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Restoring marine ecosystems: Spatial reef configuration triggers taxon-specific responses among early colonizers

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Abstract

1. The longstanding debate in conservation biology on the importance of single large or several small (SLOSS) habitats for preserving biodiversity remains highly relevant, given the ongoing degradation and loss of natural habitats world-wide. Restoration efforts are often constrained by limited resources, and insights from SLOSS studies therefore have important implications if restoration efforts can be optimized by manipulating the spatial configuration of restored habitats. Yet, the relevance of SLOSS for habitat restoration remains largely unexplored.
2. Here, we report the effects of spatial reef configuration on early colonization of marine organisms after restoring boulder reef habitats. Reefs were restored in single large (SL) and several small (SS) designs in the western Baltic Sea, where century-long boulder extraction has severely degraded large reef areas and likely exacerbated regional declines in commercially important gadoids (*Gadidae* spp.). We sampled the field sites using remote underwater video systems in a before-after control-impact (BACI) design and obtained probabilistic inferences on restoration and SLOSS effects from Bayesian hierarchical models.
3. Probabilities of a positive restoration effect were high (>95%) for gadoids, labrids and demersal gobies, moderate (60%–75%) for species richness and sand gobies, and low (<5%) for flatfish abundance. Notably, gadoid abundance increased 60-fold and 129-fold on average at SL and SS respectively. The species composition at restored reefs deviated from control sites, mainly driven by large-bodied piscivores.
4. Spatial reef configuration had the strongest effect on small-bodied mesopredators, including gobies, which were more abundant at SS and driving distinct species assemblages between the reef designs. In addition to providing suitable conditions for reef species, results suggest that SS can also benefit soft-bottom taxa, possibly through a dispersed predator-mediated effect relative to SL.
5. *Synthesis and applications.* This study demonstrates that boulder reef restoration can strongly promote the abundance of exploited gadoids (e.g. Atlantic cod) and is therefore a promising management tool to support top-down controls by

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predatory fishes in degraded marine systems. The higher abundance of meso-predators at reefs with a 'several small' configuration suggests that the SLOSS dilemma could have long-term implications for trophic structure and resilience of restored habitats, and should therefore become an important facet within restoration strategies.

KEYWORDS

Atlantic cod, BACI design, Baltic Sea, Bayesian hierarchical models, reef restoration, remote underwater video systems, rocky reefs, SLOSS

1 | INTRODUCTION

Coastal waters around the globe are facing cumulative impacts from human-induced stressors at an accelerating pace (Halpern et al., 2019). In the Baltic Sea, a combination of resource extraction, eutrophication and pollution has severely degraded coastal habitats (Korpinen et al., 2012). The seabed of the Baltic Sea is generally dominated by mud and sandy mud of smooth topography, yet large boulders are scattered across the low relief areas as a result of glacial erosion and deposition (Beisiegel et al., 2019; Kaskela & Kotilainen, 2017). Accumulations of boulders locally form geogenic reef systems, providing hard substrate and structural complexity in an otherwise homogenous environment. The hard substrate enables anchorage of macroalgae and sessile fauna, and complex reef structures such as holes, crevices and ledges offer shelter for numerous marine species. In recent history, extraction of marine boulders for the construction of harbours, jetties and other coastal structures has reduced the quality and volume of hard bottom substrate in the Baltic Sea (Dahl et al., 2003). While boulder extraction from Danish waters was prohibited in 2010 (Kristensen et al., 2017), the permanent removal of hard substrate constitutes a fundamental shift in reef availability, hampering recovery of associated flora and fauna and making habitat restoration efforts warranted (Johnson et al., 2017).

A longstanding conundrum within the field of conservation biology involves the efficacy of a single large or several small (SLOSS) habitat configuration in promoting species richness (Cole, 1981; Diamond, 1975; Simberloff & Abele, 1982). Notably, the emergence of SLOSS from equilibrium theory in island biogeography (MacArthur & Wilson, 1963) resulted in numerous studies examining SLOSS for terrestrial systems (overview in Volenec & Dobson, 2020). Single large (SL) habitats tend to provide stable conditions for large population sizes, while several small (SS) systems often include more heterogeneous habitats and cover a greater geographical extent (Rösch et al., 2015; Volenec & Dobson, 2020). However, extrapolating empirical evidence from terrestrial SLOSS studies to marine systems may not be a valid approach, given the marked differences in physical, ecological and evolutionary processes between marine and terrestrial environments (Carr et al., 2003). For example, dispersal from marine reserves may replenish neighbouring habitats and facilitate habitat connectivity across large distances (>40 km; Manel

et al., 2019), whereas the productivity of terrestrial reserves highly depends upon local fecundity, often with limited exchange among populations (Carr et al., 2003). As such, SLOSS studies from a wide range of marine systems are warranted to assess potential effects on associated marine communities and elucidate the underpinning mechanisms. To date, studies examining SLOSS for marine environments have been limited to marine reserves (Fovargue et al., 2018; Puckett & Eggleston, 2016; Stockhausen & Lipcius, 2001), coral reefs (Acosta & Robertson, 2002), concrete modules (Bohnsack et al., 1994) and seagrass beds (McNeill & Fairweather, 1993). While investigated response variables differ between studies, the majority of findings indicate $SS > SL$ with only one study concluding $SL > SS$ (Stockhausen & Lipcius, 2001) and one study finding no effect (Acosta & Robertson, 2002).

The SLOSS concept has received much attention in conservation biology, landscape ecology and reserve design, yet there remains a largely unexplored potential to synergize SLOSS theories and empirical evidence with restoration ecology (Bell et al., 1997; Metzger & Brancalion, 2017). For example, identifying the appropriate spatial configuration of restored habitat may facilitate successful recruitment of fauna (Bell et al., 1997) and optimize restoration outcomes (Belder et al., 2019). Boulder reefs provide an ideal case study to test the importance of SLOSS for restoration ecology, as boulders represent patches of isolated habitats that are easily manipulated (e.g. in spatial configuration; Chapman, 2017). In addition, boulder substrate is increasingly incorporated in ecological engineering (Liversage & Chapman, 2018), for example to diversify seawalls (Chapman & Underwood, 2011), and in restoration efforts of geogenic (Kilfoyle et al., 2013; Støttrup et al., 2017) or biogenic reefs (i.e. multi-habitat restoration; Liversage, 2020). Studies on boulder reefs have highlighted the importance of microhabitat (i.e. centimetres; Liversage et al., 2017) and geological features across large scales (i.e. kilometres; Beisiegel et al., 2018; Franz et al., 2021) in shaping reef community dynamics, but the effects of spatial reef configuration on intermediate scales (i.e. reef patches; 10–100 m) are still poorly understood. Accordingly, there is a need to examine the importance of SLOSS in shaping the marine community associated with boulder substrates and the underlying implications for restoration efforts in general.

In this study, we constructed SL and SS boulder reefs in a coastal area of the western Baltic Sea where reefs were depleted

by historical extractive activities. We monitored the field sites using remote underwater video systems (RUVS) before and after the reef restoration to address three aims. First, we assessed the effects of reef restoration on species richness and relative abundance of prevalent taxa by comparing pre- and post-restoration sites. Second, we compared these metrics for SL and SS to address SLOSS in relation to marine habitat restoration. Finally, we delineated the species composition of pre- and post-restoration sites and assessed whether reef configuration affected the composition of colonizing species.

