

Local Competition and Metapopulation Processes Drive Long-Term Seagrass-Epiphyte Population Dynamics

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Abstract

It is well known that ecological processes such as population regulation and natural enemy interactions potentially occur over a range of spatial scales, and there is a substantial body of literature developing theoretical understanding of the interplay between these processes. However, there are comparatively few studies quantifying the long-term effects of spatial scaling in natural ecosystems. A key challenge is that trophic complexity in real-world biological communities quickly obscures the signal from a focal process. Seagrass meadows provide an excellent opportunity in this respect: in many instances, seagrasses effectively form extensive natural monocultures, in which hypotheses about endogenous dynamics can be formulated and tested. We present amongst the longest unbroken, spatially explicit time series of seagrass abundance published to date. Data include annual measures of shoot density, total above-ground abundance, and associated epiphyte cover from five *Zostera marina* meadows distributed around the Isles of Scilly, UK, from 1996 to 2011. We explore empirical patterns at the local and metapopulation scale using standard time series analysis and develop a simple population dynamic model, testing the hypothesis that both local and metapopulation scale feedback processes are important. We find little evidence of an interaction between scales in seagrass dynamics but that both scales contribute approximately equally to observed local epiphyte abundance. By quantifying the long-term dynamics of seagrass-epiphyte interactions we show how measures of density and extent are both important in establishing baseline information relevant to predicting responses to environmental change and developing management plans. We hope that this study complements existing mechanistic studies of physiology, genetics and productivity in seagrass, whilst highlighting the potential of seagrass as a model ecosystem. More generally, this study provides a rare opportunity to test some of the predictions of ecological theory in a natural ecosystem of global conservation and economic value.

Citation: Lobelle D, Kenyon EJ, Cook KJ, Bull JC (2013) Local Competition and Metapopulation Processes Drive Long-Term Seagrass-Epiphyte Population Dynamics. PLoS ONE 8(2): e57072. doi:10.1371/journal.pone.0057072

Editor: Richard K.F. Unsworth, Swansea University, United Kingdom

Received: October 15, 2012; **Accepted:** January 17, 2013; **Published:** February 21, 2013

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Funding: All costs were met by volunteers. There were no “funders” as such. As a result, it is not inconsistent to state: The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

The roles of spatial scale and structure in population dynamics remain a central theme in ecological research [1–5]. A classic approach to understanding the dynamics of spatially explicit populations is the metapopulation model of Levins [6], developed by Hanski [7] amongst others. Here, habitat with the potential to be colonized by a focal species is discretized, with the resulting patches classed as either occupied or vacant. This model gives rise to the familiar ‘blinking light’ dynamics, with local occurrence moving between the two states, as a result of colonization through dispersal, and extinction [7]. However, these dynamics rely on some strong, and often biologically unrealistic assumptions. Notably that potential habitat is infinite in extent and has no structure, with an equal probability of dispersal between neighbouring patches as those far apart; also, that local population dynamics are fast compared to metapopulation scale patch turnover, with local state moving between a stable equilibrium size or zero effectively instantly. As a result, there is broad consensus that in many systems it is necessary to understand population dynamics over a range of spatial and temporal scales in order to explain observed species distributions [2,5,8].

Despite these limitations, simple metapopulation models continue to be remarkably useful tools for understanding spatial dynamics in a wide variety of circumstances [9–12]. One such area where the metapopulation scale approach has dominated our understanding is the study of epiphytes [13–15]. Epiphytes form an important component of many ecological communities, providing a substantial amount of additional biomass, carbon sequestration and niche diversity [16,17]. However, much of what is known about epiphyte population dynamics is based on terrestrial forest systems [13,14]. Here, epiphytes typically include lichens, bryophytes, ferns and relatively small flowering plants such as orchids and bromeliads. In these cases, it has often been assumed that distributions of these epiphytes are dependent on the presence or absence of host trees (metapopulation ‘patch-tracking’) rather than local environmental state variables (‘habitat-tracking’) [18,19].

Where studies of forest epiphyte distributions do include local factors relating to habitat condition, these typically take the form of environmental gradients (such as microclimate and edge effects) rather than explicitly modelling feedback between host and epiphyte populations [20–23]. Whilst including independent variation in habitat structure adds considerably to a homoge-

neous metapopulation approach [19,24], such models fail to capture important non-linearities inherent in many other, higher-turnover ecosystems. As a result, terrestrial forest communities may be unrepresentative of a range of widespread and valuable ecosystems where epiphytes are important; particularly in marine ecosystems such as those based on seagrasses or macrophytic algae.

To explore this, we turn to one of the most important [25] but still relatively poorly understood benthic ecosystems: that based on seagrass. Seagrasses are globally dispersed along coastlines, covering approximately 0.3 to 0.6 million km² [26,27]. Much of the value of seagrass meadows lies in their high levels of primary productivity, acting as a carbon and nutrient sink, providing a shelter for invertebrates or juveniles of fish species and protecting shorelines via wave attenuation and stabilization of sediments [25,26,28]. However, seagrasses are currently in rapid decline worldwide, due to a range of anthropogenic impacts, disease and climate change [29,30]. As a result, there is considerable interest in understanding the drivers of seagrass population dynamics and a general appreciation that multiple spatial scales are important (for example, local density at the sub-metre scale [31–33], the influence of clonal expansion over tens of metres [8,34,35], or even metapopulation processes spanning oceans [36]).

Due to the substantial logistical and cost constraints inherent to the observation of a submerged natural ecosystem, many studies of seagrass dynamics take the form of laboratory or within season field trials, often focusing on single spatial scales of measurement [31,32,37–40] (although see [41,42]). Therefore, there is a lack of fundamental knowledge about the long-term dynamics of seagrass and its associated flora and fauna, including a substantial epiphytic community that can account for over 30% of above ground seagrass meadow biomass [43,44]. Typically, this epiphytic community is dominated by diatoms and rhodophytes (red algae) in a healthy seagrass community; with increasing occurrence of cyanobacteria, bryozoans, hydroids and brown, green or blue-green algae populations in sub-optimal environments [16,44,45].

In this study, we present novel data from an ongoing, spatially replicated study of a comparatively unimpacted temperate seagrass-epiphyte system. In this sub-tidal environment, there are no large grazing species, such as the geese that affect inter-tidal seagrass populations [46,47], or the marine turtles and sirenians of tropical seagrass habitats [48,49]. In addition, our choice of location is an archipelago with little industrial or agricultural impact or urbanization (Fig. 1). Here, seagrass grows substantially as a natural monoculture in which we are able to not only make rare baseline observations of a seagrass ecosystem not currently in overall decline, but also test theoretical predictions on ecological processes such as enemy-victim interactions [33] and competition, which would likely be masked by trophic complexities in many other natural environments.

Our aims were to test the hypotheses that: (1) epiphytes play an important role in the long-term dynamics of their seagrass hosts; and (2) inclusion of both local and metapopulation scale interactions are necessary to explain observed population dynamics. We developed a simple population dynamic model, fitting this to observed time series at different spatial scales using mixed-effects models and model averaging techniques. Whilst local scale effects dominate seagrass dynamics, we found approximately equal support for both local and metapopulation scale influences on epiphyte abundance.

