

**Spatiotemporal variation in clam recruitment among beaches in Washington State
(USA)**

Spatiotemporal variation in clam recruitment

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Abstract

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Abundant clam populations provide ecosystem services and commercial and recreational shellfish harvests worldwide. Two non-native clams (Manila clams, *Ruditapes philippinarum*; Eastern Soft-shell clams, *Mya arenaria*) commonly populate mid-intertidal zones of coarse-sediment beaches in Washington State, USA. To better understand factors influencing their abundance, we used passive mid-intertidal spat collectors to determine the density and distribution of clam recruits (150-500 μm shell length) at eight beaches spanning over 500km and over two reproductive seasons (2016, 2017). Cumulative seasonal recruitment (clams $< 500 \mu\text{m}$) in 2016 and 2017 at +1.0 m MLLW ranged from 800 to 125,000 m^{-2} for *R. philippinarum* and 50 to 85,000 m^{-2} for *M. arenaria*, and did not differ by substrate type at small scales (gravel vs. crushed shell). At larger scales, different interannual recruitment patterns across sites did not dramatically shift the ranked order of highest and lowest recruitment sites. Cumulative recruitment tended to be lower at warmer sites, while timing of peak recruitment was not consistently related to temperature. Sites also differed in the relative recruitment of the two clam species, but most beaches had greater densities of *R. philippinarum* than *M. arenaria* at both recruitment and juvenile stages. Although recruitment densities differed by two orders of magnitude across sites, post-settlement factors eliminated initial spatial variation within a year, dampening recruitment variability among these beaches that all contribute to commercial and recreational clam production.

Key Words

recruitment variability, spatiotemporal, Manila clam, Eastern soft-shell clam, intertidal, substrate manipulation

Introduction

Recruitment variability is a hallmark of benthic marine species with complex life cycles that include a planktonic larval stage (Underwood & Fairweather, 1989). Variability often appears in multi-year time series but also can manifest in phenology (interannual variability in timing) or among sites. When recruitment is spatiotemporally variable, ecological portfolio effects may arise in which spatial asynchrony in population dynamics stabilizes metapopulations, and years of low production at one site are buffered by being offset by high production at other sites (Schindler et al., 2015). For some benthic invertebrates, the weight of evidence is against such portfolio effects, for instance due to large-scale synchrony in the timing of reproduction (mussels and oysters; Philippart et al., 2012), or because certain sections of coastline have consistently better larval settlement than others (mussels and barnacles; Broitman et al., 2008). Yet, in cases where larval development occurs primarily within bays, dynamics of recruitment in different bays can be decoupled (oysters; Wasson et al., 2016).

To further understand spatiotemporal scales of variability in recruitment of benthic marine invertebrates, we examined seasonal recruitment of two non-native clam species over two years across eight beaches in Washington State, USA. Settlement occurs at the point of metamorphosis from the planktonic larval to benthic juvenile stage. We counted small (150-500 μm) clams at two to four week intervals and refer to these as ‘recruits,’ since the abundance of recruits is influenced by settlement dynamics and post-settlement processes like growth and survival (Keough & Downes, 1982).

Our two focal species were Manila clams (*Ruditapes philippinarum* Adams and Reeve) and Eastern Soft-shell clams (*Mya arenaria* Linnaeus). Both are now grown commercially, but were originally introduced to Washington State as hitchhikers with aquaculture oysters: *M. arenaria* from the US east coast in the 1880s, and *R. philippinarum* from Japan in the 1930s

(Wonham & Carlton, 2005). Commercial shellfish production and recreational harvest in Washington State derive from a combination of planting hatchery-raised seed and natural recruitment, creating a shellfish industry totaling billions of dollars in state revenue (Dethier, 2006).

Seasonal timing of bivalve reproduction is closely linked to water temperature, among other factors (Bayne, 1976). Increasing water temperature triggers rapid gonadal development and eventually spawning, though critical spawning temperatures can vary widely between locations for both *R. philippinarum* (Mann, 1979; Delgado & Pérez-Camacho, 2007) and *M. arenaria* (Pfitzenmeyer, 1965; Porter, 1974; Brousseau, 1978). Warmer spring water temperatures triggered earlier gametogenesis for *M. arenaria* in Massachusetts (Brousseau, 1978), and a cold spring is suspected to have delayed reproduction in a population of *R. philippinarum* in Ireland (Xie & Burnell, 1994). Both clam species are capable of multiple spawns per season, and the timing of spawning depends on water temperature and geographic location (*R. philippinarum*, Williams, 1980; Bourne, 1982; Toba et al., 2007; *M. arenaria*, Pfitzenmeyer, 1965; Porter, 1974.)

Temperature can also influence the rate of larval development. *R. philippinarum* pelagic larval duration can vary from 1.5 to 4 weeks (avg. 2 weeks) (Bourne, 1982; Zhang & Yan, 2006), and the exact duration is thought to depend on water temperature and food supply (Toba et al., 1992). Larval development time for *M. arenaria* may be slightly longer, but can also vary with temperature (Stickney et al., 1964): 2 weeks in warmer water (Ayers, 1956) or even as long as 4-6 weeks in cooler water (Beal, 1994). In culture, the thermal optimum is between 18 and 32°C for *R. philippinarum* larvae (Huo et al., 2018), and 14 to 24°C for *M. arenaria* larvae (Stickney, 1964) and this difference in thermal optima could influence the timing of settlement for each species in nature, depending on the temperature of the water. Both clam species metamorphose at a shell

length of approximately 200 μm (*R. philippinarum*, Robinson & Breese, 1984; Zhang & Yan, 2006; *M. arenaria*, Jorgensen, 1946; Sullivan, 1948; Stickney, 1964).

The effects of salinity on the reproduction and larval ecology of *R. philippinarum* and *M. arenaria* are less well understood. Though *R. philippinarum* reproduction and larval growth require salinity above 20 (Robinson & Breese, 1984), optimal salinities for larval settlement are between 13 and 20 (Yamamoto, 1952; Tezuka et al., 2013). Stickney (1964) found no substantial differences between *M. arenaria* larvae raised at 10, 16, 21, and 32, but noted that growth was better above a salinity of 16.

Variation in substrate type, wave action, and salinity can also influence clam recruitment densities locally (Ishii et al., 2001; Nambu et al., 2012; Tezuka et al., 2013). In addition to abiotic factors, settling clams may actively influence their own fates via behaviors such as benthic habitat selection. Many benthic marine invertebrate larvae have advanced sensory capabilities that enable small-scale selection of settlement sites, including substrate and tidal elevation (reviewed by Hodin et al., 2017). For soft sediment marine invertebrates, the evidence is mixed (some show habitat-specific settlement, some do not) (Woodin et al., 2007). The addition of shell to beaches can enhance clam recruitment, which could result from improved chemistry for post-settlement survival (Green et al., 2009). However, in several field studies, shell addition had no effect on recruitment for *R. philippinarum* (Nosho & Chew 1972; Ruesink et al., 2014a) or *M. arenaria* (Beal et al., 2020), nor on survival for *R. philippinarum* (Greiner et al., 2018). *R. philippinarum* settlement was unrelated to substrate grain size in a laboratory study (Tezuka et al., 2013).