2 | MATERIALS AND METHODS

2.1 | Study area and design

Our study was carried out within Flensborg Fjord, a Natura 2000 designated protected area between Denmark and Germany. We selected six field sites (Figure 1a) using archived information on historic boulder extraction sites (Mammen Kruse, 2016). All sites had a depth between 6 and 7 m and were separated by at least 500 m. We used a before-after control-impact (BACI; Christie et al., 2019) sampling scheme, by assigning two control (sandy bottom) sites and four impact (restoration) sites for sampling before and after the reef restoration. Pre-restoration sampling took place on daily basis during the summer months of June and July 2016, as long as weather conditions allowed for safe boating (details provided in S1 of Supporting Information). Subsequently, we constructed boulder reefs in December 2017 and January 2018 and conducted post-restoration sampling during June and July of 2018 (i.e. approximately 5–6 months after the restoration). All field sites therefore consisted of empty sand bottoms in 2016 but were still separated into control and restoration sites (Figure 1) to disentangle natural temporal fluctuations from the restoration effects.

Reefs were constructed using boulders with a diameter of 0.5–1.5 m, obtained from a quarry in Norway. The total amount of restored habitat at each of the four restoration sites was standardized at a reef volume of 500 m³. The two remaining sites served as soft-bottom control sites (Figure 1a). At two restoration sites, the volume of boulders (500 m³) was deposited at one location to form a single large (SL) reef (Figure 1b,d), whereas boulders were distributed in a 4 × 4 configuration at the remaining two restoration sites to construct several small (SS) reefs (Figure 1c,e). All constructed reefs were 2 m in height. The sampled area was standardized for each site at 3,250 m², which encompassed the entire SS configuration (Figure 1c; including intermediate sand) and included a 25 m radius of sand habitat surrounding the SL reefs (Figure 1b).

2.2 | Data collection

We deployed unbaited RUVS (Figure 1f) to monitor the field sites. We used GoPro cameras (Hero 3, 3+ and 4; GoPro), equipped with a timer (Time Lapse Intervalometer or BlinkX; CamDo Solutions,

Canada), which programmed the cameras to record for 2 min every hour. Each deployment consisted of 24–60 two-minute recordings (i.e. recordings across 24–60 hr), which were used as individual sampling units. We deployed a maximum of 3–4 RUVS at the same field site on a given sampling day, with distances between the RUVS actively maximized within the confines of the sites. We used a side scanner (Lowrance Elite-7 Ti; Lowrance Electronics) to scan the bottom for the desired substrate (i.e. restored reef or sand). Further details on sampling procedures are provided in the Supporting Information.

2.3 | Video analyses

We analysed video recordings using VLC Media Player (VideoLan; www.videolan.org). Relative abundance of species was measured as MaxN counts (Cappo et al., 2003), a widely used metric obtained by counting the maximum number of individuals of a certain species in any video frame to avoid double counting. Observers identified individuals to the lowest possible taxonomic category. In case species-level identification was unattainable, individuals were grouped by genus or family level. The sampled marine community included all conspicuous organisms within the field of view of the camera, from slow-moving benthos (e.g. starfish) to mobile pelagic species (e.g. herring; Table S2). However, sampling notably excluded sessile taxa (e.g. ascidians, barnacles and sponges) which could not be easily identified and counted from the RUVS recordings and for which other video methods such as downward-facing towed cameras are more suitable (Beisiegel et al., 2018). While we did not identify macroalgae observed on the videos, both vegetation and boulder coverages were estimated as proportions of the total visible seabed within a video frame, to describe the sampled habitat (Figure S2). In addition, functional visibility was estimated for each hourly video sequence from rope markers deployed along the camera's field of view.

2.4 | Statistical analysis

We used Bayesian hierarchical models to analyse the effects of reef restoration and configuration on species richness and abundance of prevalent marine taxa. Specifically, we fitted generalized linear multilevel models (GLMLMs) to assess the efficacy of the restoration efforts while incorporating our BACI sampling design. The integer response variables were initially modelled using a Poisson distribution with a log-link and subsequently assessed for dispersion. Models showing overdispersion were improved using a negative binomial distribution (Figure S7), while the Conway–Maxwell Poisson distribution proved effective at dealing with underdispersion (Figure S8; Huang, 2017).

Similar to previous studies employing a BACI design (e.g. Stenberg et al., 2015), we focused on the interaction between time period (pre- and post-restoration) and treatment (Control, SL and SS) to disentangle restoration effects from temporal fluctuations