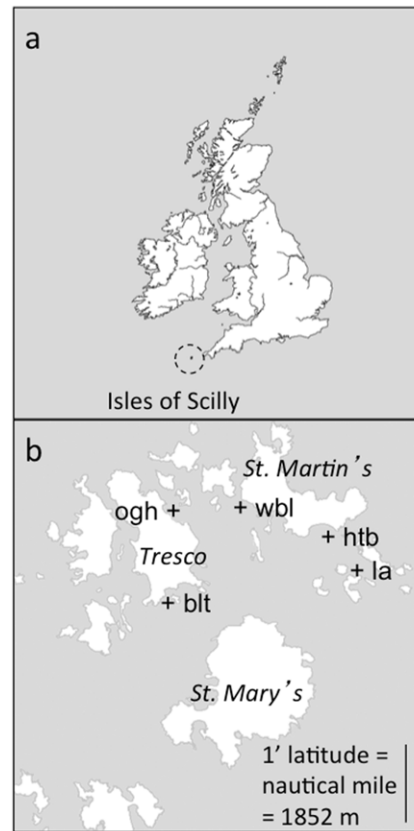


Figure 1. Study area location. Panel (a) the position of the Isles of Scilly relative to mainland United Kingdom; panel (b) the positions (marked +) of the five seagrass meadows sampled in this study: Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). doi:10.1371/journal.pone.0057072.g001

Results

Empirical Patterns

Seagrass with abundant epiphyte cover was persistent at all sites throughout the length of the study. Time series of mean epiphyte cover, as well as mean seagrass density and the proportion of occupied patches at each site are shown in Fig. 2. In order to quantify empirical relationships in the data, we explored a mixed-effects time series model incorporating sampling year and sea surface temperature (SST) as explanatory variables, as well as autocorrelation (AR1) structure between years.

There was no overall, linear, temporal trend in epiphyte cover or any measure of seagrass abundance (Likelihood Ratio tests for slope parameter: epiphyte cover, L.R. = 1.95, $p = 0.38$; local seagrass density, L.R. = 3.58, $p = 0.17$; seagrass metapopulation occupancy, L.R. = 2.04, $p = 0.36$; ‘combined’ – see Methods – scale seagrass abundance, L.R. = 3.02, $p = 0.22$). However, we did find a small but statistically significant positive association between SST and local seagrass density (L.R. = 4.85, $p = 0.028$), although this was not evident for metapopulation occupancy (L.R. = 0.130, $p = 0.72$), combined scale abundance (L.R. = 0.737, $p = 0.39$), or epiphyte cover (L.R. < 0.001, $p = 0.98$).

We found no evidence of temporal autocorrelation within local seagrass density ($\Delta\text{AIC} = 0.39$) or epiphyte cover ($\Delta\text{AIC} = 1.77$). However, first order autocorrelation was strong within time series of metapopulation patch occupancy ($\Delta\text{AIC} = 21.0$, Fig. 3), suggesting that patch turnover may operate over a slower time scale

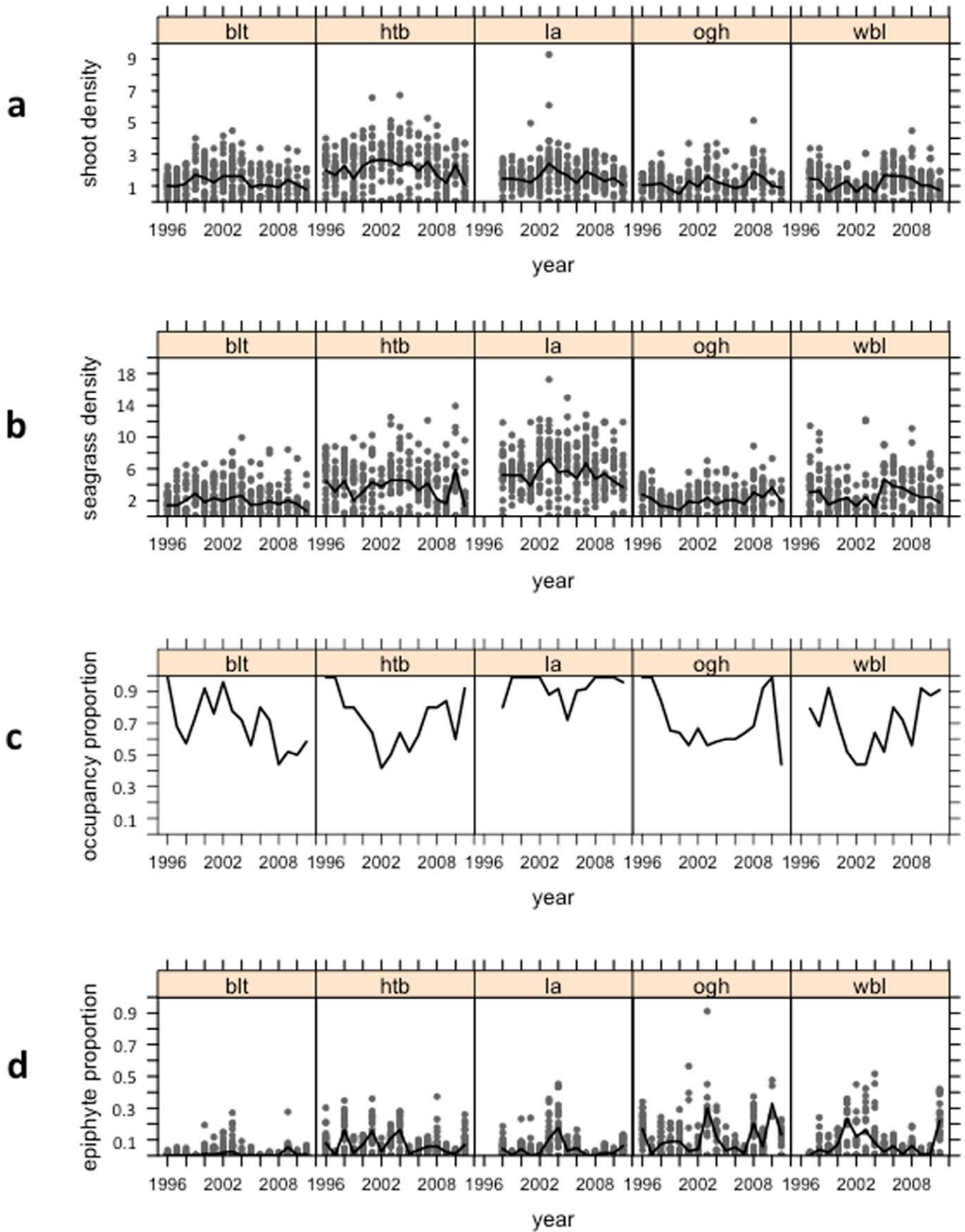


Figure 2. Time series of seagrass (*Zostera marina*) density and epiphyte cover. Panel (a) shoot density $\times 100$ per square metre; panel (b) seagrass density $\times 100$ per square metre (total metres of leaf per square metre of ground); panel (c) the proportion of quadrats occupied by seagrass in a given meadow; and panel (d) the average proportion of each leaf covered by epiphytes in a given quadrat. Grey dots show individual quadrat data; black lines show meadow averages for Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).
doi:10.1371/journal.pone.0057072.g002

than dynamics driving local seagrass density. Not surprisingly, this pattern was also observed in time series of combined scale seagrass abundance, which incorporates the patch occupancy information ($\Delta AIC = 25.8$).