Post-settlement processes often dominate over settlement in determining distributions of juveniles in benthic marine invertebrates (Hunt & Scheibling, 1997), and can be major drivers of habitat-specific bivalve distributions (Peterson, 1996; Seitz, 2011; Carroll et al., 2012). *R.*

philippinarum can settle at extremely high abundances ($>40,000 \text{ m}^{-2}$) but experience substantial juvenile mortality ($>90\%$) (Williams, 1980). Predation and synergistic abiotic stressors are documented as major drivers of post-settlement mortality in Washington State (Dethier et al., 2019a). In its native waters in the northwest Atlantic, *M. arenaria* is commonly found in intertidal sandy substrates. Settlement density can reach $400,000 \text{ m}^{-2}$ (Emerson & Grant, 1991), and post-settlement survival is typically low. Recruits $>1 \text{ mm}$ are found at densities exceeding 500 m^{-2} , and even these larger juveniles show survival of only $\sim 3.5\%$ per year (Commito, 1982). Overall, for both clam species, post-settlement mortality can be high and spatially variable.

We examined *R. philippinarum* and *M. arenaria* recruitment across eight beaches in Washington State over two years using artificial spat collectors to test whether species-specific recruitment patterns are consistent in space and time. Our hypotheses were:

- 1) Strong spatiotemporal variability in recruitment of *R. philippinarum* (Ruesink et al., 2014b) and *M. arenaria* (Emerson & Grant, 1991; Bowen & Hunt, 2009), with species-specific patterns due to differences in their reproductive biology and larval ecology, such as spawning temperatures.
- 2) Site-level variation in water properties contributing to recruitment magnitude and timing, especially earlier recruitment at warmer sites and for the species with a larval performance curve shifted to lower temperatures (*M. arenaria*, Stickney, 1964).
- 3) Weak or no small-scale (within-site) habitat selection of settling clam larvae in comparisons of two substrate types (crushed oyster shell or pea gravel). Soft-sediment invertebrate larvae including bivalves can use cues such as organics in the sediment for habitat selection (Grassle et al., 1992), but previous research is consistent with

indiscriminate settlement of *R. philippinarum* across sediment type (Nosho & Chew 1972, Tezuka et al. 2013, Ruesink et al., 2014a).

- 4) Weak or no relationships between juvenile clam densities and prior recruitment due to the dominance of post-settlement factors influencing the distribution of juveniles for *R. philippinarum* (Ruesink et al., 2014b, Dethier et al., 2019a) and marine invertebrates in general (Hunt & Scheibling, 1997).

Overall, these hypotheses emphasize an expectation that larger-scale processes will dominate over smaller-scale variability in recruitment, and that available environmental predictors will better address variability in timing rather than magnitude of recruitment. Depending on the relative importance of pre- and post-settlement processes, spatiotemporal patterns in recruitment may not be maintained into later life stages, which we address by correlating juvenile clam densities with recruitment across the eight beaches.

Methods

Study sites

We monitored eight sites in four regions of Washington State, USA (Hood Canal – HC, Southern Puget Sound – SPS, Northern Puget Trough – NPT, and Willapa Bay – WB) for clam recruitment in 2016 and 2017 (Fig. 1; Table 1). Sites within regions were 15-25 km apart, and ~200 km to other site pairs. Ultimately, because recruitment showed no more shared variation within than across regions, analyses were done at the spatial scale of sites rather than regions. Sites were located within commercial (Bowman, Chuckanut, Chapman, Hamma, Oysterville, Woody's) or recreational (Weaverling, Potlatch) shellfish beds and were selected because they had thriving natural clam populations, which were seeded nearby at Bowman and Chapman. Sediment at the

eight beaches was mostly larger than granules (32-61% >2 mm) and ranged from 1-7% fine sands or smaller (<125 μm ; Supplemental Table S2).

Spatiotemporal variation in recruitment across sites

To assess clam recruitment while controlling for differences in substrate between sites, we deployed artificial clam spat collectors at each site from May to October in 2016 and 2017. Rectangular spat collectors (10 x 12 x 2 cm) were constructed from 1.5 mm flexible vinyl mesh and filled with 240 ml of pea gravel or crushed oyster shell (Ruesink et al. 2014a,b). Spat collectors (henceforth “bags”) were placed on top of the substrate at random intervals along a 50 m transect at +1.0 m MLLW, and each bag was anchored in place to a vertically planted PVC stake with a cable tie. In 2016, five pea gravel bags were placed on site starting May or June and replaced approximately every 2 weeks ending October, resulting in 7 to 9 sampling dates per site. Over the course of each deployment period, local sediment accumulated within and partially buried each bag.

During low tide on collection days, bags were collected and thoroughly rinsed over nested sieves (500 μm , 250 μm , 150 μm). Since both clam species settle at lengths of about 200 μm (Stickney, 1964; Zhang & Yan, 2006), we considered clams with a shell length of <500 μm to be recent recruits. Only the 150-250 μm (“small”) and 250-500 μm (“large”) size fractions were kept for laboratory processing, and each size fraction was processed separately to facilitate searching for clams of various sizes (i.e. to not overlook the smallest clams). Due to the high volumes (>30 mL) of sediment often washed out of the bags and caught on the 150 μm sieve, most sample vials were sub-sampled by 1/2 to 1/8 to facilitate laboratory processing. Sub-sampled portions of each sample were examined under a stereo microscope to count newly settled clams. A live stain (Rose

Bengal) was used to help distinguish clams from sediment during sample processing. Clams were identified to species-level to the best of our ability using shell color and morphology, which was informed by past field experience (Ruesink et al., 2014a,b). Most (>95%) clams were *M. arenaria* or *R. philippinarum*, and analyses focused only on these species. Other clams were identified as native *Macoma* spp. and non-native *Nuttallia obscurata*.

The magnitude of recruitment was determined in each summer as the cumulative number of individuals in bags at each site. Seasonal recruitment in 2016 was calculated as the sum of newly settled clams from the large size fraction (250-500 μm) from all twice-monthly sampling dates, separating by species. In 2016 we did not track the position of each bag throughout the season during sample processing, and we were therefore unable to sum clams at each position along the transect. We instead randomly assigned each replicate sample a bag number (1 through 5) for each sampling date, and then summed recruits within bag numbers throughout the entire season. Seasonal recruitment for 2017 was calculated as described above, but bag position was accurately recorded at the time of sampling. To ensure a balanced design when comparing recruitment across years, 5 bags were selected at random from the 8 bags available in 2017. We randomly selected bags from shell and gravel treatments, since no difference in recruitment between shell and gravel was detected (see Results, “Substrate effects on recruitment within sites”). Thus, 5 replicates of recruitment of clams 250-500 μm were available for each year. Missing bags (3 in 2016, 5 in 2017) were assumed to contain the average of other bags at that time.

In 2016, when we counted clams of all sizes (150-500 μm) at 2-week intervals, we tested whether timing and magnitude of settlement differed in regard to local water conditions (see “Environmental predictors of recruitment magnitude and timing” below). Magnitude was based on the sum of recruits across all sampling periods from May to October in 2016. The sampling

period (1-12) when bags were collected with the highest average clam abundance was considered the recruitment peak. Due to low overall recruitment of *M. arenaria* at Oysterville (WB), this site was dropped from the analysis of peak recruitment timing.

Environmental predictors of recruitment magnitude and timing

We described some abiotic conditions at beaches including temperature and salinity based on continuous measurements just below the sediment surface, point samples of water over the site, and point samples in a nearby channel. On site visits in 2016 (five times per site, May-Oct), water temperature (°C) and salinity (PPT) were measured with a YSI Ecosense meter during low tide in approximately 0.5 m water depth (lacking only Sep. data from the WB region when water level was too low to access on the very broad tidal flats). Temperature loggers (Tidbit, Onset Computer Corporation, Bourne, MA) were continuously recording just below the sediment surface at each site from 22 Jul to 19 Aug 2016, datasets that we compiled into a site average temperature (replacing with 2017 data for Hamma, where 2016 loggers failed; 2016 and 2017 average August temperatures were within 0.2°C at other sites). Washington State Department of Ecology provided surface water (0.5-3 m depth) conditions from monthly point samples at stations close to each of our sites (BLL009 (Chuckanut); OAK004 (Chapman); DNA001 (Bowman); HCB003 (Hamma); WPA006 (Oysterville); HCB004 (Potlatch); RSR837 (Weaverling); WPA007 (Woody's)). These conditions are more reflective of nearby channels than our intertidal sites, but could affect planktonic larvae. We extracted May 2016 temperature and the temperature and salinity average of May to Sep 2016.