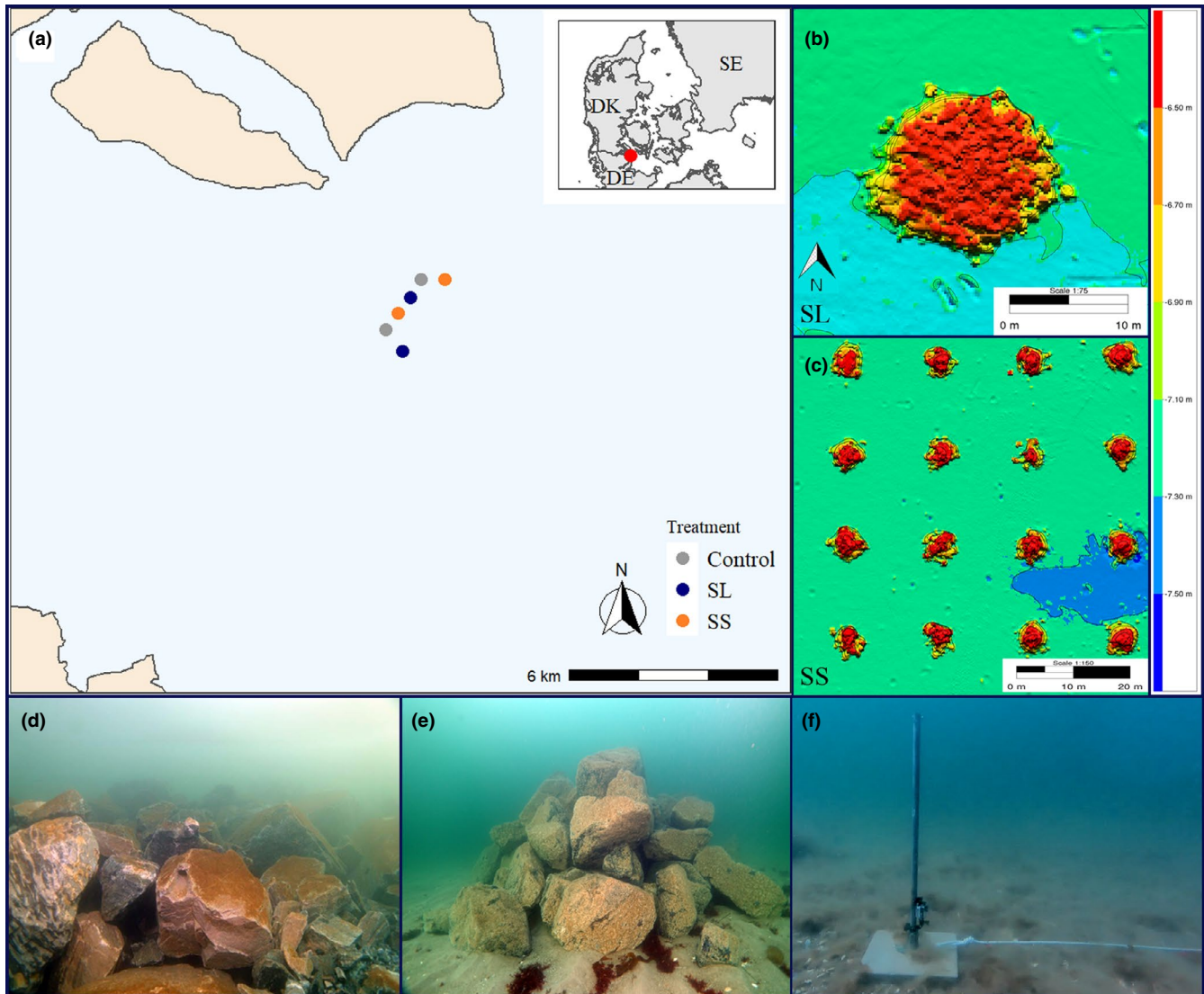


FIGURE 1 Overview of the study location and spatial reef configurations. The map shows the study area in the southwestern Baltic Sea, with colours denoting locations of the treatment replicates (a). At two restoration sites, reefs were constructed as a single large (SL) reef (b, d; diameter = 13 m), while reefs were distributed in a 4 × 4 configuration of several small (SS) reefs (c, e; diameter = 3.5 m) at the two remaining restoration sites. Two soft-bottom sites served as controls. All sites were monitored using remote underwater video systems (f)

in the system. Additional GLMLM covariates included vegetation coverage on the seabed and the natural logarithm of functional visibility (Zuur & Ieno, 2016). We defined group-level effects for each model to incorporate inherent variations due to sampling design. Specifically, varying intercepts at the site level accounted for correlations between deployments from the same site, while varying intercepts for each deployment were nested within site to account for additional correlation between hourly samples from the same camera deployment. Hierarchical models assume that residuals are independent without spatial or temporal dependencies. Given our sampling method, however, with hourly samples and multiple deployments per site, this may not be a valid assumption. We therefore tested all models for residual patterns and included a Gaussian process (exponentiated-quadratic kernel) on deployment coordinates and/or an autoregressive correlation structure on

hourly samples to account for spatial and temporal autocorrelation, respectively, if such dependencies were present. Prior predictive checks (Figure S4) were performed following the protocol described in Gabry et al. (2019). Finally, the most parsimonious model for each response variable (Table S3 and S4) was selected through leave-one-out cross-validation. This method provides estimates of out-of-sample prediction error using Pareto smoothed importance sampling (Vehtari et al., 2017), allowing for comparison of predictive accuracy between multiple candidate models.

We followed the protocol outlined by Conner et al. (2016) and employed a combination of Bayesian Markov chain Monte Carlo (MCMC) sampling and BACI ratio computation to estimate probabilities of different restoration effect sizes. First, we extracted posterior samples from all models for each time period and treatment level, with the number of samples (N) depending on the number of

post-warmup iterations for each model (Table S3). Next, we computed 'before-ratios' and 'after-ratios' as follows:

$$R_{ijSL_B} = \frac{\hat{Y}_{ijSL_B}}{\hat{Y}_{ijControl_B}}; R_{ijSL_A} = \frac{\hat{Y}_{ijSL_A}}{\hat{Y}_{ijControl_A}}; i = 1, \dots, N, \quad (1)$$

with R_{ijSL_B} denoting the 'before-ratios' and R_{ijSL_A} the 'after-ratios' for the i -th iteration of the SL treatment, while \hat{Y}_{ijSL} and $\hat{Y}_{ijControl}$ represent the fitted values (on the response scale) for the i -th iteration of the SL and control treatment respectively. The same calculations were applied to the SS treatment. We then computed 'BACI ratios' for the two reef configurations:

$$R_{ijSL_BACI} = \frac{R_{ijSL_A}}{R_{ijSL_B}}; R_{ijSS_BACI} = \frac{R_{ijSS_A}}{R_{ijSS_B}}; i = 1, \dots, N, \quad (2)$$

yielding a posterior distribution of N BACI ratios for each reef treatment. Since a BACI ratio of 1 indicates an equal 'before-ratios' and 'after-ratios', the posterior density (i.e. area under the curve) of ratios >1 is equivalent to the probability of a positive restoration effect on the response variable. Therefore, this method allows for a straightforward probability assessment of any impact effect size of interest. Finally, we calculated 'SLOSS ratios' to compare restoration effects between the two reef configurations:

$$R_{ijSLOSS} = \frac{R_{ijSS_BACI}}{R_{ijSL_BACI}}; i = 1, \dots, N, \quad (3)$$

yielding a posterior distribution of N SLOSS ratios with the density of ratios >1 being equivalent to the probability of a larger response variable at SS.

To assess the effects of both reef restoration and configuration on species composition, we performed a Bayesian ordination and multivariate regression analysis. Specifically, we fitted pure latent variable models (LVMs) to run a model-based unconstrained ordination and visualize sites with indicator species in a low-dimensional plot (Hui, 2016). This approach allows for validation of distributional and residual assumptions, as well as a comparison of information criteria values between different models. We initially used a Poisson distribution to model the multivariate species abundances, but information criteria values and model validation plots (Figure S11) indicated that using a negative binomial distribution improved the fit. We excluded species occurring in less than three camera deployments and defined a site-level row effect to account for variations in abundance per site to focus on community composition. In case of community differences, we further tested the effect of environmental parameters (i.e. reef configuration and vegetation) by fitting correlated response models and inspecting residual correlations (Hui, 2016).

All analyses were performed in R statistical software version 3.6.1 (R Core Team, 2020). The Bayesian hierarchical models were fitted using the 'brm' function in the BRMS package (Bürkner, 2017), implementing Bayesian models through the R interface of the STAN

TABLE 1 Overview of the sampling effort and descriptive statistics on the raw observations. The number of camera deployments and extracted 2-min hourly samples (excluding night recordings) is given for each of the six field sites (Figure 1), whereas descriptive statistics are pooled for each treatment (Control, SL, SS) and time (pre- and post-restoration) combination

Treatment	Pre-restoration (2016)			Post-restoration (2018)		
	Control	SL	SS	Control	SL	SS
Sampling effort (for two replicate field sites per treatment)						
Camera deployments	22	16	22	39	40	55
Two-minute samples (N)	529	341	367	1,062	1,086	1,658
Descriptive statistics: Mean count 2 min ⁻¹ (SD)						
Species richness	1.81 (1.15)	1.83 (1.12)	1.88 (1.12)	2.31 (1.29)	2.31 (1.30)	2.77 (1.41)
Gadoids	0.01 (0.10)	0.00 (0.06)	0.00 (0.04)	0.00 (0.06)	0.47 (0.87)	0.25 (0.58)
Labrids	0.01 (0.13)	0.04 (0.22)	0.03 (0.19)	0.14 (0.42)	0.26 (0.61)	0.23 (0.53)
Flatfishes	0.02 (0.16)	0.02 (0.15)	0.03 (0.17)	0.07 (0.29)	0.02 (0.14)	0.04 (0.21)
Demersal gobies	0.30 (0.80)	0.21 (0.99)	0.03 (0.19)	2.37 (3.94)	2.39 (5.70)	2.81 (7.13)
Sand gobies	0.80 (1.17)	1.23 (1.74)	1.63 (1.69)	0.43 (0.87)	0.17 (0.54)	0.70 (0.94)

programming language (Carpenter et al., 2017). Spatial and temporal autocorrelation tests were performed using the DHARMA package (Hartig, 2018) after converting the Bayesian model fits into DHARMA objects with the 'createDHARMA' function. Posterior predictive checks were performed with the BAYESPLOT package (Gabry & Mahr, 2018). The LVMs were fitted using package BORAL version 1.8 (Hui, 2016).