These empirical differences in both fixed effects (year and SST) and temporal autocorrelation structure, evident between different measures of seagrass abundance, suggest multiple ecological processes operating at different spatial scales. We went on to explore the role of spatial scale using a simple population dynamic model fitted to our time series.

Population Dynamics

We developed a Lotka-Volterra competition model in order to quantify intra- and interspecific competition between seagrass and

its epiphytes over a range of spatial scales. The exponent of the intercept, β_0 , of our local density model indicates the net reproductive rate in the absence of density dependence. We estimated the net reproductive rate of *Z. marina* to be 3.06 (95% CI: 1.44, 7.27) year^{-1} . We also quantified and compared factors that limit optimal growth at both the local and metapopulation scale.

The three measures of seagrass abundance, at different spatial scales, were correlated: Pearson's $r_{(\text{local density, metapopulation occupancy})} = 0.33$; $r_{(\text{local density, combined abundance})} = 0.59$; $r_{(\text{metapopulation occupancy, combined abundance})} = 0.90$. Therefore, we did not necessarily expect any measure of seagrass abundance to completely outweigh the other spatial scales when comparing (meta)population dynamic models. However, a difference in the relative weights

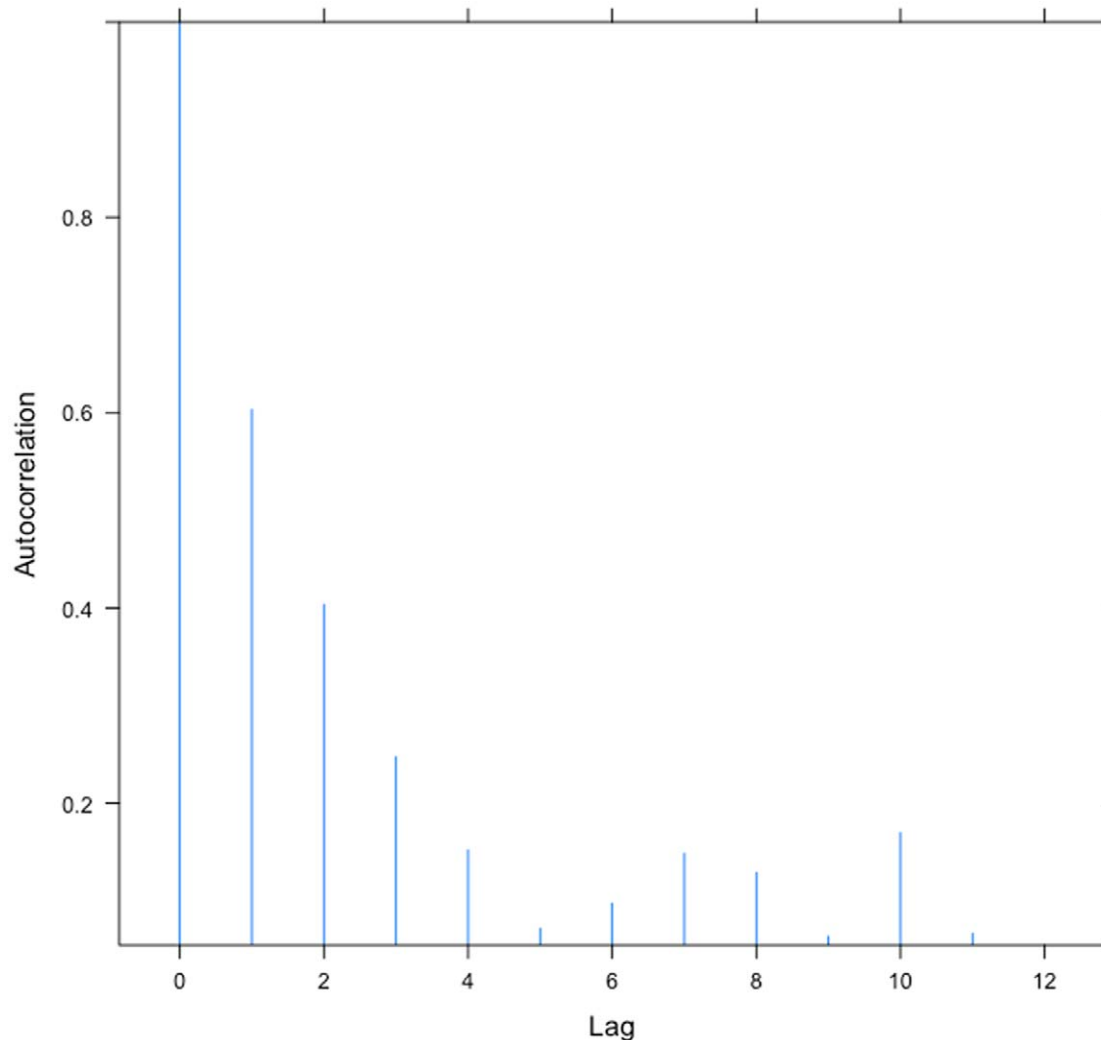


Figure 3. Seagrass metapopulation autocorrelations from the Isles of Scilly, UK. Average time-lagged empirical autocorrelations in the proportion of area (quadrats) occupied by seagrass (*Zostera marina*) within 16 year time series, sampled from five independent meadows around the Isles of Scilly.
doi:10.1371/journal.pone.0057072.g003

Table 1. Seagrass-epiphyte population dynamic modelling.

$\ln(X_t/X_{t-1}) \sim \text{Normal}(\beta_0 - \beta_1 X_{t-1} - \beta_2 Y_{t-1}, A)$ a) seagrass local population dynamics,				
spatial scale	AICc	ΔAICc	AICcWt	slope, β_1 (SE)
local	27.54	–	0.99	0.320 (0.102)
metapopulation	38.81	11.27	0.00	0.111 (0.049)
combined	39.46	11.92	0.00	0.056 (0.038)
$\ln(X_t/X_{t-1}) \sim \text{Normal}(\beta_0 - \beta_1 X_{t-1} - \beta_2 Y_{t-1}, A)$ b) seagrass metapopulation dynamics,				
spatial scale	AICc	ΔAICc	AICcWt	slope, β_1 (SE)
local	–70.32	–	0.90	0.056 (0.016)
metapopulation	–65.64	4.67	0.09	0.056 (0.022)
combined	–61.79	8.53	0.01	–0.082 (0.052)
$\ln(Y_t/Y_{t-1}) \sim \text{Normal}(\beta_0 - \beta_1 Y_{t-1} - \beta_2 X_{t-1}, A)$ c) epiphyte population dynamics,				
spatial scale	AICc	ΔAICc	AICcWt	slope, β_1 (SE)
local	199.64	–	0.34	0.445 (0.185)
metapopulation	199.72	0.09	0.33	0.880 (0.342)
combined	199.73	0.09	0.33	0.289 (0.158)

We explored three population dynamic models of intra- and inter-specific competition between seagrass and its epiphytes: (a) $\ln(X_t/X_{t-1})$ represents the population growth rate of local seagrass density; (b) $\ln(X_t/X_{t-1})$ describes the net colonization/extinction rate of available habitat by seagrass; and (c) $\ln(Y_t/Y_{t-1})$ represents the population growth rate of epiphytes on seagrass leaves. In each case, we compared the relative weight of evidence (AICcWt) for local, metapopulation and ‘combined’ scale (average local density including unoccupied patches) seagrass abundance as drivers of population dynamics.

doi:10.1371/journal.pone.0057072.t001

of each measure of seagrass abundance is informative for determining the contributions of different spatial scales to dynamics [50]. Calculating Akaike Weights (AICcWt) between models incorporating each of the measures of seagrass abundance, we found that local seagrass density was clearly the dominant spatial scale limiting seagrass dynamics within occupied habitat patches (Table 1a), and similarly that metapopulation patch occupancy took the form of a stationary distribution with little influence from within patch seagrass density (Table 1b). Here, there was little evidence for any interaction between local and metapopulation scales. However, making the same comparison between seagrass abundance measures in the model explaining local epiphyte dynamics, we found close to equal weighting between all three spatial scales (Table 1c).