Substrate effects on recruitment within sites

To test the influence of micro-habitat selection on the abundance and distribution of recruiting clams, we manipulated substrate in the recruitment bags in 2017. Bags were filled with either pea gravel (n=4 per site) or similarly sized (0.5-1 cm diameter) crushed oyster shell (*Magallana gigas*; n=4 per site), and randomly assigned placement along the same 50 m transect used in 2016. All eight bags were deployed June 2017 to September 2017 and replaced once monthly, resulting in just three sampling dates. Only the large (250-500 μm) size fraction was processed in 2017 to account for clam shell growth during the first few weeks post-settlement. Due to this difference in methods, only large clams (250-500 μm) were included in analyses directly comparing 2016 and 2017 clam recruitment. In all other aspects, the sampling protocol in 2017 was similar to the 2016 protocol.

Recruit-juvenile relationship

To determine if juvenile clam densities were related to the magnitude of prior recruitment, we quantified juvenile clams at each site in 2017, one year after we began monitoring recruitment in 2016. We assessed the density of juveniles in June 2017 along the same 50 m transect where spat bags were deployed. We took surface sediment samples (10 cm x 90 cm x 5 cm deep) at 10 randomly selected locations along the transect. The sediment was sieved to 2 mm, and clams <20 mm were counted as juvenile clams (Dethier et al., 2019a).

Data Analysis

Spatiotemporal variation in recruitment across sites - Spatiotemporal recruitment variability was examined by analyzing cumulative recruitment in each year for each species at each site, based on the sum of the large (250-500 μm) size fraction clams recorded per bag at each 2- to 4-week

interval. Cumulative recruitment was $\log(x+1)$ -transformed prior to analysis, and the transformed data met the assumptions of normality and homogeneity of variance.

The response variable of cumulative recruitment per species was tested for fixed effects of species, site, and year, and their interactions (n=5 per Species, Site, and Year; Analysis of Variance). The interactions would indicate spatiotemporal effects overall and subset for each species (Site x Year), whether *R. philippinarum* and *M. arenaria* had similar spatial patterns of recruitment (Species x Site), and whether these patterns changed over time (Species x Site x Year). Any main effect of year could be due to differences in sampling time intervals between years; spat bags were collected every two weeks in 2016 and every four weeks in 2017. As the three-way interaction proved significant, we subset the data to examine spatiotemporal patterns for each species separately, that is, testing recruitment with respect to Site, Year, and Site x Year.

Environmental predictors of recruitment magnitude and timing – We compiled a suite of site-level predictors and used a model comparison approach to evaluate relationships with recruitment in 2016 (n=8 sites for each clam species). A similar approach to 2017 data was not possible because the sampling provided less resolution on timing (1-mo intervals) and magnitude (no individuals <250 μm counted). Cumulative recruitment was log-transformed and then met Gaussian error assumptions (linear model), whereas the sampling time of peak recruitment was evaluated assuming Poisson distribution, as it was restricted to an integer value between 1 and 12 (generalized linear model). Predictor variables were species and seven measurements of temperature and salinity covering different time periods (gametogenesis in May vs. entire summer) and positions (water over the tidal flat, sediment, nearby channel; Table 1). Channel temperature was too highly correlated (above 0.6) with salinity to include in a single model, and temperature

variables were correlated in such a way that only a total of three appeared in a single model. The combinations of uncorrelated predictors, plus a null model with no predictors, resulted in a total of 60 models. Only main effects were included as predictors, not interactions. Models were compared by Akaike's information criterion, adjusted for small sample size (AICc), which penalizes model fit by model complexity. Models within two units of the best model (smallest AICc) were considered equivalent (Burnham & Anderson, 2003).

Substrate effects on recruitment within sites - Recruitment differences by substrate type were analyzed for 2017, when an equal number of bags were filled with gravel and crushed shell at each site. We summed recruits across months for each bag position to determine cumulative recruitment of each species ($\log(x+1)$ -transformed for normality and homogeneity of variance). Due to our focus on small-scale substrate choice, the model was constructed with fixed effects of clam species, substrate type, and their interaction, and random effect of site, with bag nested in site to account for both species of clams detected in each bag. We ran a linear mixed-effects model, followed by analysis of variance (ANOVA) to test for significant predictors of recruitment.

Recruit-Juvenile Relationship – Site-specific counts of juvenile clams of each species in 2017 were used as the response variable in a linear model, and predictor variables were species and cumulative recruitment for clams of all sizes (150-500 μm) at each site in 2016. Both recruit and juvenile abundances were log-transformed to improve data distribution. Each site was considered a sample in this analysis ($n=8$ sites for each clam species).

All statistical analyses were conducted in R (v.3.6.0; R Core Team 2019).

Results

Spatiotemporal variation in recruitment across sites

The timing of peak clam recruitment in 2016 varied between species and sites, but some notable regional trends emerged: at both sites in NPT peak recruitment occurred in August for both species, while at sites in SPS *R. philippinarum* recruitment had two peaks (June, September) while *M. arenaria* recruitment peaked once (August) (Fig. 2). Cumulative numbers of large clams (250-500 μm) were higher in 2016 than 2017 at Weaverling, while other sites were relatively similar between years (Fig. 3). Numbers of newly settled clams per bag varied highly among sites and dates (Fig. 2 and 3), from 0 to 2,000 individuals per bag (over 160,000 ind.m⁻²). Recruitment variability among the spat-collector bags was evident: coefficients of variation on any particular collection date, for the five replicates in 2016 or eight in 2017, were generally >1 for both clam species unless the average recruitment exceeded 1000 m⁻² (12 per bag). Thus recruitment was less patchy within a site at times and places of higher recruitment (Supplemental Figure S1).

In statistical analysis of clam recruitment magnitude, the three-way interaction of Species, Year, and Site was significant (Table 2; Fig. 2, 3), suggesting species-specific spatiotemporal patterns of recruitment. At the same time, the two species showed highly correlated recruitment across beaches ($r=0.74$ in 2016 and $r=0.57$ in 2017 for $\ln(R_p)$ vs $\ln(M_a)$, $n=8$); that is, “high” recruitment beaches applied to both species. Overall, *R. philippinarum* represented 71% of recruits in 2016 and 77% in 2017, and its contribution was relatively most variable at Oysterville, where it made up 99% and 53% in the two years. However, Oysterville was ranked 7th or 8th (lowest) in clam recruitment for both species in both years, so the relatively variable contributions were immaterial to spatiotemporal trends. To examine spatiotemporal variation for each clam species, we carried out species-specific two-factor ANOVA (Site, Year, Site x Year). Both clam species

showed significant Site x Year effects in recruitment, but despite significant year to year variation between sites, recruitment in the two years was strongly correlated: $r=0.73$ for *R. philippinarum* and $r=0.84$ for *M. arenaria* ($n=8$).

Environmental predictors of recruitment magnitude and timing

Based on model comparisons, magnitude of recruitment differed by clam species and by summer water temperature in nearby channels; one model fit substantially better than all others (Table 3). Clams recruited at higher abundance at sites where channel temperatures were cooler, and *R. philippinarum* had 2.8 times higher recruitment than *M. arenaria*. We had hypothesized that clams would recruit earlier where temperatures were warmer but instead found inconsistent patterns among models with equal support: the top model for timing was the null model, with others indicating earlier recruitment at warmer temperatures (Table 3).

