Local–regional richness relationship in fouling assemblages – Effects of succession

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Abstract

The number of species in a local habitat depends on local and regional processes. One common approach to explore ecological saturation of local richness has been to plot local versus regional richness. We expand this approach by incorporating two dimensions of diversity – taxonomic and functional – and different successional ages of marine fouling communities. In four different biogeographic regions (Mediterranean Sea, NE Atlantic, Western Baltic Sea and North Sea) 60 experimental units made from artificial substratum were deployed for colonization. Local richness was assessed as the average number of species and functional groups (FG) per unit area while regional richness was estimated as the estimated (Jack 2) asymptote of the accumulation curves for species or FG in local panel communities. Our findings indicate that the nature of the relationship between local and regional diversity is sensitive to successional stage and the dimension of diversity considered. However, as a general pattern, for taxonomic and functional richness, the slope of the local–regional relationship increased in the course of succession. We discuss how this pattern could have been produced by a combination of low number of recruiting species and incomplete competitive exclusion as is typical for early succession.
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Zusammenfassung

Die Artenanzahl in lokalen Lebensräumen ist abhängig von lokalen und regionalen Prozessen. Eine häufig angewandte Methode, um die Beziehung zwischen lokaler und regionaler Diversität zu untersuchen, ist das graphische Auftragen der lokalen gegen die regionale Vielfalt. Wir haben diesen Ansatz erweitert durch die Berücksichtigung zweier Dimensionen der Diversität (taxonomisch und funktional) sowie unterschiedlicher Sukzessionsalter von marinen Siedlungsgemeinschaften. In vier unterschiedlichen biogeographischen Regionen (Mittelmeer, NO Atlantik, Westliche Ostsee und Nordsee) wurden 60 künstliche Substrate der natürlichen Besiedlung ausgesetzt. Die lokale Vielfalt wurde als der Mittelwert der Artenanzahl, bzw. Anzahl funktionaler Gruppen (FG) pro Substrateinheit

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definiert, während die regionale Vielfalt als die geschätzte (Jack2) Asymptote der Arten- bzw. FG-Akkumulations-kurven auf den lokalen Siedlungsgemeinschaften basiert. Unsere Ergebnisse zeigen, dass die Beziehung von lokaler und regionaler Diversität sensitiv gegenüber dem Sukzessionsstadium und der verwendeten Dimension der Diversität ist. Im allgemeinen jedoch nahm die Steigung der lokal-zu-regional-Beziehung im Laufe der Sukzession zu. Dies könnte auf die Kombination aus einer begrenzten Anzahl rekrutierender Arten und unvollständiger Exklusionskonkurrenz zurückzuführen sein wie es für frühe Sukzession typisch ist.

Introduction

The number of species in one location has been reported to depend on two categories of processes: local and regional (Caley & Schluter 1997; Ricklefs 2004; Shurin & Srivastava 2005). The terms 'local' and 'regional' are related to the spatial scale at which ecological and biogeographic processes prevail. Local processes include predation, parasitism, abundance, competition or disturbance while long-distance dispersal, speciation or extinction are considered as regional processes (Cornell & Lawton 1992). A widely used approach for evaluating the relative influence of local versus regional processes on local assemblages has been to plot local against regional richness (RR), a method originally employed by Terborgh and Faaborg (1980). Since their publication in 1980, the local–regional relationship has been investigated in more than a hundred studies for different taxonomic groups, spatial scales and habitats (Russell, Wood, Allison, & Menge 2006). In most studies, the plotted relationships were positive and linear which has been interpreted as regional species richness driving local species richness with little richness limitations imposed by local processes (see Lawton 1999; Shurin & Srivastava 2005; Srivastava 1999). For such relationships, local communities are referred to as 'unsaturated' or 'type I'. Conversely, if the plot shows a relationship where local species richness reaches an asymptote at high levels of regional richness, local communities are referred to as 'saturated' or 'type II' and local limiting processes seem important (Cornell 1985; Cornell & Lawton 1992).

In recent years, however, the use of the local–regional richness plots to examine species saturation has been criticized on a number of different grounds (see Hillebrand 2005; Hillebrand & Blenckner 2002; Shurin & Srivastava 2005). Thus, Hillebrand and Blenckner (2002) pertain that the local–regional richness relationship is sensitive to the definition of local and regional scales, i.e. a linear relationship could be caused by autocorrelation if the local area is relatively large as compared to the regional area considered. This problem can be avoided using independent data-sets to measure the local and regional richness (Srivastava 1999) as well as by selecting scales for sampling local richness that are sufficiently small, to reduce internal environmental heterogeneity (Harrison & Cornell 2008). Drawbacks can also emerge by inappropriate statistical analysis. For example, if local diversity is underestimated and/or regional diversity overestimated, a phenomenon recognized as *pseudosaturation* may occur (Cornell 1993; Srivastava 1999). However, suggestions have been made recently to circumvent this setback: underestimation of true local richness can be corrected using indices that take into account the presence/absence of rare species (e.g. non-parametric estimators), while regional overestimation can be avoided by including in the regional richness only those species capable to recruit into the local habitat (Harrison & Cornell 2008).