We went on to analyze seagrass and epiphyte inter-dependency using phase plots (Fig. 4). Here, zero-isoclines mark no net population growth of both seagrass and its epiphytes, parameterized from our fitted population model. The downward slopes of the epiphyte isoclines indicate that both local and metapopulation scale seagrass abundance limit epiphyte cover, with a slightly steeper slope attributed to local density. Likewise, non-vertical seagrass isoclines illustrate the negative effects of epiphyte cover on both local seagrass density and patch occupancy. On this axis, the scales, so slopes, are not comparable. We infer that competitive processes operating over multiple spatial scales affect epiphyte cover and this feeds back on both seagrass density and extent to drive long-term seagrass-epiphyte population dynamics.

Discussion

In this study we investigated the long-term dynamics of a natural seagrass-epiphyte community. Seagrass and its epiphytes persisted in a competitive interaction, where stability was ensured by the domination of intraspecific (or perhaps more accurately in the case of epiphytes, intra-guild) competition within focal populations, compared to the effects of interspecific competition. In order to confirm that the Isles of Scilly *Zostera marina* population

was comparable to healthy populations elsewhere, we estimated the maximum net reproductive rate of *Z. marina* in its natural setting. The estimated annual multiplication rate of ≈ 3 compares favourably with other measures of recruitment for this species (in the range 0–3), reviewed by Duarte et al. [51], and could be seen as a baseline figure from a ‘healthy’ population, against which studies of threatened populations might be compared. Our estimate averages over long-term stochastic fluctuations in a way that comparable measures from short-term studies do not. On the other hand, our model assumes no inter-annual survival of seagrass leaves (probably reasonable – Fig. 1 in [44] – but not confirmed) and does not partition between vegetative reproduction and recruitment from seeds. As with other aspects of our study, these findings provide a useful addition to information derived from detailed short-term investigations, rather than seeking to overturn them. Importantly, we also found that multiple spatial scales of seagrass distribution contributed to long-term epiphyte dynamics.

In contrast to studies of terrestrial systems, where the emphasis is on the effects of hosts on epiphytes, there is a history of investigating the contribution of epiphytes to overall seagrass ecosystem value; and of short-term, manipulative studies into the impact of epiphytes on seagrass growth. Epiphytes add primary productivity to the system [52–54], as well as providing a food source to a broader range of grazing invertebrate species than seagrass alone [55]. In addition, epiphytes contribute up to 60% of carbon flux in seagrass ecosystems [56]. The majority of studies (reviewed in [57]) suggest that where epiphytes influence seagrass growth and survival, the effect is negative. However, there is some evidence for the opposite effect: Fixation by epiphytes is thought to increase nitrogen availability to seagrass through the decomposition of dead epiphyte grazers [58]. In addition, data from Sand-Jensen [59] (Fig. 3 in that study) indicated that seagrass photosynthesis might actually proceed at a higher rate in plants with heavy epiphyte loadings than bare plants, although no mechanism for this was suggested. Conversely, seagrass may increase nutrient availability to their epiphytes by transporting

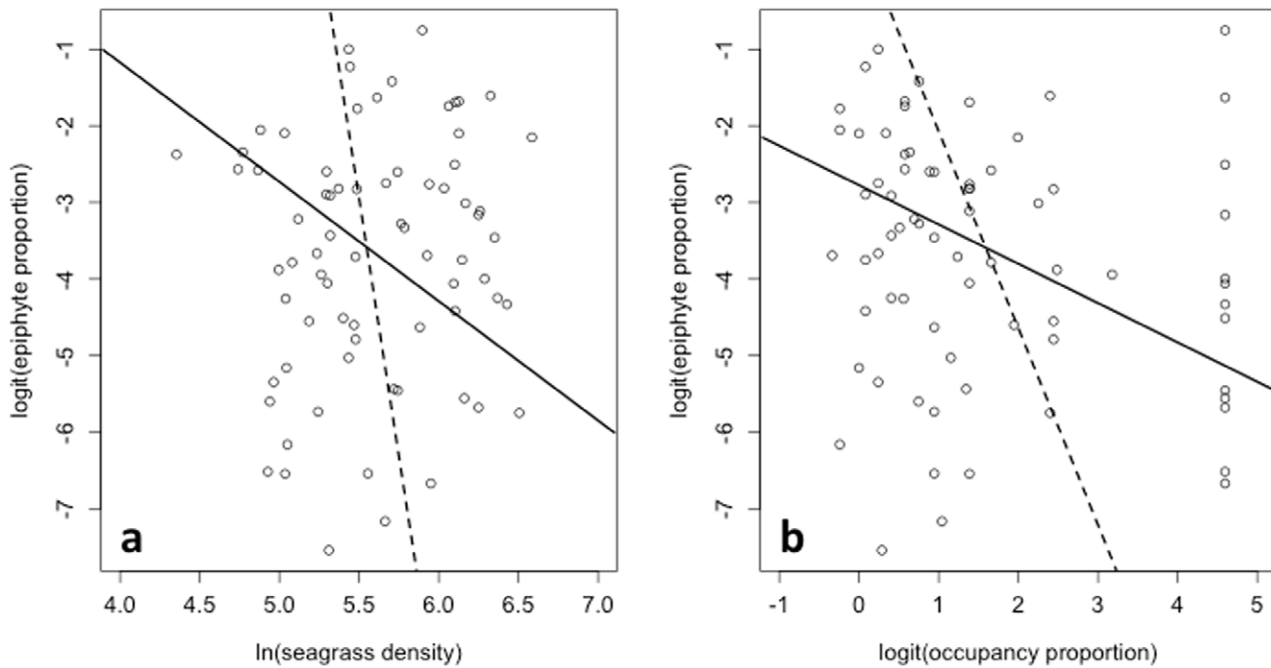


Figure 4. Phase plots of seagrass-epiphyte competition. Panel (a) average quadrat seagrass density plotted against epiphyte cover from 16 year time series, sampled at five independent *Zostera marina* meadows around the Isles of Scilly, UK; panel (b) the proportion of sampled area (quadrats) occupied by seagrass plotted against epiphyte cover (where seagrass patch occupancy proportion = 1, this was substituted with 0.99 for logit-transformation). Solid lines show epiphyte zero isoclines (no net population growth); dashed lines show *Z. marina* zero isoclines. doi:10.1371/journal.pone.0057072.g004

nutrients from substrate to leaf surface [60] (somewhat analogous to the ‘habitat-tracking’ concept), as well as simply providing a stratum for epiphyte attachment (‘patch-tracking’).