Substrate effects on recruitment within sites

In 2017, clam recruitment did not differ for either species between gravel and shell substrate ($F_{1,64}=0.01$, $p=0.92$) but was four times greater for *R. philippinarum* than *M. arenaria* ($F_{1,64}=71.0$, $p<0.001$). There was no significant interaction between Species and Substrate ($F_{1,64}=0.18$, $p=0.68$).

Recruit-Juvenile Relationship

R. philippinarum reached higher juvenile densities than *M. arenaria* for a given amount of recruitment (Species $t_{1,13}=2.6$, $p=0.02$), but without any positive correlation with prior recruitment density (Recruitment $t_{1,13}=0.2$, $p=0.8$). That is, post-recruitment survival appeared higher in *R.*

philippinarum than *M. arenaria*, but across sites, first-year survival differences obscured distribution patterns set up at the point of recruitment (Fig. 4). *R. philippinarum* varied by two orders of magnitude in recruit density across sites, but only by a factor of three in juvenile density, so the later life stages converged in terms of density. For *M. arenaria*, at two of the sites we detected no juveniles, despite seeing them as recruits the year before.

Discussion

Clam recruitment patterns and environmental predictors

Recruitment of two non-native clam species was variable across sites in our two year study of beaches in Washington State, which supports our first hypothesis for strong spatiotemporal variability. We also found some species-specific patterns of recruitment; site-specific recruitment changed annually in each species, and recruitment magnitude was higher for *R. philippinarum* than *M. arenaria* on all the beaches we surveyed. However, shifts between years were not dramatic or purely stochastic since high recruitment sites remained high in both years. *M. arenaria* made up a substantial portion of all recruits (30-50%) in the two Northern Puget Trough sites (Weaverling and Chuckanut) but made up <10% at all sites in Hood Canal and South Puget Sound. This regional difference is consistent with cooler optimal temperatures for reproduction of *M. arenaria* than *R. philippinarum*. Yet in other ways, clam recruitment across sites was not a straightforward function of temperature and salinity, not even for recruitment timing, which we expected would be accelerated at warmer sites (hypothesis 2) (Table 3).

High densities of new recruits have been documented for these two clam species in their native and non-native ranges. At one of our sites with highest recruitment of *R. philippinarum* (Bowman, SPS), recruitment reached 38,000 ind. m⁻² in 2016 (250-500 μm size fraction only) and

33,000 ind. m⁻² in 2017, similar to previous reports from Puget Sound (46,000 ind. m⁻², Williams, 1980) or Japan (50,000 ind. m⁻², Sekiguchi et al., 1995; 57,000 ind. m⁻², Tezuka et al., 2012). At the site with highest recruitment of *M. arenaria* (Weaverling, NPT), recruitment reached 85,000 ind. m⁻² in 2016 and 12,000 ind. m⁻² in 2017, compared to settlement densities of 400,000 ind. m⁻² in its native range (Emerson & Grant, 1991).

Our study design avoided some factors that might confound our estimates of recruitment, for instance, we used passive spat collectors at all sites to control for beach grain size, and monitored throughout the season to account for disjunct recruitment timing. Although the spat collectors decoupled clam recruitment from beach sediment properties and tended to protect post-settlement clams from predation (Ruesink et al., 2014a) they did not necessarily provide a perfect index of settlement. First, the time lag between settlement and pickup of bags introduced opportunities for clam mortality and movement. Second, bags that accumulated sediment also tended to have high clam counts, although the reverse was not true: low-sediment bags included the full range of recruitment.

We documented high variation in clam recruitment across sites (Fig. 3), but the suite of environmental predictors that we expected to explain recruitment timing and magnitude had little or no influence. One potential constraint was that the point samples we incorporated as physical predictors may not have been accurate indicators of the mean or extreme conditions influencing clams. May temperatures differed among sites by nearly 10°C, average summer temperatures by 4°C, and salinity by 10 units (although all above 19). Another factor could have been that regional scale phenomenon may have masked the influence of natural environmental variation. Our 2016 sampling season was during a major marine heatwave ('the blob') that affected the Northeast Pacific from 2013 to 2016, and coincided with periods of elevated water temperature and

freshwater input in the Puget Sound (Khangonkar et al. 2021). The marine heatwave may have impacted clam recruitment, as it altered plankton productivity in parts of the Puget Sound (Winans et al., 2023) and disrupted invertebrate spawning patterns in Oregon (Shanks et al., 2019). Yet, we did not find any evidence to suggest that the blob explicitly affected clam recruitment here, since there was not a significant difference between recruitment in 2016 (during the marine heatwave) and 2017 (following the heatwave).

Despite being highly variable, the temperature and salinity values we measured were generally not outside documented tolerances of the two clam species at larval stages (Stickney, 1964; Robinson & Breese, 1984; Chew, 1989; Numaguchi, 1998). In a study of *M. arenaria* recruitment in Maryland, *M. arenaria* were absent from weekly recruitment collectors when average surface water temperatures exceeded 21°C (Pfitzenmeyer, 1962), and Stickney (1964) has reported an upper limit of 24°C for *M. arenaria* larvae. Temperature and salinity can both influence *M. arenaria* larval growth rates (Stickney, 1964) and larval and juvenile shell building processes (Strasser et al., 2008). *R. philippinarum* larval development is also influenced by temperature, though larvae can tolerate up to 30°C (Robinson & Breese 1984; Numaguchi, 1998). *R. philippinarum* recruitment increases as salinity decreases until a lower limit of 13 (Tezuka et al., 2013). For both clam species in the present study, recruitment magnitude was negatively related to warm springtime (May) or summer water temperature at our sites in 2016, even though site conditions were well within ranges considered optimal for these clams. The species-specific thermal tolerances were consistent with *M. arenaria* being relatively more abundant at sites in the coolest region (NPT; Fig. 3). It's also possible that regional differences in the effects of the marine heatwave in the Salish Sea (Khangonkar et al. 2021) could have contributed to differences in spring and summer water temperature between our sites, and therefore impacted recruitment.

Our models were inconclusive regarding accelerated recruitment timing at warmer spring or seasonal temperatures (Table 2), although other bivalves can recruit earlier at warmer times and places (*Macoma* sp., Philippart, 2003). The absence of a consistent species-specific difference in timing of recruitment could reflect *M. arenaria* spawning at lower temperatures but developing longer before recruitment. *R. philippinarum* larvae spend around 1.5-4 weeks in the plankton (Bourne, 1982; Zhang & Yan, 2006), while the planktonic stage of *M. arenaria* can be 2-6 weeks (Ayers, 1956; Abraham & Dillon, 1986; Beal, 1994). Other factors that may have influenced clam recruitment magnitude and timing that we did not incorporate into our analysis include local and regional hydrodynamic conditions, such as water residence time (Butman, 1987; Peterson et al., 1996), which is thought to influence settlement densities of clam species including *M. arenaria* (Ayers, 1956) and *Cardium edule* (Cockle) (Kreger, 1940; Baggerman, 1953). Food availability can limit the survival of larval and post-larval bivalves (Philippart et al., 2003; Bos et al., 2006) and therefore overwhelm temperature signals. Although we do not have direct evidence of food availability across our study sites, we do have data on growth rates of newly-settled *R. philippinarum* at most sites (Ruesink et al. 2014a, Dethier et al. 2019). The only site with stunted juvenile clam growth was Chuckanut, which was likely a function of low-tide temperatures that made conditions too stressful for fast growth (Dethier et al. 2019). Chuckanut was a relatively low-recruitment site, particularly for *R. philippinarum* (Fig. 3). One additional possibility for general insensitivity of recruitment to temperature was that we tested peak timing rather than the initiation of seasonal recruitment, because the peak was clearly identifiable in the time series, but first recruitment was harder to detect.