3 | RESULTS

3.1 | Sampling effort and observed community

Field sampling resulted in a total of 383 camera deployments of which 106 deployments were completed pre-restoration and 277 deployments post-restoration, yielding 9,949 two-min hourly video samples (Table 1). We identified 40 unique species, including 30 marine fishes, 9 invertebrates and 1 marine mammal, belonging to 23 families. During pre-restoration sampling, we recorded 28 unique species (20 species at control, 18 at SL and 20 at SS), while 33 species were recorded post-restoration (26 at control, 24 at SL and 31 at SS). We grouped MaxN counts of the most prevalent fish species on family or order level to model responses of these prominent taxa to the reef restoration. The five focal groups included gadoids (*Gadidae* spp.), which are mobile predatory fishes comprised mainly of economically important Atlantic cod *Gadus morhua* and saithe *Pollachius virens*, as well as labrids *Labridae* spp. (mostly goldsinny wrasse *Ctenolabrus rupestris*), flatfishes *Pleuronectiformes* spp. (including both left-eyed and right-eyed species) and gobies *Gobiidae* spp. Given the differences in habitat association within the goby family, we divided gobies into demersal gobies (including two-spotted goby

Gobiusculus flavescens and transparent goby *Aphia minuta*) and sand gobies *Pomatoschistus* spp. and black goby, *Gobius niger*. A complete overview of observed species and focal groups is provided in the Supporting Information (Table S2).

3.2 | Reef restoration effects

Species richness (number of species per hourly recording) increased on average 8.5% and 22% at restored SL and SS reefs respectively, relative to control sites (Table 2). Notable observations contributing to post-restoration increases included Atlantic pollock *Pollachius pollachius* at SL, two species of sculpin *Myoxocephalus scorpius* and *Taurulus bubalis* at SS, and rock gunnel *Pholis gunnellus* and saithe at both reef treatments (Table S2). However, the posterior distribution of BACI ratios indicated substantial uncertainty around the posterior averages, revealing a moderate 64.1% (SL) and 74.8% (SS) probability of a positive restoration effect on species richness (Figure 2). The gadoid family showed a strong positive restoration response (Figure 3a). Specifically, gadoid abundance increased 60-fold and 129-fold on average at SL and SS, respectively, relative to control sites. The BACI ratio distributions indicated a probability of 99.8% for both configurations that reef restoration resulted in higher gadoid abundance (Figure 3a). The labrid family also responded positively to the reef restoration, with 1.8-fold (SL) and 3.6-fold (SS) average increases in abundance, relative to control sites. Probabilities for a positive restoration effect on labrid abundance were moderate for SL at 82.8%, but high for SS at 95.5% (Figure 3b).

In contrast, flatfishes showed a negative response to the restoration efforts. The average BACI ratios were similar between reef

TABLE 2 Summary of average BACI ratios (R_{BACI} ; computed according to the protocol described in Conner et al., 2016) with 2.5 and 97.5 percentiles of the ratio distributions in parentheses and probabilities (between 0 and 1) of differential restoration effect sizes across the columns

	R_{BACI}	$p(R_{\text{BACI}} > 1)$	$p(R_{\text{BACI}} > 2)$	$p(R_{\text{BACI}} > 10)$	$p(R_{\text{BACI}} > 100)$
Species richness					
SL	1.09 (0.70–1.69)	0.64	0.00	0.00	0.00
SS	1.22 (0.69–2.21)	0.75	0.05	0.00	0.00
Gadoids					
SL	60.4 (6.1–1510)	0.99	0.99	0.95	0.52
SS	129.2 (7.2–4478)	0.99	0.99	0.96	0.66
Labrids					
SL	1.8 (0.4–12.6)	0.83	0.57	0.05	0.00
SS	3.6 (0.8–24.1)	0.95	0.81	0.17	0.00
Flatfishes					
SL	0.34 (0.09–1.23)	0.04	0.01	0.00	0.00
SS	0.35 (0.10–1.07)	0.03	0.00	0.00	0.00
Demersal gobies					
SL	0.4 (0.1–2.7)	0.25	0.05	0.00	0.00
SS	8.3 (1.8–99.8)	0.99	0.97	0.58	0.02
Sand gobies					
SL	0.27 (0.04–1.32)	0.05	0.01	0.00	0.00
SS	1.69 (0.20–14.1)	0.67	0.40	0.05	0.00

