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The right place at the right time: improving the odds of biogenic reef restoration

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Abstract

Habitat restoration is an international priority. With this demand there is a need for ecological knowledge to underpin restoration projects to ensure their success and cost-effective delivery. This study is the first temperate marine restoration project to examine the role seasonality and location may have on restoration projects. The study found that the settlement of *Serpula vermicularis,* a rare biogenic reef forming species of conservation importance, was up to three times higher on materials deployed during July than other months. The results also found similar differences in settlement between restoration sites. These results suggest that the timing and location of a restoration effort could affect its overall success in the medium to long term. For the restoration of marine biogenic species of conservation importance, targeted spatial and temporal pre-restoration experiments can greatly increase a project's chance of success as well as making large-scale restoration programs more cost efficient.

KEY WORDS: Biogenic reef, Settlement, *Serpula vermicularis*, Sea Loch, UN Decade on Ecosystem Restoration

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Introduction

The restoration of habitats are a global priority and the restoration of degraded ecosystems is central to the Aichi biodiversity targets 14 and 15 set by of the Convention on Biological Diversity (CBD Secretariat, 2010). New and even more ambitious restoration targets are likely to be set at the fifteenth Conference of the Parties in 2021, in response to the UN decade on Ecosystem Restoration, stating in 2021 (UN 2020).

Even though the corresponding scientific literature has increased by nearly two orders of magnitude in the last two decades (Nilsson *et al.,* 2016), the scientific reporting of best practice in restoration and its applications are still rare. There are universal concerns over cost implications and inefficiencies whether it's the restoration of forests, grasslands or marine habitats (Aradóttir *et al.,* 2013; Crouzeilles *et al.,* 2016; Mayfield, 2016; Nunes *et al.,* 2016).

Marine biogenic reefs, from tropical coral reefs to temperate shellfish reefs are in decline globally (Beck *et al.,* 2011; IPBES, 2019). This loss in habitat forming organisms has led to the loss of ecosystem services such as carbon sequestration and a decline in biodiversity (Ulanowicz and Tuttle, 1992; Sebens, 1994; Cook *et al.,* 2013; Lee *et al*., 2020). The natural recovery of these reefs, if possible, can take tens to hundreds of years (Hall-Spencer and Moore, 2000; Cranfield *et al.,* 2004; Trigg and Moore, 2009; Cook *et al.,* 2013). Therefore, restoration is increasingly being investigated as an option to reverse the trends of habitat degradation and loss (Fariñas-Franco *et al.,* 2018; zu Ermgassen *et al*., 2020).

For any restoration program to be successful, an ecological understanding of how that ecosystem functioned before it was degraded or lost is highly beneficial (Clewell and Rieger, 1997; Hobbs, 2007). This ecological knowledge is often elusive for rare, threatened habitats with a limited distribution. As the degradation or loss of that habitat may have removed the ability to study potential restoration techniques, or establish baselines against which restoration success can be judged (Hawkins *et al.,* 2002; Hobbs, 2007).

Serpula vermicularis (Linnaeus, 1767) is a tube-dwelling polychaete that rarely forms dense aggregations or biogenic reefs (Holt *et al.,* 1998) of calcium carbonate in enclosed water bodies. The distribution of these reefs is extremely limited with records from Ardbear Lough, Killary Harbour and Blacksod Bay in Ireland; and Loch Creran, Loch Ailort and Loch Teacuis in Scotland (Neff, 1969; Bosence, 1973; Minchin, 1987; MERC Consultants, 2008; Dodd *et al.,* 2009; Moore *et al.,* 2009; Moore, 2019). Loch Creran has the largest known extant reef at 108 ha and the reefs in the Loch are highly vulnerable to physical anthropogenic disturbance, caused by mooring chains, dredging and aquaculture installations (Moore *et al.,* 2009). Reefs reported from Linne Mhuirich in Loch Sween disappeared during the 1990's, and recently unexplained declines have been reported in Loch Teacuis and Loch Creran (Moore *et al.,* 2020; Kamphausen, 2015).