Substrate effects on clam recruitment

We found no evidence that *M. arenaria* or *R. philippinarum* recruits selected crushed oyster shell or pea gravel habitat preferentially, supporting our third hypothesis for weak small-scale habitat selection. At a within-site scale, neither *R. philippinarum* nor *M. arenaria* larvae appeared selective of substratum in our comparison of pea gravel and oyster shell. Potential differences between gravel and shell substrates such as localized pH differences or chemical cues were not important drivers of variation in clam recruitment. The addition of shell to substrate may not alter porewater pH in the short-term (24 h; Dethier et al., 2019a), but can have an effect over a longer time period (1 mo.; Greiner et al., 2018). Nevertheless, our study adds to a growing body of work showing no benefit of having shell hash present for clam recruitment or survival (Ruesink et al., 2014a; Greiner et al., 2018; Dethier et al., 2019a; Beal et al., 2020; but see Green et al., 2009), although the large particles of shell may help reduce predation on clams. Some planktonic larvae can control their distribution through sensory-mediated vertical swimming and benthic habitat selection (Hodin et al., 2017), which may contribute to preferences of *M. arenaria* larvae for certain sediments and associated biota (Snelgrove et al., 1999). Micro-hydrodynamic conditions can also affect spatial patterns of settlement (Butman, 1987), including artificial reefs and breakwaters that may concentrate larvae (Mottet et al., 1981). The comparison in the present case (pea gravel vs. shell) does not span the full range of microhabitats available in the field, but strongly indicates that shell was not a preferred recruitment substrate over gravel at any site.

Recruit-juvenile relationships & post-settlement processes

For both *R. philippinarum* and *M. arenaria*, recruitment densities in the first year of our study did not correlate with juvenile densities the following year, validating our fourth hypothesis that post-settlement factors including mortality and displacement can obscure the relationship

between recruit and juvenile clam densities. Information regarding the relative importance of pre- and post-settlement factors for species' abundance has been compiled for many benthic marine invertebrates (Hunt & Scheibling, 1997; Frascetti et al., 2002), and post-settlement processes can have a stronger influence on clam population density and distribution than settlement (Tezuka et al., 2012). For *R. philippinarum*, recruitment variability among sites was substantially greater than the amount of variability in juvenile densities; that is, beaches were much more similar in their juvenile clam abundance than would be expected from our observed recruitment patterns (Fig. 4, Table S1). *M. arenaria* juveniles were generally found at lower densities than *R. philippinarum*, except at Bowman (SPS). Surprisingly, we found no *M. arenaria* juveniles at Weaverling (NPT), despite the extremely high magnitude of *M. arenaria* recruitment the previous year.

Post-settlement mortality is commonly very high for clams, especially immediately following settlement (Williams, 1980; Tezuka et al., 2012; Beal et al., 2018). For *R. philippinarum*, juvenile densities may have been inflated by seed clams outplanted at some sites, including Chapman and Bowman, during 2016 since those are active *R. philippinarum* aquaculture beaches. For *M. arenaria*, the recruitment signal is natural since this species is not commercially seeded or harvested in the region. Relatively high densities of predators may have eaten many of the clams recruiting at particularly high abundance at Weaverling and Bowman (Dethier et al., 2019a). Small *M. arenaria* are more vulnerable to crushing predation by shore crabs than *R. philippinarum* (Dethier et al., 2019b), and predator exclusion can enhance juvenile *M. arenaria* densities by nearly 900 times (Beal et al., 2018). Therefore, species-specific variation in vulnerability to predation could have contributed to differences in juvenile abundances between the two species at some sites (e.g. Weaverling).

Active or passive migration of spat can also influence the distribution of juveniles (Hunt and Mullineaux, 2002; Nambu et al., 2012; Whitton et al., 2015); for example, post-settlement transport of *M. arenaria* via bottom currents and bedload sediment transport can significantly alter population distribution (Emerson & Grant, 1991; Hunt, McLean & Mullineaux, 2003).

Conclusion

Clam beaches along a shoreline create a potential ecological portfolio, if they vary asynchronously in productivity and therefore through statistical averaging reduce overall variance in the aggregate stock (Schindler et al., 2015). A longer time series with identical methods in each year will be necessary to resolve whether there are synchronous low- and high-recruitment years throughout Washington State. From this two-year study, sites of higher and lower recruitment suggest that these eight beaches may not represent an ecological portfolio. The first issue comes from consistent spatial order; for instance, *M. arenaria* recruited disproportionately in one region, and high recruitment occurred on a few beaches. The second issue comes from the decoupling of clam production from recruitment, since spatial variation in recruits was substantially compressed within a year. All of these beaches were selected for study due to their known importance for commercial and recreational clamming, and the species became established in this intertidal system within the past 150 years (Wonham and Carlton, 2005). These factors may predispose the study species to be successful in most years at all sites.

Data availability statement

The data that support the findings of this study are openly available in Mendeley Data at doi: 10.17632/nr9t27p4d9.1.

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Tables

Table 1. Average (\pm SE or \pm SD) temperature ($^{\circ}$ C) and salinity in 2016 at each clam study site in Washington State, USA. “Flat” temperature and salinity measurements were taken in water over the tidal flat with a YSI Ecosense meter (0.5 m depth), “Sediment” temperature measurements

were recorded with Tidbit loggers placed just below the sediment surface at each site and “Channel” temperature and salinity measurements were taken from the Washington Department of Ecology water column monitoring database at the stations nearest to each site (0.5-3 m depth). Correlations >0.6 occurred among the following variables: Flat Temp May-Oct and Sediment Temp, Channel Temp May and May-Sep, and the two salinity variables. Channel temperatures were also negatively correlated with salinity. The last row indicates the number of temperature or salinity measurements (# samples, in months or days) and whether the Standard Error (SE), Standard Deviation (SD) or neither (na) are included.

Site (Region)	Flat Temp.		Sediment Temp.	Channel Temp.		Salinity May-Sep/Oct	
	May	May-Oct	Aug	May	May-Sep	Point	Channel
Weaverling (NPT)	14.6	15.7±1.5	17.6±1.7	10.5	11.8±0.5	28.1±0.6	28.7±0.6
Chuckanut (NPT)	13.9	17.5±2.2	21.4±1.7	13	15.3±0.8	27.5±0.7	27.5±0.2
Bowman (SPS)	16.2	16.8±1.2	19.8±1.1	12	14.4±0.6	26.5±0.9	28.8±0.4
Chapman (SPS)	18	19.2±1.9	20.6±5.5	14.6	17±0.7	21.4±1.8	27.3±0.4
Hamma (HC)	16.9	17.4±1.8	20.8±	17.4	17.2±1.0	23.6±1.5	25.7±1.3
Potlatch (HC)	17.2	15.6±1.7	17.8±2.4	18.2	17.5±0.7	19.2±3.5	25.2±1.0
Oysterville (WB)	23.9	17.6±2.1	19.6±1.1	15	17.3±0.7	25.0±2.1	28.9±0.8
Woody's (WB)	19.6	16.6±1.8	19.7±0.9	15.4	18.1±0.7	23.4±2.6	28.5±0.8
# samples ±SD or SE	n=1 mo. na	n=5 mo. SE	n=31 d. SD	n=1 mo. na	n=5 mo. SE	n=4-5 mo. SE	n=5 mo. SD

Table 2. Statistical results for analysis of variance (ANOVA) examining the effects of Species (Sp), Site, and Year (Yr) on cumulative clam recruitment (250-500 µm) for *Ruditapes philippinarum* (Rp) and *Mya arenaria* (Ma) in Washington State, USA. Species were also subset to test for spatiotemporal effects (Site x Year). (***) P<0.001