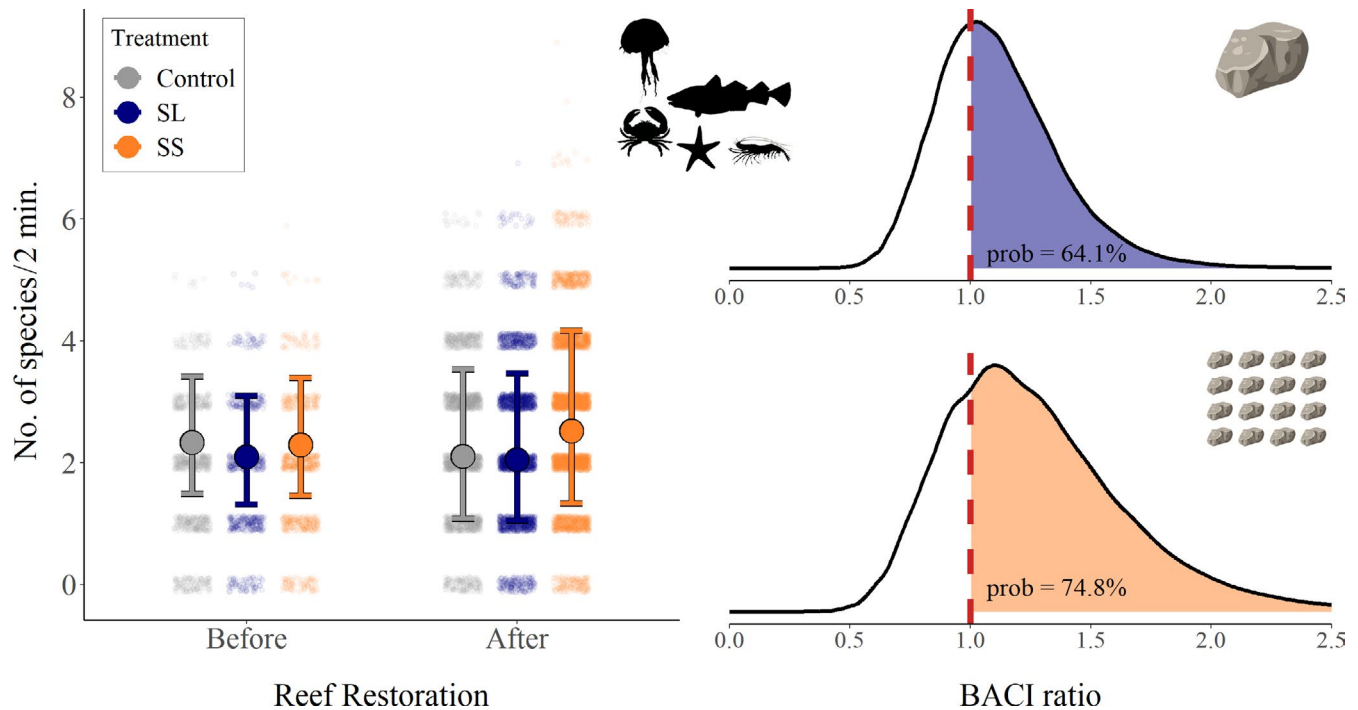


FIGURE 2 Reef restoration effects on species richness (no. of species/2 min. video). Restoration involved deployment of a single large (SL) reef and several small (SS) reefs. Left-hand side plot shows the posterior means and 95% credible intervals, with small semi-transparent circles representing raw observations that are jittered to improve visual representation. Right-hand side curves show the posterior distribution of BACI ratios for both reef configurations (SL and SS). BACI ratios were computed using Equations 1 and 2, with a ratio of 1 indicating equal values before and after the restoration (red dashed line). The probability (i.e. area under the curve) of a positive effect is indicated within the shaded area for each treatment

treatments, with a ratio of 0.35 indicating a 65% decrease on average in flatfish abundance, relative to control sites (Table 2). This decrease was also reflected in very low probabilities of 4.4% (SL) and 3.1% (SS) of a positive restoration effect (Figure 3c). Within the goby groups, restoration responses strongly depended on reef configuration. Demersal gobies decreased on average 60% in abundance at SL compared with control sites, with a 24.8% probability of a positive restoration effect (Figure 3d). In contrast, demersal gobies increased on average 730% in abundance at SS relative to control sites, with a 99.2% probability of a positive restoration effect. Sand gobies decreased 73% in abundance at SL contrary to a 69% increase at SS, relative to control sites, yielding a 5.1% probability of a positive restoration effect at SL, compared with 66.7% at SS reefs (Figure 3e).

3.3 | Reef configuration effects

Configuration of the reefs had a moderate effect on species richness, with on average 15% more species at SS and a probability of 70.3% that SS promoted richness over SL (Figure 4a). For gadoids, we found an average 1.6 times higher abundance at SS compared with SL and a 65.6% probability that SS promoted gadoid abundance (Figure 4b). Labrid abundance was on average 1.9 times higher at SS relative to SL with a 78.5% probability of higher labrid abundance at SS (Figure 4c). The negative restoration response of flatfish was not

affected by the reef configuration, as indicated by the 52.7% probability of higher abundance at SS (Figure 4d). The average SLOSS ratio for demersal gobies indicated that 26.7 times more gobies were observed at SS relative to SL reefs, while the density curve showed a 99.6% probability that SS resulted in higher demersal goby abundance (Figure 4e). Similarly, sand gobies were on average 7.9 times more abundant at SS, with a 98.6% probability of SS promoting sand gobies relative to SL reefs (Figure 4f).

3.4 | Community composition

Results from the LVMs indicated a unique species composition at the restored reefs that was clearly distinct from pre-restoration sites and post-restoration controls (Figure 5a). The distinct composition at restored reefs was mainly driven by large-bodied piscivores; including cod *G. morhua*, saithe *P. virens* and greater sandeel *Hyperoplus lanceolatus*, and a ctenophore; Northern comb jelly *B. infundibulum*. Furthermore, the exclusion of reference sites revealed distinct communities at SL and SS reefs (Figure 5b), with a number of small-bodied mesopredators (*G. niger*, *Caridea* sp. and *C. maenas*) showing associations with SS. Vegetation coverage was substantially higher at one of the SL sites (Figure S3), yet accounting for this environmental factor in a correlated response model indicated that vegetation was not the driver of the distinct communities, as evidenced by the