Given the limited global distribution, sensitivity and decline of *Serpula vermicularis* reefs, there is a pressing need to understand aspects of their ecology which would underpin any future restoration project. For example, a recruitment peak has been described in late summer (Cotter *et al.,* 2003; Chapman *et al.,* 2007) and seasonal larval maxima and settlement patterns have been observed for many biogenic reef forming species in temperate latitudes (Seed and Brown, 1977; Soria *et al.,* 2014; Maathuis *et al.,* 2020). Following the removal of anthropogenic pressures from an ecosystem the commonly acknowledged second step in any restoration project is to enhance natural recruitment. This is commonly addressed through increased habitat provision and stock enhancement (Brumbaugh *et al.,* 2006; Elliott *et al.,* 2007; Mann and Powell, 2007; Brumbaugh and Coen, 2009). Seasonal timing in the deployment may have a profound effect on restoration success: As there are potential trade-offs between the formation of attractive biofilms (Rodriguez-Perez *et al.,* 2019) and the formation of competitive epibionts on settlement material (Evensen *et al.,* 2019). This is a consideration that appears to have been overlooked in temperate reef restoration projects to date.

The aim of the present study was to investigate if deployment period and location would influence the settlement success of a biogenic reef-forming species onto deployed restoration materials. The null hypotheses being. H0: There will be equal abundances of *S. vermicularis* settled on restoration materials deployed at different times. H0: Restoration materials deployed at different locations will have equal abundances of settled *S. vermicularis.*

Methods

Study site and sampling procedure

Loch Creran is a fjordic sea loch on the west coast of Scotland, comprised of two main basins. In the lower basin a belt of scattered *Serpula vermicularis* reef runs around the margin of the loch between depths of 1 to 13 m BCD (Moore *et al.,* 2009). The main study site (Main Site) was located near the southern shore of Loch Creran in the lower basin (56° 31.371' N, 05° 19.989' W). An additional three sites were spaced around the lower basin with one further site in the upper basin (Figure 1). Previous work Chapman *et al.,* (2007) and Moore *et al.,* (2009) indicated settlement and reef density were greatest between 2-9 m below chart datum, therefore all sites were located at 6 m below chart datum to ensure optimum settlement rates. Sites were selected to provide broad geographic coverage within the area of known reef distribution in the loch. Three sites were in areas with limited reef development (Upper Basin, Mussel Farm and Kelco) and two were in areas with well-established reef aggregations (Main Site, Rubha Mòr; Moore *et al.,* 2009). The substrate was similar at all sites and consisted of mixed poorly sorted muddy sediment.

Settlement tiles were used to test the effects of deployment timing and location on recruitment and post settlement survival. The 10 cm x 10 cm tiles were made from quartzite and attached vertically in pairs to canes. At each site, the canes were pushed into the sediment at random points within an area of uniform substrate type. There was a minimum spacing of 4 cm between tiles on a cane and a separation of 1 m to 1.5 m between canes. All tiles were positioned facing north to remove any effects relating to orientation.

The effect of deployment timing was investigated by deploying 10 tiles at the Main Site on each of 6 occasions. These deployments were conducted at 2 monthly intervals between January 2012 and November 2012; all tiles were then removed in November 2013. This gave deployment durations of between 12 and 22 months. The tiles are referred to throughout the present study by the month of their deployment.

The effect of location on recruitment and post settlement survival within the loch was tested by deploying an additional 10 tiles at each of the 5 sites in February 2013. These tiles were then removed 12 months later.

Hydrolab MS5 minisondes fitted with salinity and temperature sensors were deployed on the seabed at each site between February 2013 and February 2014 to record temperature and conductivity at one-hour intervals. Salinity was calculated in Parts Per Thousand (PPT) by the instruments using the algorithm outlined by Miller *et al.,* (1988). The sondes were recovered approximately every two months, cleaned, downloaded and re-calibrated to ensure accurate measurements before redeployment. The sondes were rotated between sites over the year to remove any instrument-based bias. Additionally, a Valeport model 602 CTD was deployed at 3 sites across the two basins approximately every 2 months. These data were used to validate the data recorded by the sondes.