Factor	Degrees of freedom	Mean square	F, P	Mean square	F, P	Mean square	F, P
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Species	1	123.5	264.1***	Rp	Rp	Ma	Ma
Site	7	41.3	88.4***	19.9	48.8***	28.9	54.9***
Year	1	0.02	0.04	3.4	8.4**	4.1	7.9**
Site x Yr	7	6.6	14.1***	4.6	11.3***	3.5	6.7***
Site x Sp	7	7.5	16.1***	-	-	-	-
Yr x Sp	1	7.6	16.1***	-	-	-	-
Site x Yr x Sp	7	1.6	3.4**	-	-	-	-
Residual	128 (64 for species-specific test)	0.5	-	0.4	-	0.5	-

Table 3. Statistical results for top models testing for environmental predictors of cumulative recruitment and peak timing of recruitment in 2016, for two clam species (125-500 μm): *Ruditapes philippinarum* (Rp) and *Mya arenaria* (Ma). Models are considered equivalent if within 2 units of the top model based on Akaike’s information criterion, adjusted for small sample size (AICc); only one top model emerged for cumulative recruitment, and five equivalent top models (i.e. within 2 units of the model with the lowest AICc value) for recruitment timing. Many predictors were highly correlated and therefore not tested in the same model. The table identifies the predictors in the top models (listed in the last row) and provides the coefficient describing the relationship with clam recruitment. “Tideflat” temperature and salinity measurements were taken in water over the tidal flat with a YSI Ecosense meter (0.5 m depth), and “Channel” temperature and salinity measurements were taken from the Washington Department of Ecology water column monitoring database at the stations nearest to each site (0.5-3 m depth).

Model Equation	df	AICc	weight
Cumulative Recruit = $17.98 + \text{Sp}(\text{Rp} > \text{Ma}) - 0.68 * T_{\text{SC}}$	4	64.2	0.40
Recruitment Timing = 1.856	1	63.9	0.17
= $2.563 - 0.04 * T_{\text{M}}$	2	65.6	0.071
= $3.335 - 0.087 * T_{\text{ST}}$	2	65.7	0.067
= $1.091 + 0.031 * \text{Sal}_{\text{T}}$	2	65.7	0.065
= $1.946 + \text{Sp}(\text{Rp earlier than Ma})$	2	65.8	0.062

Sp = clam species, T_{SC} = Avg summer Channel temp., T_{M} = May Tideflat temp., T_{ST} = Avg summer Tideflat temp. Sal_{T} = Avg Tideflat salinity

Figure legends

Figure 1. Map of Western Washington State, USA showing (A) the four regions where intertidal clam recruitment was monitored during 2016 and 2017, and the two sites within each region located in (B) Willapa Bay and (C) the Salish Sea.

Figure 2. Seasonal patterns of *Ruditapes philippinarum* (*Rp*; grey) and *Mya arenaria* (*Ma*; black) recruitment in 2016 throughout eight sites in Washington State. The average of replicate recruitment collectors (clams 150-500 μm ; $n=5$; ind. m^{-2}) is shown for each time point, and error bars are standard error. Individual replicates are plotted as points and jittered by 6 days for clarity. Note very different y-axes within and among panels; a secondary vertical axis was to facilitate comparison between species with different magnitudes of recruitment densities.

Figure 3. Recruitment of clams (250-500 μm) at eight sites in Washington State, displayed as box-and-whisker plots of cumulative recruitment (ind. m^{-2}); *Ruditapes philippinarum* (top) in 2016 and 2017, and *Mya arenaria* (bottom) in 2016 and 2017 with points showing individual replicates ($n=5$). Note different axis scales due to much higher recruitment at Weaverling. Codes correspond to eight sites (WE:Weaverling, CK:Chuckanut, BO:Bowman, CP:Chapman, HA:Hamma, PO:Potlatch, OY:Oysterville, WO:Woody's).

Figure 4. Relationship between the average cumulative clam recruitment densities (clams 150-500 μm ; ind. m^{-2}) in 2016 and average juvenile densities (clams >20 mm; ind. m^{-2}) in 2017 *Ruditapes philippinarum* (*Rp*; triangles) and *Mya arenaria* (*Ma*; circles) across eight sites in Washington State, USA. Juvenile densities were higher for *R. philippinarum* than *M. arenaria*

(linear model; “Species” $t_{1,13}=2.6$, $p=0.02$), but juveniles were not positively correlated with prior recruitment densities (linear model; “Recruitment” $t_{1,13}=0.2$, $p=0.8$). Horizontal and vertical error bars show standard error. Note a log-scale x-axis is used for cumulative recruitment to facilitate comparison between sites with different magnitudes of recruitment densities.