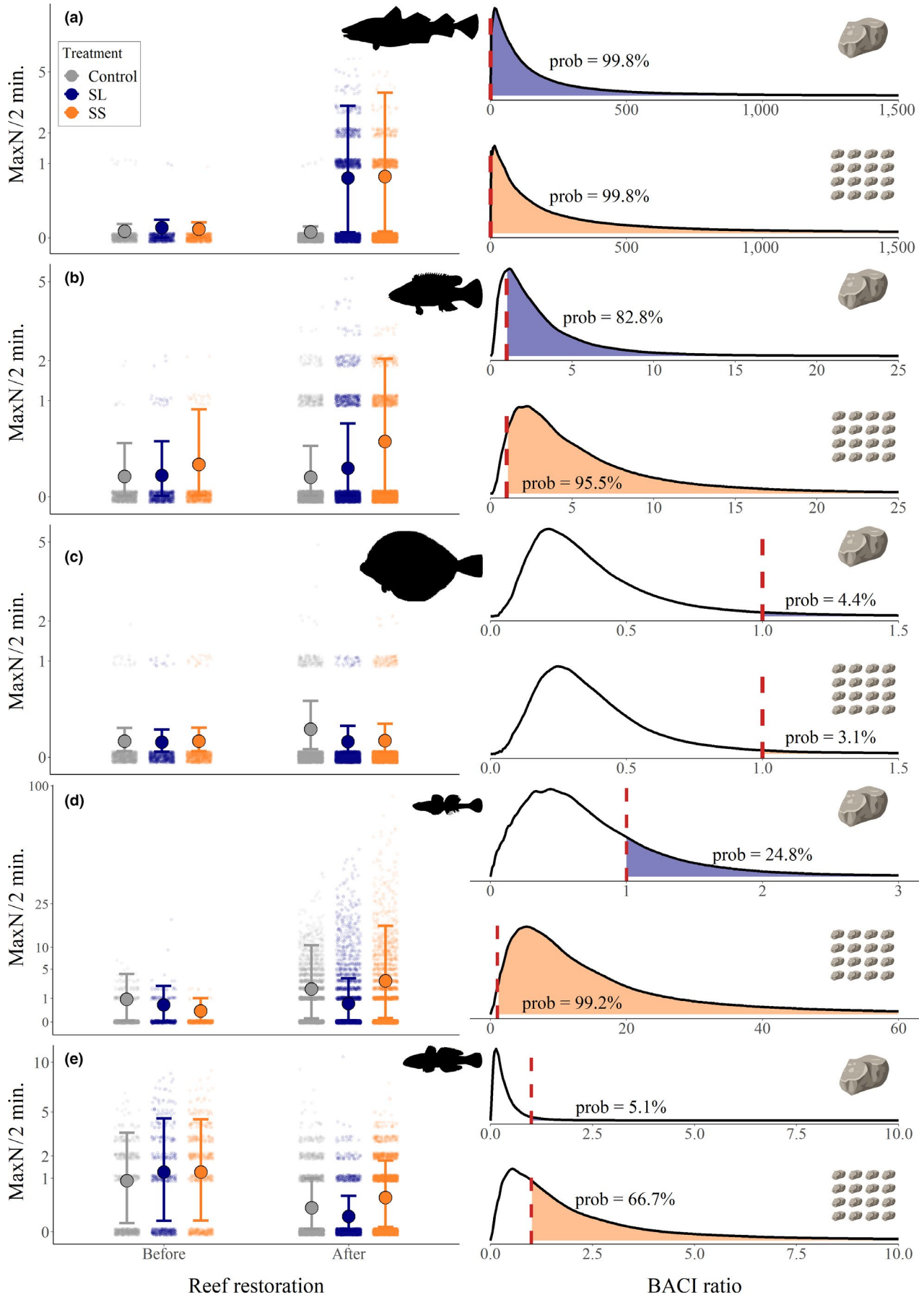


FIGURE 3 Reef restoration effects on relative abundance (MaxN/2 min. video) of the most prevalent taxa. Interpretation of left- and right-hand side plots is described in caption of Figure 2. Y-axes in left-hand side plots were root transformed to highlight fine-scaled variations in abundances between treatments. Density curves on the right-hand side show the posterior distributions of BACI ratios for all focal taxa, including (a) gadoids *Gadidae* spp., (b) labrids *Labridae* spp., (c) flatfishes *Pleuronectiformes* spp., (d) demersal gobies *Gobiidae* spp. and (e) sand gobies *Gobiidae* spp.

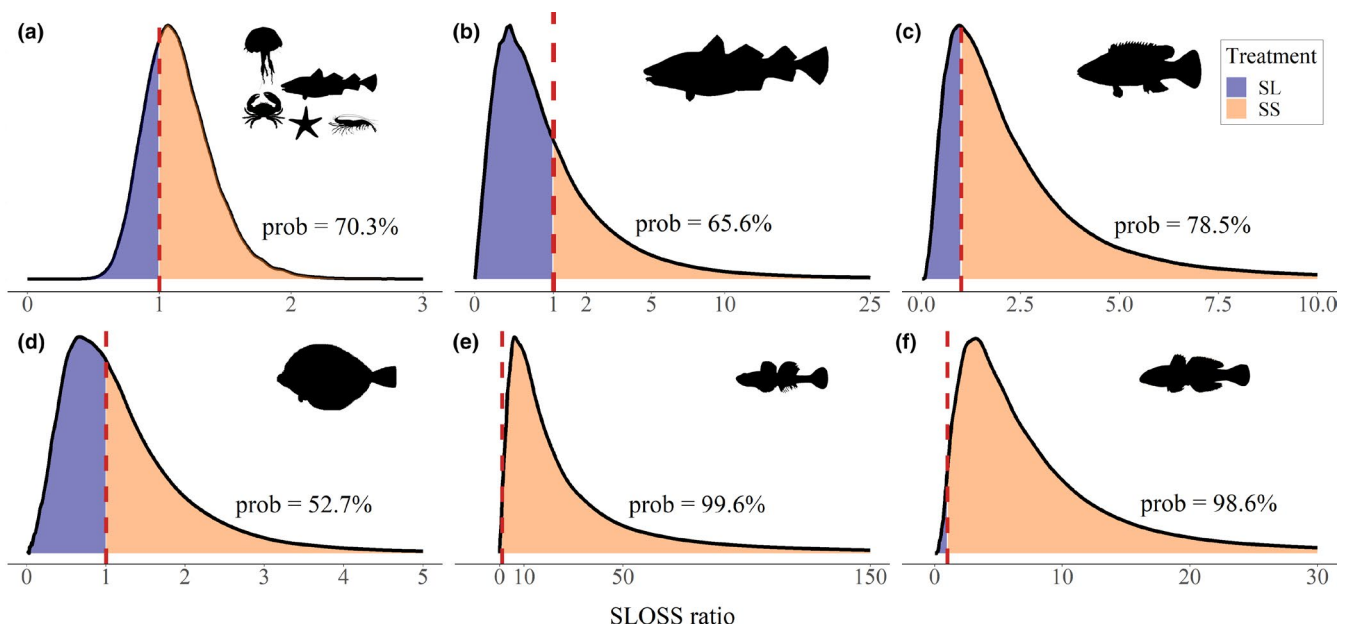


FIGURE 4 Posterior distributions of SLOSS ratios computed according to Equation (3). SLOSS ratios represent a direct comparison of the restoration effect at SL versus SS. A ratio of 1 corresponds to an equal restoration effect for both reef treatments (red dashed line). The probability (area under the curve) of a larger response variable at SS relative to SL sites is indicated next to each curve. SLOSS posterior distributions are shown for: (a) species richness; (b) gadoids *Gadidae* spp.; (c) labrids *Labridae* spp.; (d) flatfishes *Pleuronectiformes* spp.; (e) demersal gobies *Gobiidae* spp. and (f) sand gobies *Gobiidae* spp.

lack of overlap between the confidence ellipses (Figure 5c). Instead, accounting for reef configuration resulted in no residual patterns (Figure 5d), confirming that SLOSS was the main driver of the distinct communities.

4 | DISCUSSION

This study restored boulder reefs to recover hard substrate availability for reef-associated fauna in a coastal area of the Baltic Sea, where century-long boulder extraction has severely degraded and removed large areas of reef habitat. We constructed reefs in a SL and SS design to examine the importance of spatial habitat configuration for reef restoration in terms of colonizing marine taxa. Video monitoring revealed that a range of marine species colonized the reefs within 6 months. Most notably, the strong increases in relative abundance of commercially exploited gadoids suggest that boulder reef restoration is a promising management tool to help recover predatory fish stocks in degraded temperate waters. Spatial reef configuration did not have a pronounced effect on species richness, but instead triggered taxon-specific responses with small-bodied mesopredators strongly promoted at SS. Our results indicate that SLOSS should become an important facet within restoration strategies and highlight

the importance of collecting relative abundance data for taxonomic groups to move beyond the traditional focus on species richness and presence–absence data in evaluating SLOSS dynamics (Deane et al., 2020).

The combination of MCMC sampling and BACI ratio computation allows for easy to interpret probabilistic inference on the effect of impact events (Conner et al., 2016) and revealed that reef restoration in this study had a high probability of strongly increasing gadoid abundance (Table 2). These results confirm the importance of hard substrate for gadoids as highlighted in previous studies (Gotceitas & Brown, 1993; Rhodes et al., 2020), and stress the need for continued reef conservation and restoration efforts in areas where gadoids are heavily exploited, such as the Baltic Sea. Labrids and demersal gobies also responded favourably to the reef restoration, as expected from their strong association with diverse reef structures such as holes and crevices (Sayer et al., 1993; Utne-Palm et al., 2015). As common mesopredators, labrids and gobies may exert strong top-down effects on macrophyte communities by reducing mobile mesograzers (Östman et al., 2016). Management actions promoting healthy piscivorous fish stocks can therefore strengthen top-down controls and prevent cascading negative effects from mesopredator release (Östman et al., 2016). While restoration efforts seemed to trigger an increase in mesopredators in this study, the concurrent