These contrasting findings suggest that the relationships between seagrass and its epiphytes are highly non-linear over the full range on naturally occurring seagrass density. Our data are from a relatively pristine seagrass habitat and observed plant densities only span a fairly narrow range. Therefore we chose to model density dependence with linear functional forms but caution strongly against extrapolating this baseline model to seagrass that is heavily impacted by human interference or disease. Rather, our model forms an appropriate null hypothesis of the long-term interaction between seagrass and its epiphytes, against which studies of threatened or declining seagrass should be compared. In particular, many studies of seagrass-algae interactions are motivated by the widespread threat to seagrass by eutrophication. In such cases, excessive algal blooms threaten seagrass by reducing available light in the water column, smothering seagrass leaves and directly competing for nutrients [61].

In our system, while we found evidence of a reciprocal negative interaction between seagrass and its epiphyte community, at the same time both seagrass and epiphytes were persistent throughout the study period. Observed heterogeneity in equilibrium epiphyte abundance, both within and between meadows (Fig. 2), is likely to result from environmental factors such as turbidity. However, long-term seagrass-epiphyte coexistence is achieved through the balance of within and between species processes, here with intraspecific competition outweighing interspecific competition. This is illustrated using phase plots (Fig. 4), with zero isoclines – lines in parameter space denoting no net population growth – crossing at the predicted equilibrium abundances of seagrass and epiphytes. Hence while interspecific competition is evident in the long-term population dynamics, it has only a quantitative effect,

modifying the equilibrium abundance, rather than a qualitative effect, leading to competitive exclusion. It would be interesting to investigate whether adverse environmental conditions, such as eutrophication, can push the relationship between seagrass and its epiphytes from one of stable coexistence towards competitive exclusion.

This long-term study was not aimed at uncovering specific mechanisms underpinning observed processes. However, there is a broad consensus that availability of light is the major limiting resource in healthy and undisturbed seagrass populations [51,62–64]. Light attenuation is also likely to present a limitation to algal epiphyte growth, although it is largely unknown how much seagrasses compete with their epiphytes for nutrients [44]. Persistent coexistence in this seagrass-epiphyte system, regulated around a stable equilibrium, suggests that different resources ultimately limit seagrass and its epiphytes (strong interspecific competition for the same resource predicted to lead to competitive exclusion [65]). Consistent with this, epiphyte abundance is commonly related to nutrient levels in the water column [66] and even used as an indicator of eutrophication [67]. Competitive interference for nutrients between epiphyte species has been postulated by Romero et al. [68] but detailed knowledge of the factors that limit epiphyte growth is recognized as a knowledge gap.

In this study, we did not attempt to identify specific epiphytes, but rather treated all visible epiphytes as a functional group, likely to have a similar effect on seagrass growth by restricting light reaching the photosynthetic surface of leaves. In reality, the epiphytic community of *Zostera marina* is typical of many seagrasses, dominated by algae but comprising a range of invertebrate species as well [44]. There is known to be substantial spatial and temporal heterogeneity in epiphyte distributions on the leaves of *Z. marina* [69,70]; a phenomenon also found in other seagrass genera, such

as *Amphibolis* [71] and *Posidonia* [72]. This diversity in epiphytic species is likely to be structured by rich and, as yet, uncharted population dynamics. We have certainly observed between meadow variation in some species, particularly the snakelocks anemone (*Anemonia viridis*) and the nationally important stalked jellyfish species *Halicystus* sp., *Lucernariopsis campanulata* and *L. cruxmelitensis*, and recognize that further work is warranted to resolve fine grain epiphyte community structure. However, our finding that both local and metapopulation scale processes influence overall epiphyte abundance is consistent with the hypothesis that epiphyte dynamics are largely driven by recruitment [44], with metapopulation scale processes limiting epiphyte dispersal and local scale processes limiting vegetative reproduction in epiphytes.

Further, manipulative experiments would be needed to determine whether the influence of local vs. metapopulation scale processes is partitioned between different epiphytic species, or affect all epiphyte species similarly. The former would suggest that fluctuations in the total abundance of epiphytes should be accompanied by shifts in the composition and possibly species richness of the epiphyte community. However, in a nearby (Plymouth, UK), similar seagrass habitat, epiphyte composition was relatively uniform within seagrass meadows and 99% of *Z. marina* epiphytes were found to be filamentous or coralline algae [44]. More broadly, studies have found little variation in species composition at the local scale [45,69,73,74], making differential responses between epiphyte species an unlikely explanation for the importance of multiple spatial scales observed in our study. This is supported indirectly by an earlier study of the infaunal (but not epiphytic) invertebrate community at three of our study sites (blt, htb, wbl), which found that between meadow differences substantially outweighed within meadow differences in assemblage composition, even though some within patch variation was observed [75]. Therefore, we infer from the relative invariance of the epiphytic community at the scale we measured it, that seagrass distribution (local density and regional distribution) is likely to affect both the dispersal and vegetative growth rates of individual epiphyte species, rather than for example local seagrass density limiting vegetative growth of one epiphyte group and seagrass patch distribution limiting dispersal success in a different group. However, this could only be confirmed by intensive surveys of epiphyte identities over a range of temporal and spatial scales.

Ultimately, epiphyte accumulation will be curtailed by longevity of seagrass. *Z. marina* is known to grow in annual or short-lived perennial forms, with individual leaves surviving for up to 100 days [44]. It is apparent from our study site that older seagrass leaves tend to support greater epiphyte cover and the shedding of these leaves provides a potential mechanism to mitigate the negative impact of epiphytes. Therefore, the survival of seagrass in a given situation is likely to have a substantial impact on epiphyte dynamics but this remains a knowledge gap in our system. More generally, epiphyte species richness has been shown to increase with time but no clear successional pattern is evident [76–78]. Our study was carried out at the same time each year, so largely controlling for within season accumulation (although there will inevitably be environmental stochasticity in this respect). While within season variation in epiphyte distributions is well charted [52,53,79–81] none of these provide the inter-annual data necessary to test hypotheses on long-term population dynamics.

In conclusion, our long-term study complements, and to an extent synthesizes, existing short-term investigations of specific mechanisms in the interaction between seagrass and its epiphyte community. We show how ecological processes, detailed elsewhere using manipulative studies, contribute to the inter-annual fluctu-

ations of a natural ecosystem. This should help to establish baseline understanding of a globally important habitat and help to formulate predictions and responses to future threats and disturbances. Currently, there is an increased awareness of the need to understand the natural restoration potential of seagrass meadows [82] and our findings highlight the importance of measuring local density as well as wider extent in *Zostera marina* habitat in this context. It would also be useful to continue developing metrics to understand how ecological patterns and processes scale in seagrass meadows (for example, Cunha et al. [83,84]). More broadly, particularly in marine environments, there is a shortage of data testing ecological theory on the roles of spatial scaling and structure, which is vital if conservation management is to be underpinned by relevant mechanistic understanding.