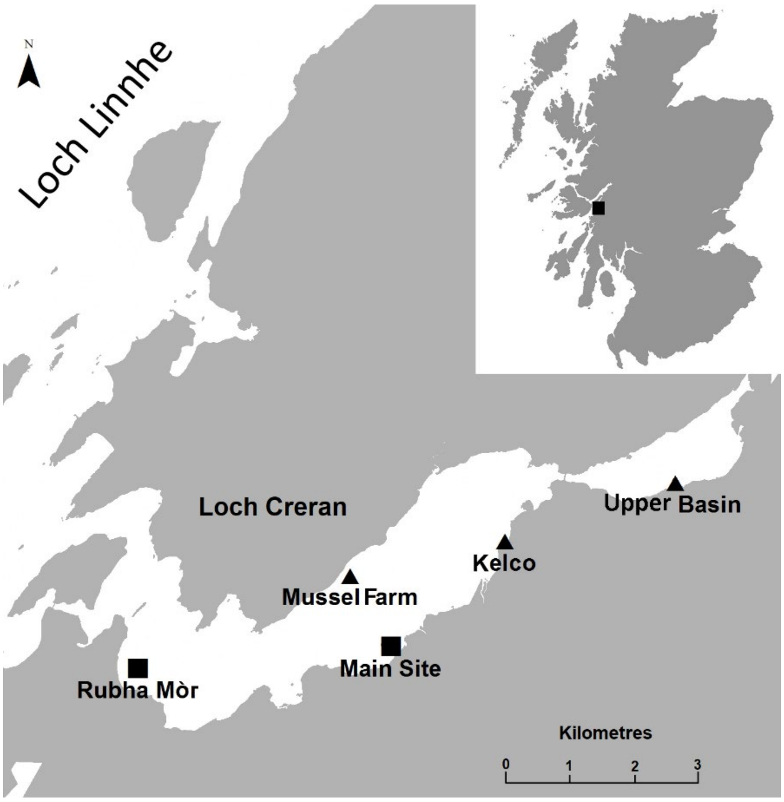

Figure 1. Loch Creran study site. Black squares indicate the location and names of the two study sites with existing reefs, the triangles indicate the sites with no extant reefs present.

Analysis

All tiles were stored in seawater and examined alive under a dissection microscope within 1 week of recovery. Serpulids were identified to species level and counted, small serpulids less than 2mm in length were recorded as Serpulidae spp.

Data analysis was conducted in R, with graphical interpretations conducted using the ggplot2 package (Wickham, 2009; R Core Team, 2015). Generalised Linear Models (GLMs) were used to test for spatial, temporal effects on recruitment and post settlement survival and interactions with the most abundant species. Negative binomial regression models were fitted using the lme4 package (Bates *et al.,* 2013), to account for the non-normal data and to control over dispersion in the model. These techniques proved to be the most appropriate for non-normally distributed count data (Ver Hoef and Boveng, 2007; Bolker *et al.,* 2009; O'Hara and Kotze, 2010). Null hypotheses were tested using an F test of deletion, by comparing the original model to a reduced model. F tests were used over Likelihood Ratio (LR) tests as they have proved more reliable for small sample sizes (Bolker *et al.,* 2009). Pairwise analysis of categorical response variables were conducted when a significant difference was detected using the general linear hypothesis routine (glht) within the multcomp package (Hothorn *et al.,* 2008). A Generalised Linear Mixed Model (GLMM) was used to test for the effect of "reef presence" using the lme4 package (Bates *et al.,* 2013). The model was fitted using a poisson error structure, to account for the non-normal count data (Bolker *et al.,* 2009; O'Hara and Kotze, 2010). Site was specified as a random effect within the model, and reef presence as the categorical fixed factor. Site was used as a random factor to account for the spatial pseudoreplication within the model (Millar and Anderson, 2004). The null hypotheses of no reef effect was tested using an LR test of deletion, by comparing the original model to a reduced model.

Salinity and temperature data were reviewed and outlying data points caused by instrumentation error such as low power or fouling were removed. These data were then averaged to give one reading per variable, per day, per site, they were also not normally distributed or conformed to any common distribution without transformation. Tests for differences in the salinity and temperature between sites were conducted using non-parametric Kruskal Wallis tests. If significant, pairwise comparisons were then conducted using a pairwise Wilcox test with a Bonferroni correction (Crawley, 2007).