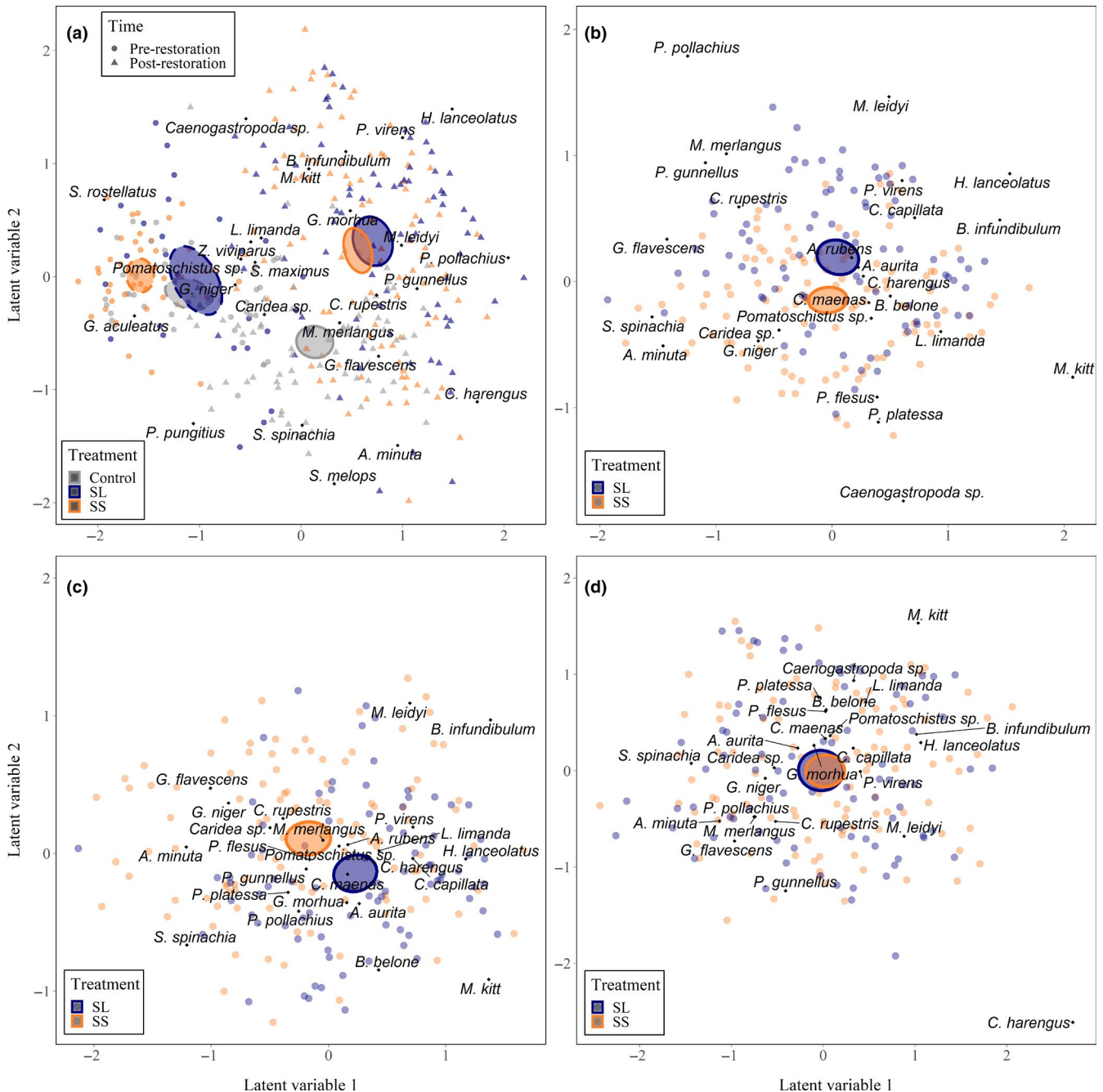


FIGURE 5 Biplots of unconstrained ordinations based on pure latent variable models (LVMs) and residual ordinations from correlated response models (CRMs). Species composition for each camera deployment is regressed against a set of unknown parameters (the latent variables) for low-dimensional visualization of community patterns. Each of the small symbols corresponds to a single camera deployment, while ellipses represent the 95% confidence intervals for the centroids of pre-restoration (dashed ellipses) and post-restoration (solid ellipses) treatments. LVMs were run on all data pooled to assess restoration effects (a) and separately on post-restoration reef data to assess the SLOSS effects (b) on species composition. To identify the driver(s) of distinct community patterns between restored SL and SS reefs, we assessed residual ordinations from CRMs that included vegetation coverage (c) and spatial reef configuration (d) as environmental variables. Positions of the 25 most important indicator species (based on their latent variable coefficients) are superimposed as small black dots to visualize their association with the different time treatment combinations. For example, species showing positive coefficients for both latent variables in (a) are associated with the restored reefs (e.g. *Pollachius virens* and *Hyperoplus lanceolatus*), whereas a negative latent variable 1 coefficient indicates an association with pre-restoration sites (e.g. *Gasterosteus aculeatus*)

increase in gadoids suggests that reef restoration may reinforce top-down controls by piscivorous fishes and possibly enhance resilience in degraded marine systems.

In contrast, flatfishes responded negatively to the reef restoration independent of the configuration of the reefs. Since flatfishes are ambush predators found predominantly on featureless sandy

bottoms (Vinagre et al., 2005), the decrease in flatfish abundance in our study is a direct effect of the decline in soft-bottom area utilized by flatfish at the site level (~3,250 m²). However, similar to offshore wind farms (Glarou et al., 2020), adverse effects at such small spatial scales are unlikely to impact population levels of soft-bottom species, particularly in regions with extensive soft-bottom areas such as the South Baltic Sea (Kaskela & Kotilainen, 2017). In general, we note that our results are merely representative of the early stages of succession following the reef restoration. At time of sampling, the 6-month-old reefs were overgrown with ephemeral algae which support low faunal density and richness (Christie et al., 2009), implying that the associated community may change over time if reefs are gradually colonized by macroalgae of higher complexity and longevity. Consequently, a well-developed reef could indirectly promote soft-bottom species (e.g. flatfish) in the reef vicinity, by inducing spill-over effects on infaunal prey communities from algal food sources (Posey & Ambrose, 1994). However, the reef construction could also adversely affect ecosystem resilience over time by facilitating the colonization of invasive species, with potential deleterious effects on native taxa (Bulleri & Airoidi, 2005). Two invasive species in the Baltic that are sufficiently conspicuous for RUVS sampling include the round goby *Neogobius melanostomus* and comb jelly *Mnemiopsis leidyi*. We did not record any round gobies in this study and found no evidence that the restored reefs promoted comb jelly, which is a holoplanktonic species (Jaspers et al., 2018), relative to reference sites (Table S2). Still, these mechanisms highlight the importance of investigating effects of reef construction on soft-bottom taxa (Puckeridge et al., 2021) and of conducting long-term monitoring studies to assess temporal variabilities in restoration effects.