Materials and Methods

Seagrass Meadow Locations

We monitored five seagrass meadows around the Isles of Scilly, UK (Fig. 1), from 1996 to 2011, using consistent and rigorous survey methodology [33,85]. Access to sampling sites is not a restricted activity and no permits were required. GPS positions and chart datum depths for the centres of these meadows are: Broad Ledges, Tresco (blt: 49° 56.4' N, 06° 19.6' W, depth: 0.2 m); Higher Town Bay, St. Martin's (htb: 49° 57.2' N, 06° 16.6' W, depth: +0.5 m drying height); Little Arthur, Eastern Isles (la: 49° 56.9' N, 06° 15.9' W, depth: 1.0 m); Old Grimsby Harbour, Tresco (ogh: 49° 57.6' N, 06° 19.8' W, depth: 0.6 m); and West Broad Ledges, between Tresco and St. Martin's (wbl: 49° 57.5' N, 06° 18.4' W, depth: 0.6 m). Mean low water springs is 0.7 m; mean high water springs is 5.7 m. Gradients across meadows are insubstantial, with typically less than 0.5 m depth variation across individual meadows.

Survey Techniques

Seagrass (*Zostera marina*) was surveyed annually, during the first week of August, by placing 25 quadrats (0.0625 m²) in each meadow. Quadrat positions were predetermined as random rectangular coordinates (x, y) translated into polar coordinates (*distance, bearing*), radiating from the centre of the meadow. Randomization of quadrat locations was renewed each year and the maximum distance was 30 m from the focal point, close to the centre of each meadow.

Measurements recorded within each quadrat included: number of shoots (shoot density) visible above the surface of the sand (these are connected by unobserved networks of rhizomes in the substrate); the number of leaves per shoot; and length of the longest leaf on each shoot. 'Shoot size' was calculated as the number of leaves \times longest leaf length on a given shoot and, hence, seagrass density as the sum of shoot sizes per quadrat.

Currently, there is substantial interest making global meta-analyses and developing universal metrics of seagrass of seagrass abundance [30,57]. Consequently, for comparison with other studies, our 'seagrass density' was scaled to per square metre. *Zostera marina* leaves are strap like, showing no striking variation either along the length of the leaf or between leaves. An assumption of uniform leaf diameters would make this proportional to the Leaf Area Index found in studies of many other vegetation types. Finally, although we do not analyze it here, we also present time series of shoot density (shoots m⁻²) in addition to the fully worked-up 'seagrass density'.

These seagrass meadows are typical of many marine landscapes [86], taking the form of patchily distributed vegetation, with bare sand forming the interstitial matrix [87]. Quadrats placed on sand

were recorded as zero abundance. This allowed the relative contributions of local and metapopulation scales to be quantified. For each meadow, we calculated: the average seagrass density in occupied quadrats (local scale); the proportion of occupied quadrats in a meadow (metapopulation scale); and the average density in all quadrats, including empty quadrats ('combined' local and metapopulation scale).

In addition, we recorded the proportions of individual leaves visibly covered in epiphytic growth, based on an accepted categorization: ($a=0$), ($0<b<0.02$), ($0.02<c<0.25$), ($0.25<d<0.5$), ($0.5<e<0.75$) and ($0.75<f<1$) [88]. Percentages were averaged by equating categorical scores to the mean of the corresponding proportion bracket.

Population Modelling

We began with the familiar Lotka-Volterra competition model for two species, X and Y , competing for a shared, limiting resource [65]:

$$\frac{dX}{dt} = r_X X \left(\frac{K_X - X - \alpha_{Y,X} Y}{K_X} \right);$$

$$\frac{dY}{dt} = r_Y Y \left(\frac{K_Y - Y - \alpha_{X,Y} X}{K_Y} \right)$$

Here, r represents the exponential growth rate of the focal species in the absence of density dependence and K is the carrying capacity of the local environment that sets the equilibrium density in the absence of interspecific competition, α , from the other species. By integration [89], the discrete time analogue of this type of equation becomes:

$$\ln(X_t/X_{t-1}) = r_X \left(\frac{K_X - X_{t-1} - \alpha_{Y,X} Y_{t-1}}{K_X} \right).$$

The discrete time equation can be fitted to time series data as a linear statistical model, taking the form:

$$z_t = \beta_0 - \beta_1 X_{t-1} - \beta_2 Y_{t-1}; \quad \text{where} \quad z_t = \ln(X_t) - \ln(X_{t-1}),$$

$$\beta_0 = r, \quad \beta_1 = r/K, \quad \text{and} \quad \beta_2 = r\alpha/K.$$

References

- MacArthur RH (1972) Geographical ecology. New York: Harper and Row.
- McLaughlin JF, Roughgarden J (1992) Predation across spatial scales in heterogeneous environments. *Theor Pop Biol* 41: 337–353.
- Bonsall MB, Bull JC, Pickup NJ, Hassell MP (2005) Indirect effects and spatial scaling affect the persistence of multispecies metapopulations. *Proc Roy Soc Lond B* 272: 1465–1471.
- Bull JC, Pickup NJ, Hassell MP, Bonsall MB (2006) Habitat shape, metapopulations processes and the dynamics of multispecies predator-prey interactions. *J Anim Ecol* 75: 899–907.
- McGlinn DJ, Hurlbert AH (2012) Scale dependence in species turnover reflects variance in species occupancy. *Ecology* 93: 294–302.
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc America* 15:237–240.
- Hanski I (1999) Metapopulation ecology. Oxford: Oxford University Press.
- Kendrick GA, Duarte CM, Mårba N (2005) Clonality in seagrasses, emergent properties and seagrass landscapes. *Mar Ecol Progr Ser* 290: 291–296.
- Sutcliffe OL, Thomas CD, Yates TJ, Greatorex-Davies JN (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia* 109: 235–241.
- Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, et al. (1997) Inbreeding and extinction in a butterfly metapopulation. *Nature* 392: 491–494.
- Keymer JE, Galajda C, Muldoon R, Austin R (2006) Bacterial metapopulations in nanofabricated landscapes. *Proc Natl Acad Sci USA* 103: 17290–17295.
- Peck SL (2012) Networks of habitat patches in tsetse fly control: Implications of metapopulation structure on assessing local extinction probabilities. *Ecol Modelling* 246: 99–102.
- Snäll T, Ehrlén J, Rydin H (2005) Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology* 86: 106–115.
- Johansson V, Ranius T, Snäll T (2012) Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology* 93: 235–241.
- Fedrowitz K, Kuusinen M, Snäll T (2012) Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem. *J Appl Ecol* 49: 493–502.
- Moncreiff CA, Sullivan MJ, Daehnick AE (1992) Primary production dynamics in seagrass beds of Mississippi Sound: The contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Mar Ecol Progr Ser* 87: 161–171.
- Coleman VL, Burkholder JM (1994) Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. *J Exp Mar Biol Ecol* 179: 29–48.
- Thomas CD (1994) Extinction, colonization, and metapopulations: Environmental tracking by rare species. *Conservation Biol* 8: 373–378.
- Snäll T, Ribeiro PJ Jr, Rydin H (2003) Spatial occurrence and colonisations in patch-tracking metapopulations of epiphytic bryophytes: local conditions versus dispersal. *Oikos* 103: 566–578.
- Borum J (1985) Development of epiphytic communities on eelgrass *Zostera marina* along a nutrient gradient in a Danish estuary. *Mar Biol* 87: 211–218.