Results

Temporal effects

From the 60 tiles deployed bimonthly, there was no significant relationship between the duration tiles had been deployed and the abundance of *S. vermicularis* ($F = 0.0185$, $P = 0.8869$), deployment duration was only able to explain 0.03% of the variance in the abundance of *S. vermicularis*. There was however a significant difference in the abundance of *S. vermicularis* due to deployment month (Figure 2: $F = 5.237$, $P >0.001$). Pairwise tests found significantly more individuals on tiles deployed in July, compared to tiles deployed in January, March, September and November, with F always >3.001 and P always <0.03. Additionally, the pairwise tests found significantly more individuals on tiles deployed in May than November ($F = 3.16$, $P = 0.01$). Deployment month was able to explain 32.7 % of the variance in the abundance of *S. vermicularis*.

The most abundant species recorded on the tiles over time was *Spirobranchus triqueter* (Linnaeus, 1758). A GLM revealed there was no significant interaction effect of *S. triqueter* on the abundance of *S. vermicularis* with deployment duration ($F = 0.433$, $P = 0.823$). A further GLM with *S. triqueter* abundance as the response variable, detected a significant difference in the abundance of *S. triqueter* due to deployment month (Figure 2: $F = 3.402$, $P = 0.009$). Pairwise tests found significantly higher abundances in May compared to January and September with Z always >3.5 and P always <0.005.

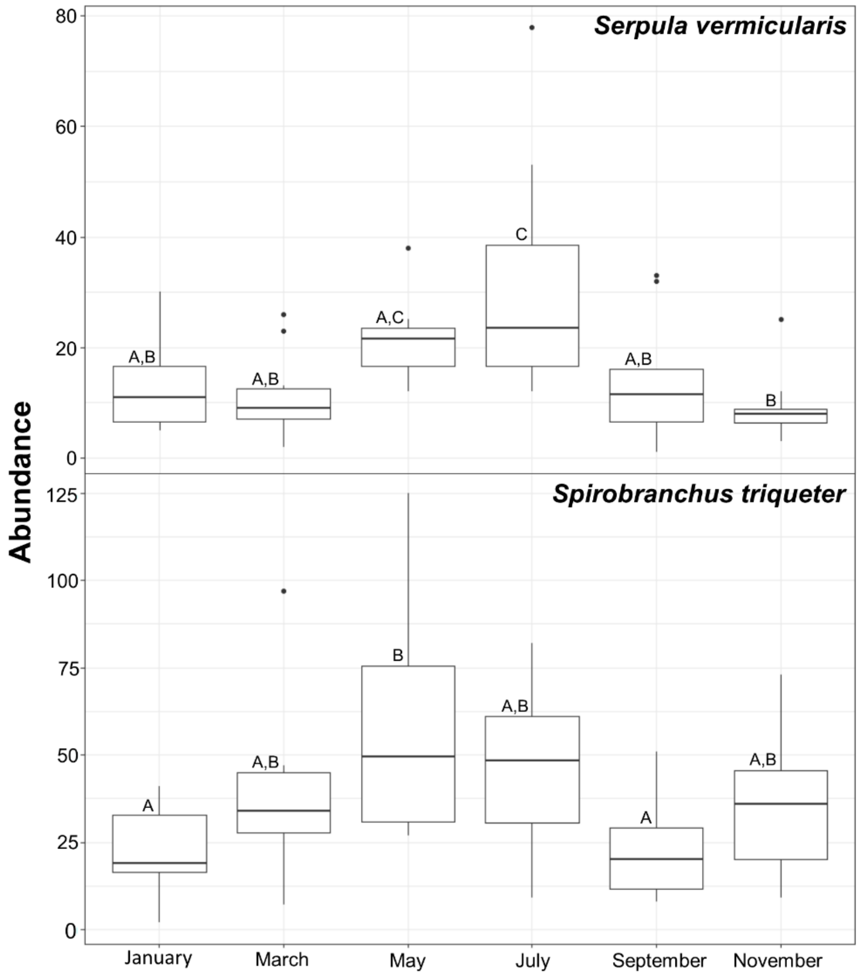

Figure. 2. Abundance of *Serpula vermicularis* and *Spirobranchus triqueter* per settlement tile from tiles deployed bimonthly during 2012. Box plots represent inter-quartile range, median, maximum and minimum values or points representing outliers if greater than 1.5x the inter quartile range. Sites not sharing a capital letter are significantly different (p<0.05).