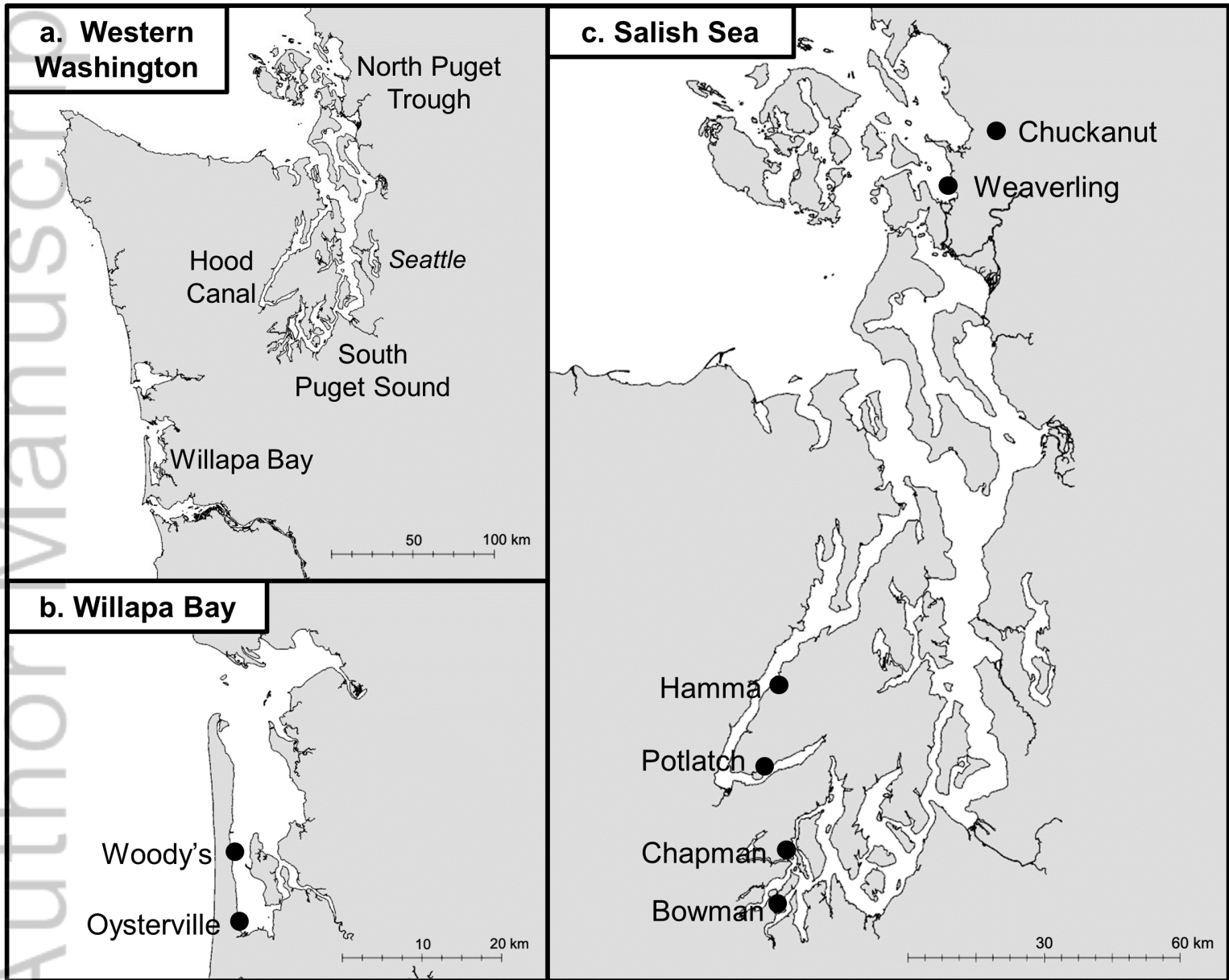


Fig 1.png

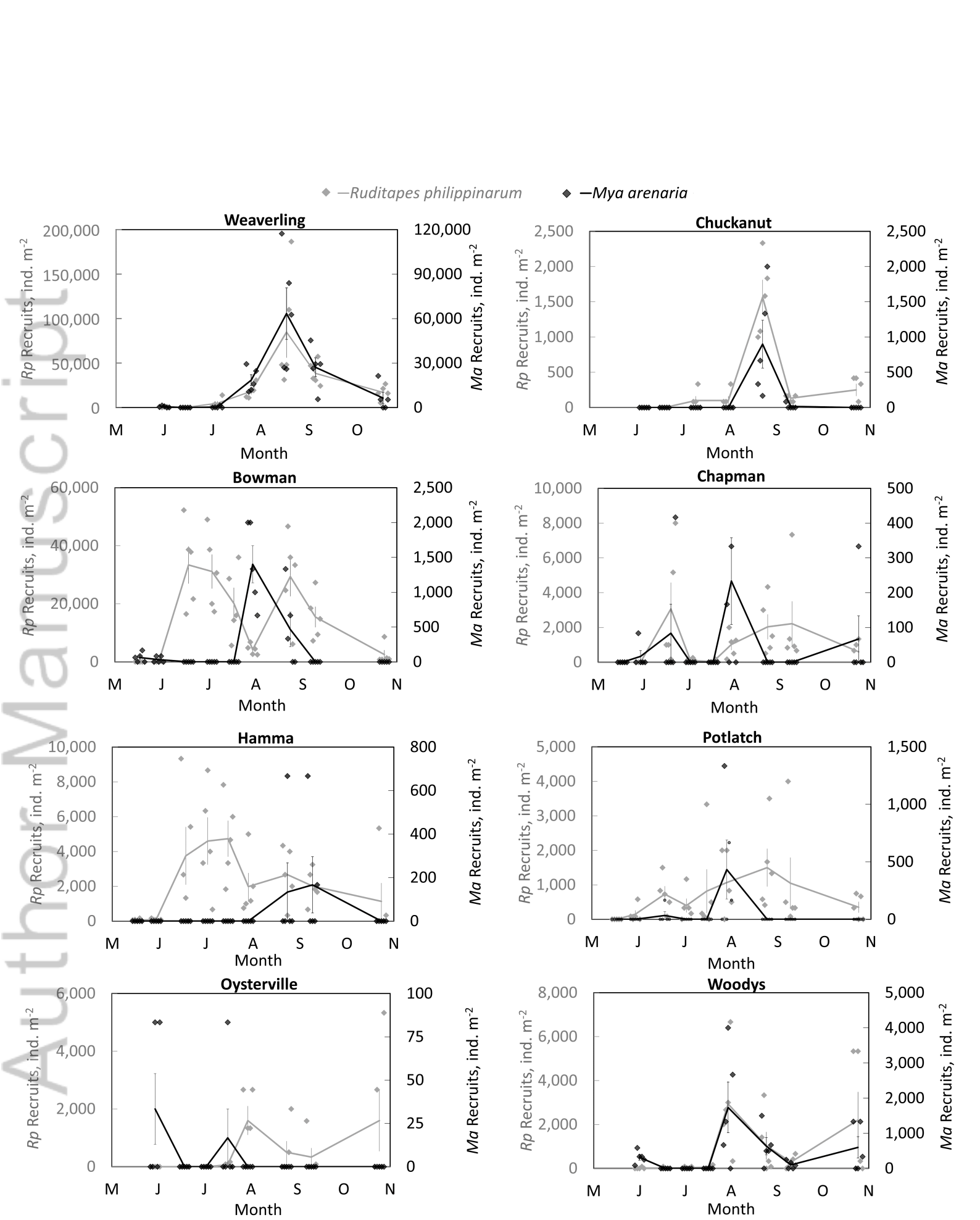


Fig 2.png