At the metapopulation scale, the Levins model of patch occupancy can be written in an equivalent form [90]. In this case, X is the proportion of occupied patches. Where previously r = birth rate – death rate, here, r = habitat patch colonization rate – extinction rate, and K represents the equilibrium patch occupancy, usually assumed to result from density-dependent colonization.

Therefore, we developed three separate models: (a) seagrass within patch dynamics (dX/dt = rate of change of local density); (b) seagrass metapopulation dynamics (dX/dt = rate of change of the proportion of occupied patches); and (c) epiphyte dynamics (dY/dt = rate of change of epiphyte cover). In each case, our three different scale measures of seagrass abundance ('local', 'metapopulation', or 'combined') were incorporated separately as explanatory variables (nine models in total – see Table 1). We quantified evidence for the influence of each measurement scale using Akaike Weights for each set of three seagrass explanatory variables, based on the second order Akaike Information Criterion, AICc [50].

Linear models were fitted to our spatially replicated time series data in a mixed-effects framework [91]. Seagrass density as an explanatory (independent) variable was log-transformed; proportions of occupied patches and epiphyte cover as explanatory variables were logit-transformed. Spatial heterogeneity (within meadow heteroscedacity and between meadow correlation) was modelled with an empirical variance-covariance matrix, Λ . Gaussian noise has been shown to be appropriate descriptor of stochastic processes in spatially explicit systems [92].

All statistical and population dynamic modelling was performed using R 2.14.1 (<http://www.r-project.org>).

Acknowledgments

We are grateful to a large number of volunteers who have collected data for the Isles of Scilly seagrass project over many years. In particular, we thank Cyril Nicholas (Natural England) for expert local knowledge and logistical support.

Author Contributions

Literature review: DL. Conceived and designed the experiments: JCB EJK KJC. Performed the experiments: JCB EJK KJC. Analyzed the data: JCB. Contributed reagents/materials/analysis tools: JCB KJC. Wrote the paper: DL JCB.