Spatial effects

From the 50 tiles deployed at the 5 sites, 49 were recovered because one tile was lost at Rubha Mòr. There was a significant difference in the abundance of *S. vermicularis* due to location (Figure 3: F = 7.59, P <0.001). Pairwise tests found significantly lower abundances at Rubha Mòr compared to Mussel Farm, Kelco and Upper Basin (Z = 3.7-4.2, P always <0.002). The Main Site also had significantly fewer individuals compared to Kelco, Mussel Farm and Upper Basin (Z = 3.95-4.44, P always <0.001).

A GLMM found the reef sites to have significantly less *S. vermicularis* than the non-reef sites, with site specified as a random factor (LRT = 22.196 P <0.001). Sites with existing reefs areas (Main Site and Rubha Mòr) had on average only a third of the *S. vermicularis* colonists that were recorded at the non-reef sites (Mussel Farm, Kelco and Upper Basin), with average abundances of 9.1 and 32.9 individuals per tile respectively.

The most abundant species recorded across the 5 sites was *S. triqueter*. A GLM revealed there was no significant interaction effect of *S. triqueter* on the abundance of *S. vermicularis* across the sites (F = 1.62, P = 0.342). A further GLM with *S. triqueter* abundance as the response variable, detected a significant difference in the abundance of *S. triqueter* due to location (Figure3: F = 7.11, P <0.001). Pairwise tests found significantly more individuals at the Rubha Mòr site compared to all other sites, with Z always >3.02 and P always <0.02.

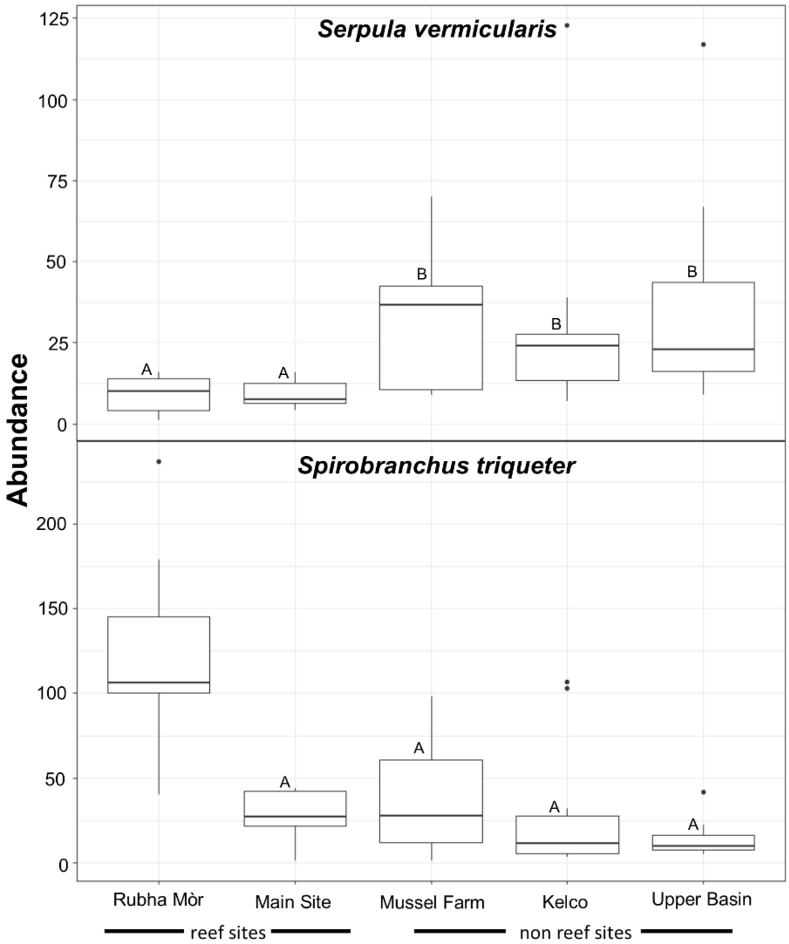

Figure. 3. Abundance of *Serpula vermicularis* and *Spirobranchus triqueter* per settlement tile at the 5 sites in Loch Creran during 2012. Box plots represent inter-quartile range, median, maximum and minimum values or points representing outliers if greater than 1.5x the inter quartile range. Sites not sharing a capital letter are significantly different (p<0.05).