Our study is the first to link the evaluation of reef restoration with SLOSS by examining if restoration efforts can be optimized by manipulating the spatial configuration of a given volume of reef material. We found no pronounced SLOSS effect on richness of early colonizers, yet there were strong taxon-specific differences in relative abundance among the focal groups. There is general agreement within the SLOSS literature that contiguous habitats are vital in supporting large and stable population sizes, partly explained by higher niche and resource availability relative to small patches (Root, 1973). However, there is still a limited understanding of how habitat fragmentation drives relative abundances among taxa, which ultimately depends on functional traits (e.g. body size and feeding strategy), species interactions (e.g. predator-prey dynamics) and the surrounding environment (e.g. matrix habitat and connectivity Deane et al., 2020; Drakare et al., 2006; Ewers & Didham, 2006). The sites in our study represent benign habitat matrices (sensu Fahrig, 2020), in which the aquatic medium allows organisms to cross habitat boundaries from reef to sand patches and vice versa, as opposed to a hostile matrix (e.g. water for insular mammals) with limited permeability for inhabitant species. We note that effects of spatial reef configuration were most apparent in gobies and to a lesser degree in labrids (Figure 4), and suggest that the observed SLOSS patterns likely resulted from a combination of high intra- and inter-site connectivity with trait-mediated responses across focal taxa. First,

gobies and labrids are small-bodied generalists, feeding on a variety of mesograzers and benthic invertebrates (Fjøsne & Gjørseter, 1996; Miller, 1986). A small body size implies lower area requirements to establish high population densities (Marquet et al., 1990), while a generalist feeding style facilitates rapid colonization and efficient resource exploitation within the habitat matrix (Holt, 2014). Therefore, SS may have provided sufficient area for high densities of small-bodied taxa at the patch level (i.e. single reef patch in Figure 1c) and richer food sources at the site level through a higher perimeter-area ratio (i.e. more edge habitat) yielding increased access to infaunal prey, relative to SL. Second, gobies and labrids are sedentary reef fishes relative to transient gadoids. While sedentary species are highly associated with fine-scaled habitat within the matrix, transient species respond to habitat features on seascape scales (i.e. km's) with species-specific drivers determining visitation rates to reef patches (Harborne et al., 2017). Our results are reflective of this pattern, as the difference in fine-scaled habitat features between SL and SS (e.g. amount of edge habitat or relative reef isolation) did not affect the abundance of transient gadoids at the site level. Still, the spatial distribution of gadoids was clearly more dispersed at SS as opposed to spatially aggregated at SL (Figure S12), which likely caused increased mortality of prey species at SL (Overholtzer-McLeod, 2006) and thereby SS > SL for small-bodied taxa at the site level. Interestingly, the higher abundance of sand gobies at SS suggests that this configuration could benefit soft-bottom species in addition to reef species. Similar to small-bodied reef taxa, we hypothesize that this was partly a predator-mediated effect since the spatial distribution of sand gobies at SL was seemingly inversely related to the distribution of gadoids (Figures S12 and S13). We note that effects on soft-bottom species would remain obscured when merely sampling focal habitat (here reef patches) and therefore argue that studies on habitat fragmentation within highly connected systems require a sampling design incorporating the entire habitat matrix to assess community dynamics across habitat boundaries.

Finally, the aquatic medium facilitates immigration and emigration of organisms among local populations and enables marine taxa with sedentary adult life stages to colonize and replenish relatively isolated habitats via larval dispersal in the water column (Carr et al., 2003). This implies that the observed SS > SL pattern in sedentary taxa could have resulted from differential larval input if the SS configuration yielded higher larval settlement and survival, relative to SL reefs. Investigating the effect of spatial reserve design on oyster recruitment, Puckett and Eggleston (2016) found that SS reserves promoted greater larval connectivity than a few large reserves, which mostly relied on local larval retention. For reef fishes, there is increasing evidence that local larval retention (or self-recruitment) is more common than previously considered (Almany et al., 2017; Jones et al., 2009). While we were unable to infer the relative contribution of larval dispersal and retention at the two reef designs, we hypothesize that both mechanisms could result in lower larval settlement and survival at SL, relative to SS. At the patch level, distance to the nearest reef patch was 15 m at SS (Figure 1c), but 500–1,500 m for SL (distance between sites). At the

site level, the higher perimeter–area ratio at SS could increase the rate at which larvae encounter or locate the reef habitat (McNeill & Fairweather, 1993). Therefore, the combined effects of relative isolation, lower perimeter–area ratio and aggregation of predators at SL may have substantially reduced larval settlement and survival, relative to SS. We note, however, that distance to the nearest reef for SL (500–1,500 m) is still within range even of short-distance dispersers (1.7 km median distance for a confamilial goby; D'Aloia et al., 2015) and that larval connectivity is more likely shaped by geographic setting rather than the fine-scaled habitat features of SL and SS in our study (Jones et al., 2009). As such, there is a promising opportunity in emerging technologies such as otolith microchemistry to provide insights into source populations of larvae and the effect of habitat boundaries on dispersal capabilities of aquatic organisms (Kaemingk et al., 2019; Rogers et al., 2019).

In conclusion, we demonstrated that boulder reef restoration is a promising tool to recover essential habitat for reef-associated fauna in degraded aquatic systems. The positive restoration effects on gadoids are particularly noteworthy and highlight the importance of continued reef conservation and restoration efforts to help sustain commercially exploited gadoid populations in the Baltic Sea. We acknowledge that large individuals recorded in our study were most likely attracted to the newly constructed reefs instead of locally produced (alluding to the 'attraction vs. production' debate; Bohnsack, 1989), since the reefs were only 6 months old at time of sampling. However, we concurrently note that we selected restoration sites based on historical knowledge and archived nautical maps to target sites where reefs were historically present but extracted entirely over the past decades. As such, this fundamental shift in reef availability likely rendered hard substrate to become a limiting factor for reef-associated fauna at the study area, implying substantial scope for productivity enhancement from reef construction over time (Folpp et al., 2020; Layman & Allgeier, 2020). We furthermore acknowledge that our results are based on a small number of reef replicates (two replicates per treatment) and that the study area of the Baltic Sea is characterized by unique conditions of low salinity levels and a multitude of anthropogenic stressors (Reusch et al., 2018). However, we emphasize that our results should be interpreted strictly within a substrate-limiting context and accordingly suggest that boulder reef restoration likely constitutes a similarly promising management action to help recover reef-associated fish populations in other temperate waters where hard substrate is limiting. SLOSS remains an important issue for conservation biology, as managers and practitioners often prioritize the preservation of contiguous, large habitats over several small patches, despite the majority of empirical evidence highlighting the conservation value of small habitats (Fahrig, 2020). From a restoration ecology perspective, we showed that restored SS reefs promoted early colonization of small-bodied mesopredators while none of the response variables were elevated at SL relative to SS reefs. Still, we note that this does not necessarily imply a higher restoration success rate at SS. Specifically, large numbers of mesopredators could exert cascading top-down effects in favour of ephemeral algae (Östman et al., 2016),

potentially hampering the development of macrophyte communities with higher complexity and longevity at SS over time. While both SL and SS strongly promoted predatory gadoids of higher trophic level, suggesting a high potential for top-down control on mesopredators, the true extent of trophic resilience at the restored reefs could not be assessed from the fish community metrics alone. This highlights a need for future restoration efforts to incorporate trophic dynamics within the BACI framework to obtain a more comprehensive evaluation of restoration success (Loch et al., 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest with the publication of this article.

AUTHORS' CONTRIBUTIONS

J.C.S., J.G.S., H.B. and B.M.K. designed the study; T.J.G.W., P.H.N., J.C.S. and B.M.K. collected the data; T.J.G.W., P.H.N. and H.B. analysed the data; T.J.G.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.vt4b8gtq8> (Wilms et al., 2021a). An R script with computational details for running the analysis and producing the figures is archived on Zenodo <https://doi.org/10.5281/zenodo.5268843> (Wilms et al., 2021b).

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