21. Löbel S, Snäll T, Rydin H (2006) Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *J Ecol* 94: 856–868.
22. Winkler M, Hülber K, Hietsch P (2009) Population dynamics of epiphytic orchids in a metapopulation context. *Ann Bot* 104: 995–1004.
23. Caruso A, Thor G, Snäll T (2010) Colonization-extinction dynamics of epiphytic lichens along a decay gradient in a dynamic landscape. *Oikos* 119: 1947–1953.
24. Roberge J-M, Johansson S, Wulff S, Snäll T (2011) Edge creation and tree dieback influence the patch-tracking metapopulation dynamics of a red-listed epiphyte. *J Appl Ecol* 48: 650–658.
25. Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. (1997) The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
26. Duarte CM, Chiscano CL (1999) Seagrass biomass and production: A reassessment. *Aquat Bot* 65: 159–174.
27. Duarte CM (2002) The future of seagrass meadows. *Envir Cons* 29: 192–206.
28. Gillanders BM (2007) Seagrasses, fish and fisheries. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 503–536.
29. Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW (2006) A global crisis for seagrass ecosystems. *Biosci* 56: 987–996.
30. Waycott M, Duarte C, Carruthers T, Orth R, Dennison W, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci USA* 106: 12377–12381.
31. Olesen B, Sand-Jensen K (1994a) Biomass-density patterns in the temperate seagrass *Zostera marina*. *Mar Ecol Progr Ser* 109: 283–291.
32. Olesen B, Sand-Jensen K (1994b) Demography of shallow eelgrass (*Zostera marina*) populations: shoot dynamics and biomass development. *J Ecol* 82: 379–390.
33. Bull JC, Kenyon EJ, Cook KJ (2012) Wasting disease regulates long-term population dynamics in a threatened seagrass. *Oecologia* 169: 135–142.
34. Reusch TBH, Stam WT, Olsen JL (1999) Microsatellite loci in eelgrass *Zostera marina* reveal marked polymorphism within and among populations. *Mol Ecol* 8: 317–322.
35. Zipperle AM, Coyer JA, Reise K, Stam WT, Olsen JL (2011) An evaluation of small-scale genetic diversity and the mating system in *Zostera noltii* on an intertidal sandflat in the Wadden Sea. *Ann Bot* 107: 127–133.
36. Rozenfeld AF, Arnaud-Haond S, Hernandez-García E, Eguiluz VM, Serrão EA, et al. (2008) Network analysis identifies weak and strong links in a metapopulation system. *Proc Natl Acad Sci USA* 105: 18824–18829.
37. Cambridge ML, Chiffings AW, Brittan C, Moore L, McComb AJ (1986) The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquat Bot* 24: 269–8.
38. Plus M, Deslous-Paollet J-M, Aubry I, Dagault F (2001) Factors influencing primary production of seagrass beds (*Zostera noltii* Hornem.) in the Thau lagoon (French Mediterranean coast). *J Exp Mar Biol Ecol* 259: 63–84.
39. Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat Bot* 27: 15–26.
40. Moore KA, Wetzel RL, Orth RJ (1997) Seasonal pulses of turbidity and their relation to eelgrass (*Zostera marina* L.) survival in an estuary. *J Exp Mar Biol Ecol* 215: 115–134.
41. Marbà NN, Duarte CM, Cebrián J, Gallegos ME, Olesen B, et al. (1996) Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. *Mar Ecol Progr Ser* 137: 203–213.
42. Rasheed MA, Unsworth RKF (2011) Long-term climate associated dynamics of a tropical seagrass meadow: implications for the future. *Mar Ecol Progr Ser* 422: 93–103.
43. Orth RJ, van Monfrans J (1984) Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: A review. *Aquat Bot* 18, 43–69.
44. Borowitzka MA, Lavery P, van Keulen M (2007) Epiphytes of seagrasses. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 441–461.
45. Saunders JA, Attrill MJ, Shaw SM, Rowden AA (2003) Spatial variability in the epiphytic algal assemblages of *Zostera marina* seagrass beds. *Mar Ecol Progr Ser* 249: 107–115.
46. Zipperle AM, Coyer JA, Reise K, Stam WT, Olsen JL (2010) Waterfowl grazing in autumn enhances spring seedling recruitment of intertidal dwarf eelgrass (*Zostera noltii*). *Aquat Bot* 93: 202–205.
47. van der Heide T, Eklöf JS, van Nes EH, van der Zee EM, Donadi S, et al. (2012) Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. *PLoS ONE* 7: e42060.
48. Thayer GW, Bjorndal KA, Ogden JC, Williams SL, Ziemann JC (1984) Role of larger herbivores in seagrass communities. *Estuaries* 7: 351–376.
49. Fourqurean JW, Manuel S, Coates KA, Kenworthy WJ, Smith SR (2010) Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to a loss of seagrass meadows in Bermuda. *Mar Ecol Progr Ser* 419: 223–232.
50. Burnham KP, Anderson DR (2002) Model selection and multi-model inference: A practical information theoretic approach. New York: Springer.
51. Duarte CM, Fourqurean JW, Krause-Jensen D, Olesen B (2007) Dynamics of seagrass stability and change. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 271–294.
52. Wear DJ, Sullivan MJ, Moore AD, Millie DF (1999) Effects of water-column enrichment on the production dynamics of three seagrass species and their epiphytic algae. *Mar Ecol Progr Ser* 179: 201–213.
53. Heijs FML (1984) Annual biomass and production of epiphytes in three monospecific seagrass communities of *Thalassia hemprichii* (Ehrenb.) Aschers. *Aquat Bot* 20: 195–218.
54. Silberstein K, Chiffings AW, McComb AJ (1986) The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook F. *Aquat Bot* 24: 355–371.
55. Deegan LA, Wright A, Avyazian SG, Finn JT, Golden H, et al. (2002) Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquat Cons Mar Freshwater Ecosys* 12: 193–212.
56. Borowitzka MA, Lethbridge RC (1989) Seagrass epiphytes. In: Larkum AWD, McComb AJ, Sheppard SA, editors. *Seagrasses: With special reference to the Australasian region*. Amsterdam: Elsevier, pp. 458–499.
57. Thomsen MS, Wernberg T, Engelen AH, Tuya F, Vanderklift MA, et al. (2012) A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. *PLoS ONE* 7: e28595.
58. Yamamuro M (1999) Importance of epiphytic cyanobacteria as food sources for heterotrophs in a tropical seagrass bed. *Coral Reefs* 18: 263–271.
59. Sand-Jensen K (1977) Effect of epiphytes on eelgrass photosynthesis. *Aquat Bot* 3: 55–63.
60. Harlin MM (1975) Epiphyte-host relations in seagrass communities. *Aquat Bot* 1: 125–131.
61. Cardoso PG, Pardal MA, Lillebo AI, Ferreira SM, Raffaelli D, et al. (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *J Exp Mar Biol Ecol* 302: 233–248.
62. Duarte CM, Kalf J (1987) Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes. *Can J Fish Aquat Sci* 44: 1759–1764.
63. Ruiz JM, Romero J (2001) Effects of *in situ* experimental shading on the Mediterranean seagrass *Posidonia oceanica* (L.) Delile. *Mar Ecol Progr Ser*, 215: 107–120.
64. Zimmerman RC (1987) Light and photosynthesis in seagrass meadows. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 303–321.
65. Townsend CR, Begon M, Harper JL (2008) *Essentials of Ecology*. Oxford: Wiley-Blackwell.
66. Frankovich TA, Fourqurean JW (1997) Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Mar Ecol Progr Ser* 159: 37–50.
67. Stankelis RM, Naylor MD, Boynton WR (2003) Submerged aquatic vegetation in the mesohaline region of the Patuxent estuary: Past, present and future status. *Estuaries* 26: 186–195.
68. Romero J, Lee K-S, Pérez M, Mateo MA, Alcoverro T (2007) Nutrients dynamics in seagrass ecosystems. In: Larkum AWD, McComb AJ, Sheppard SA, editors. *Seagrasses: With special reference to the Australasian region*. Amsterdam: Elsevier, pp. 227–254.
69. Cullinane JJ, Mahoney O, Whelan P (1985) Algal epiphytes of subtidal *Zostera marina* L. on the south coast of Ireland. *Cryptogam Algal* 6: 239–251.
70. Johnson MP, Edwards M, Bunker F, Maggs CA (2005) Variation in assemblage structure from individual leaves to regional scale. *Aquat Bot* 82: 12–26.
71. Lethbridge RC, Borowitzka MA, Benjamin K (1988) The development of an artificial *Amphibolis*-like seagrass of complex morphology and preliminary data on its colonization by epiphytes. *Aquat Bot* 31: 153–168.
72. Piazzoli L, Cinelli F (2000) Effects of the introduced Rhodophyceae *Antithamnion preissii* and *Womersleyella setacea* on the macroalgal community of *Posidonia oceanica* rhizomes in the western Mediterranean Sea. *Cryptogam Algal* 21: 291–300.
73. Vanderklift MA, Lavery PS (2000) Patchiness in assemblages of epiphytic macroalgae on *Posidonia coriacea* at a hierarchy of spatial scales. *Mar Ecol Progr Ser* 192: 127–135.
74. Lavery PS, Vanderklift MA (2002) A comparison of spatial and temporal patterns in epiphytic macroalgal assemblages of the seagrass *Amphibolis griffithii* and *Posidonia coriacea*. *Mar Ecol Progr Ser* 236: 99–112.
75. Bowden DA, Rowden AA, Attrill MJ (2001) Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *J Exp Mar Biol Ecol* 259: 133–154.
76. Bultuis DA, Woelkerling WJ (1983) Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquat Bot* 16: 137–148.
77. Heijs FML (1985) The seasonal distribution and community structure of the epiphytic algae on *Thalassia hemprichii* (Ehrenb.) Aschers. from Papua New Guinea. *Aquat Bot* 21: 295–324.
78. Borowitzka MA, Lethbridge RC, Charlton L (1990) Species richness, spatial distribution and colonization pattern of algal and invertebrate epiphytes on the seagrass *Amphibolis griffithii*. *Mar Ecol Progr Ser* 64: 281–291.
79. Alcoverro T, Duarte CM, Romero J (1997) The influence of herbivores on *Posidonia oceanica* epiphytes. *Aquat Bot* 56: 93–104.
80. Reyes J, Sansón M, Afonso-Carillo (1998) Distribution of the epiphytes along the leaves of *Cymodocea nodosa* in the Canary Islands. *Bot Mar* 41: 543–551.
81. Lepoint G, Havelange S, Gobert S, Bouquegneau JM (1999) Fauna vs flora contribution to the leaf epiphytes biomass in a *Posidonia oceanica* seagrass bed (Revellata Bay, Corsica). *Hydrobiologia* 394: 63–67.

82. Cunha AH, Marbá NN, van Katwijk MM, Pickerell C, et al. (2012) Changing paradigms in seagrass restoration. *Restoration Ecol* 20: 427–430.
83. Cunha AH, Santos R, Gaspar AP, Bairros M (2005) Seagrass landscape-scale changes in response to disturbance by barrier-islands dynamics: A case study from Ria Formosa (South of Portugal). *Estuar Coast Shelf Sci* 64: 636–644.
84. Cunha AH, Santos R (2009) The use of fractals to assess seagrass landscape stability: A case study from the barrier island system of Ria Formosa (South of Portugal). *Estuar Coast Shelf Sci* 84: 584–590.
85. Cook KJ (2002) Isles of Scilly *Zostera marina* monitoring 2001: expedition report. Report to Natural England, Truro, UK.
86. Robbins BD, Bell SS (1994) Seagrass landscapes: A terrestrial approach to the marine subtidal environment. *Trends Ecol Evol* 9: 301–304.
87. Jackson EL, Higgs S, Allsop T, Cathray A, Evans J, et al. (2011) Isles of Scilly seagrass mapping. Natural England Commissioned Report Number 087.
88. Burdick DM, Short FT, Wolf J (1993) An index to assess and monitor the progression of wasting disease in eelgrass *Zostera marina*. *Mar Ecol Progr Ser* 94: 83–90.
89. Royama T (1992) *Analytical population dynamics*. London: Chapman & Hall.
90. Amarasekare P (1998) Allee effects in metapopulation dynamics. *Am Nat* 152: 298–302.
91. Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-Plus*. New York: Springer-Verlag.
92. Bonsall MB, Hastings A (2004) Demographic and environmental stochasticity in predator-prey metapopulation dynamics. *J Anim Ecol* 73: 1043–1055.