Environmental data

Temperature and salinity were recorded for 194 days at Kelco, 144 at the Mussel Farm, 354 at Rubha Mòr, 302 at the Main Site and 357 at the Upper Basin. The CTD measurements taken during the study were always within the inter site variability of the sonde measurements, supporting their validity (Figure 4). Temperature did not vary by more than 1 ˚C between the sites over the year, and followed an expected seasonal trend, with maximum seawater temperatures reached in September and minimum temperatures in March. Salinity was much more variable throughout the year and followed no obvious seasonal trend. There were also greater variations in salinity between sites. A substantial decline in salinity of at least 3.5 ppt was recorded in January 2012 at all sites. This corresponded with an extreme rainfall event combined with significant snow melt in the catchment (Hannaford *et al.,* 2014).

Due to logger failures at different periods of the year, statistical comparisons could only be made between Rubha Mòr, Main Site and the Upper Basin over the same 284 days for temperature, and 227 days for salinity. There was no significant difference between the temperatures recorded at the 3 sites (Chi-Squared = 0.142, P = 0.931). There was however a significant difference in the salinity between the three sites (Chi-Squared = 95.59, P = <0.001). The Main Site had on average slightly higher salinities through the year than the other sites (31.95 ± 1.23 PPT), and the Upper Basin site had lower salinities with a greater range (30.92 ± 2.03 PPT) (Figure 4). Pairwise tests found these differences in salinity to be significant between all three sites, with P always <0.01.

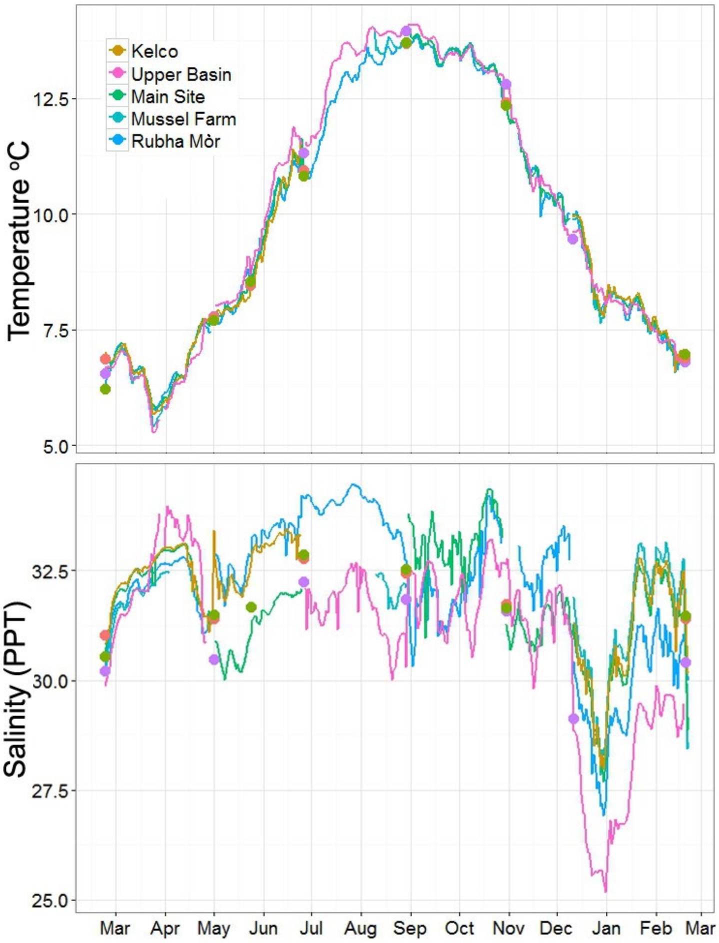

Figure 4. Daily averages for temperature and salinity at the 5 study sites, form February 2013 to February 2014. Spot data points represent CTD readings at a depth of 6m.

Discussion

This work is a unique pre-restoration study that investigated the potential for success of restoring a rare marine biogenic habitat of high conservation importance (Moore *et al.,* 1998; Chapman *et al.,* 2011; Nilsson *et al.,* 2016). The study showed significant differences in the settlement of *S. vermicularis* on restoration materials caused by deployment timing and location such that the null hypotheses are rejected. Settlement success was shown to be up to 3.3 times more if the habitat material was deployed in the optimum month and up to 3.5 times more if placed in the optimum location. These findings have implications for the growing number of temperate biogenic reef restoration projects (e.g., Pogoda *et al*., 2020).