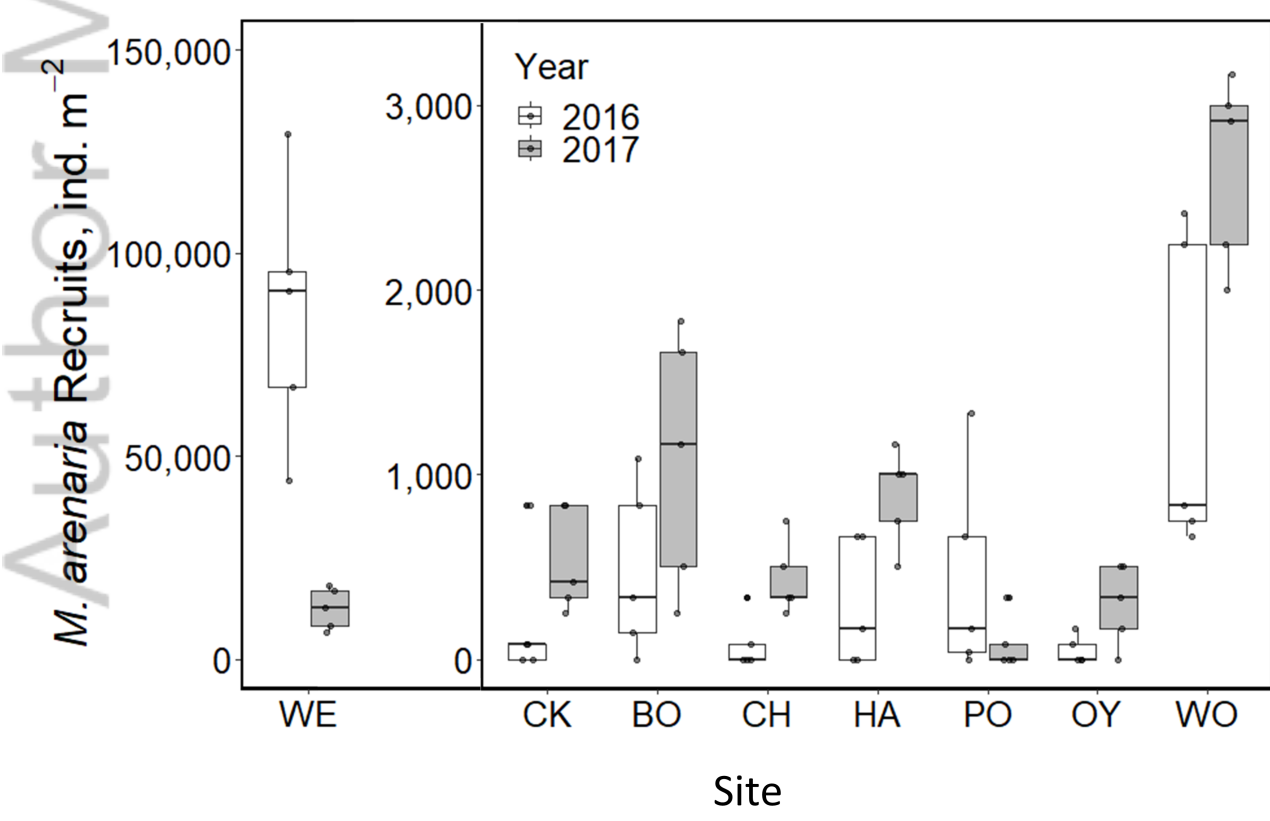
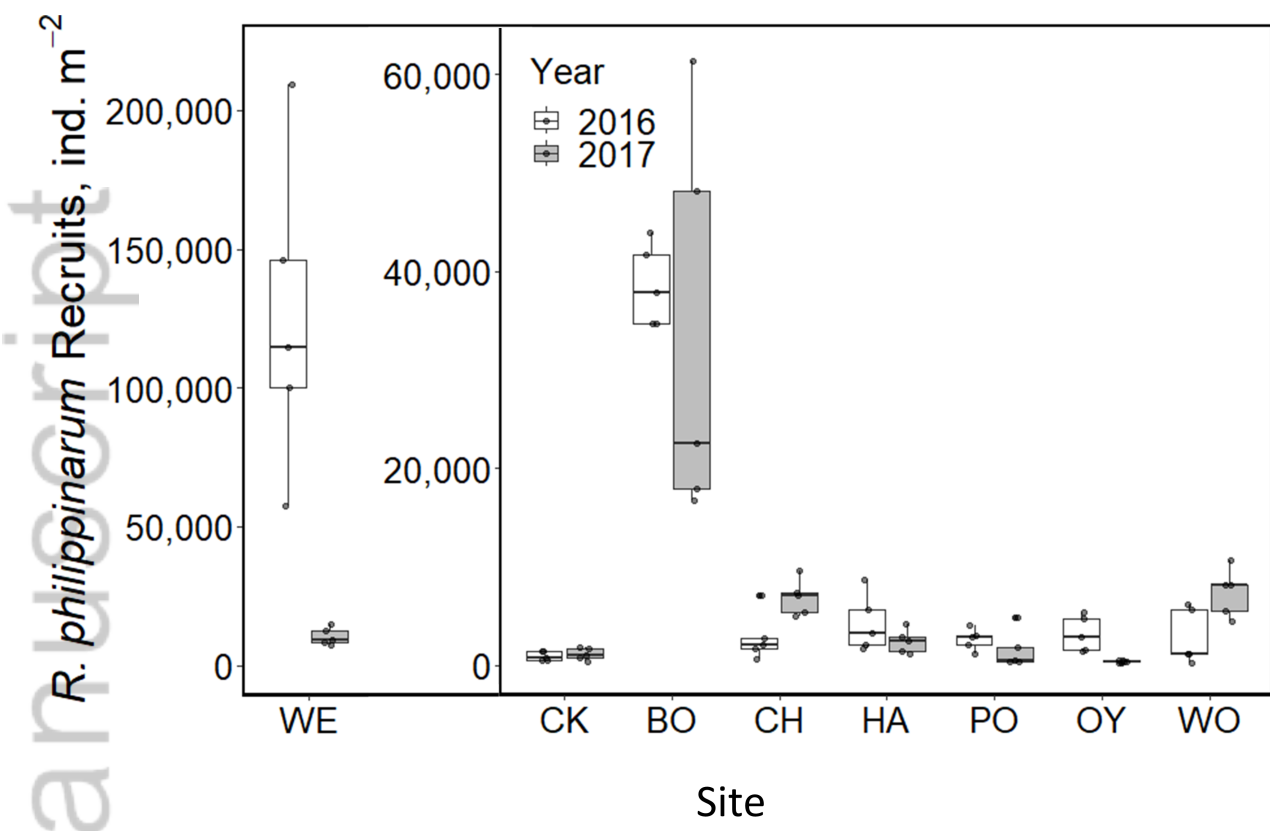


Fig 3.png

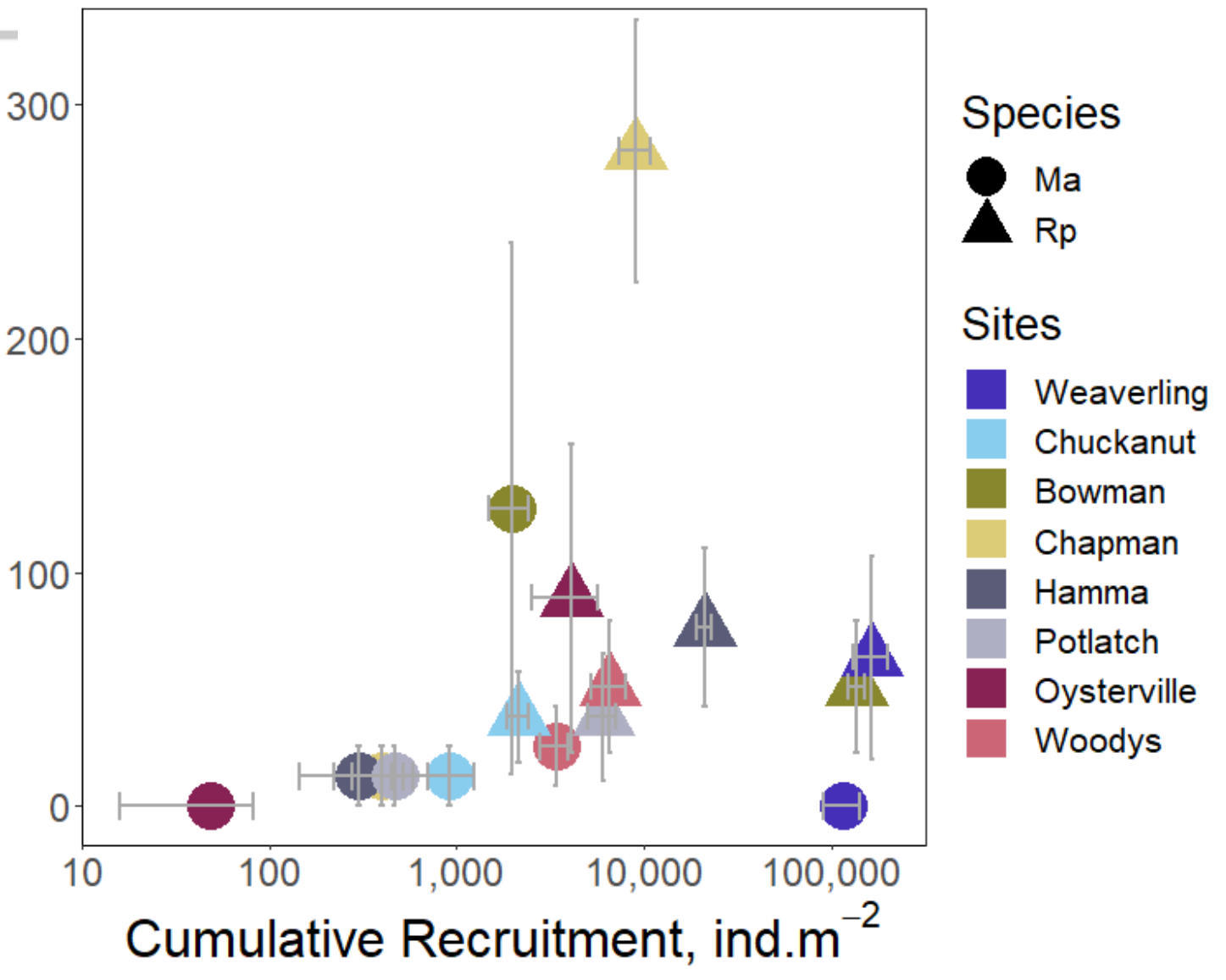


Fig 4.tiff