Effects of deployment timing and location

Materials deployed in July had significantly more *Serpula vermicularis* colonists than tiles deployed at other times of the year (Figure 2). The greatest difference was between tiles deployed in July, which had 3.3 times more colonists than tiles deployed in November, confirming earlier observations by Cotter *et al.,* (2003) and Chapman *et al.,* (2007), but highlighting that these differences persist in post-settlement survival for over 12 months and despite subsequent settlement events.

Whilst the cause of the difference due to deployment timing could not be explored during the project, *in-situ* observations revealed that tiles deployed before July were not colonised by any other visible macroscopic organisms, which may have outcompeted or inhibited *S. vermicularis* recruitment. The establishment of biofilms on the tiles may have contributed to these differences. Although biofilm development has been shown to both inhibit or increase invertebrate larval settlement (Chan and Walker, 1998; Hamer *et al.,* 2001; Dobretsov *et al.,* 2013; Rodriguez-Perez *et al.,* 2019).

Sites without pre-existing reefs had on average 3.6 times more colonists than the sites in amongst existing reefs. This supports the view that larval supply away from existing reefs is not a limiting factor in reef development within the enclosed waterbody of Loch Creran. However, location within the loch still does significantly affect the settlement of *S. vermicularis*.

The explanation for the lower rates of larval settlement on tiles in areas with abundant reefs is unclear. Existence of *S. vermicularis* reefs in Loch Creran implies a gregarious settlement response. However, evidence for a gregarious settlement response in *S. vermicularis* might appear mixed because solitary individuals also occur on cobbles in Loch Creran (Bosence, 1979; Ten Hove, 1979; Chapman *et al.,* 2007). In the native European Oyster (*Ostrea edulis*), Rodriguez-Perez *et al*., (2019) found strong settlement preferences and settlement rates in response to conspecifics and weaker but nevertheless significant responses to hard substrata with a natural biofilm. It seems likely that biogenic habitats-forming species, found aggregated in nature, probably share these gradients of settlement responses.

Existing reefs in the present study, therefore, might have provided a stronger settlement cue to the larvae at small spatial scales, such that a higher proportion settled on adjacent reefs rather than on other available near-by substrates such as tiles. Away from these reefs and/or as the larvae age, they may become less choosy and therefore more likely to settle on tiles. However published evidence for decreasing selectivity in feeding larvae, particularly serpulid larvae, is mixed and these differences between sites with and without existing reefs may also be caused by other factors (Elkin & Marshall 2007; Toonen and Pawlik, 1994; 2001).

The present experiment was run over a 2-year period, whereas *S. vermicularis* aggregations are estimated to contain individuals of at least 6 years old (Hughes *et al.,* 2008). Therefore, the recorded initial high recruitment at sites without existing reefs cannot be taken as a certain indicator of future reef development because there are other biotic or abiotic factors that may contribute to successful long-term reef development.

Conclusions and restoration best practice

There is an increasing global need for habitat restoration to replace lost biodiversity and ecosystem services and to meet goals including the restoration of at least 15% of degraded habitats (CBD Secretariat, 2010). To meet these ambitions an ecological understanding is required to underpin restoration projects (Egoh *et al.,* 2014; Crouzeilles *et al.,* 2016; Miller *et al.,* 2016; Zu Ermgassen *et al*., 2020).

The provision of additional substrate to improve recruitment is a well-established worldwide practice dating back at least 2000 years (Mann and Powell, 2007). However, the greater the knowledge of an ecosystem the greater the probability that a restoration project will be successful with the minimum required resources (Simenstad *et al.,* 2006; Hobbs, 2007; Miller *et al.,* 2016). This study is the first to show that, although providing additional substrate can improve recruitment, the seasonal timing and appropriate location of a temperate marine restoration project can substantially affect its success in the medium term.

Overall, this study is rare in the field of marine restoration where a lack of supporting science often limits the scope for the adaptive design and management of restoration initiates (Baggett *et al.,* 2015; zu Ermgassen *et al*., 2020). Biogenic reef restoration programs, whether for oysters, mussels or polychaetes, must enhance the recruitment of the habitat forming species (Mann and Powell, 2007; Brumbaugh and Coen, 2009). Since the present study shows that optimum timing and location can more than treble successful recruitment, the findings probably have widespread application to the planning and execution of temperate biogenic reef restoration.

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