Several studies seeking a better understanding of the local–regional richness relationship have determined regional richness by questioning experts or consulting available species inventories (e.g. Rivadeneira, Fernandez, & Navarrete 2002; Witman, Etter, & Smith 2004). This approach can both under- and overestimate the regional number of relevant species. Thus, in many regions fauna and flora are only incompletely inventoried. On the other hand, a variable proportion of the species listed may never colonize the habitat of interest because they have been registered in different areas or seasons. Therefore, assessments only based on species lists may distort regional richness by an unknown amount in an unknown direction. For that reason, the statistical assessment of regional richness based on a limited number of replicates (e.g. estimators), constitutes an important alternative (Colwell & Coddington 1994; Gotelli & Colwell 2001).

Several evaluations on the performance of different estimators have been conducted (for review see Walther & Moore 2005). Generally, the estimators Chao1 (Chao 1984), Chao2 (Chao 1984, 1987; Colwell 2005), first order Jackknife (Jack1 – Burnham & Overton 1979; Heltshe & Forrester 1983) and second order Jackknife (Jack2 – Smith & van Belle 1984) are reported as the most appropriate choices (Walther & Moore 2005).

However, the occurrence of rare species in a habitat/data-set may affect the quality of the estimation as recognized by Foggo, Attrill, Frost, and Rowden (2003) and Ugland and Gray (2004).

One central aspect ignored in most previous studies is that the drivers of the relationship, and as a consequence the resulting relationship, may differ between the various successional stages of a community and, thus, change during community assembly (Morton & Law 1997). Only a few theoretical and observational studies have postulated a successional shift of the local–regional richness relationship (Fukami 2004; Mouquet, Mungia, Kneitel, & Miller 2003; Munguia 2004; Starzomsky, Parker, & Srivastava 2008). Mouquet et al. (2003) predicted, in a theoretical model, saturation at early stages of the assembly process since only a limited subset of the regional species pool may be available for colonization. At an intermediate successional stage, an unsaturated relationship is expected because competitive exclusion of species takes time. At last, when communities reach an equilibrium, competition should produce a saturated relationship (Mouquet et al. 2003).

Assuming that saturation of local assemblages is produced by local processes such as competition, we predict that this process should be more intense and saturation reached faster when species functionally overlap with regard to the limiting resource(s). A recent study on the number of functional groups (FG) that may coexist in a community and its relationship with regional species richness (Canning-Clode & Wahl, unpublished data) suggests that the local–regional richness relationship is sensitive to succession as well as to the dimension of diversity (taxonomic versus functional) considered.

Here, we investigate the local–regional relationship in marine fouling assemblages using an expanded approach. During the assembly of fouling communities in four different biogeographic regions located in the northern hemisphere we assessed species identity, functional identity and specific abundances (percent cover) at three different successional ages (3, 6 and 12 months). We hypothesized that the relationship between local and regional richness in fouling assemblages would be affected by the successional stage of a community as predicted by Mouquet et al. (2003) as well as by the dimension of diversity used (taxonomic versus functional richness).

Materials and methods

Study system and functional richness

The experiment lasted for 12 months and was conducted, simultaneously, in four different regions located in the northern hemisphere: Athens, Greece, Mediterranean Sea (37°53′32″N, 23°43′04″E), Madeira Island, NE Atlantic (32°44′30″N, 16°42′40″W), Kiel Bight, Germany, Baltic Sea (54°21′57″N, 10°08′54″E) and Helgoland Island, North Sea (54°10′49″N, 07°53′20″E). Hereafter, these regions are referred to as Mediterranean, NE Atlantic, Baltic Sea and North Sea regions, respectively.

At the staggered beginning of the experiment (March–May 2006), 60 polyvinylchloride (PVC) panels ($15 \times 15 \times 0.3$ cm) distributed in 6 PVC rings (60 cm diameter, 25 cm height) hung from a buoy at approximately 0.5 m depth, were exposed for colonization at each region. The minimum distance between rings was 2 m. Communities colonizing the experimental units over the next 12 months were structurally analyzed by measuring percent cover of all sessile species larger than 1 mm at three different successional ages: 3 months (July–August 2006), 6 months (September–November 2006) and 12 months (March–May 2007). Three-month-old communities comprise early recruits that only settled in spring and early summer. Six-month-old communities encompass species that settled during spring and summer while twelve-month-old panels represent all year's settlers, excluding species that disappeared in the course of succession. Total percent cover could exceed 100% in case of multi-strata growth. Prior to the experiment we randomly determined 20 panels for each survey. Each panel was used only once to avoid carry-over effects between surveys.

Functional groups are either defined by their ecosystem services (Halpern & Floeter 2008) or by the way in which they use various resources (Arenas, Sanchez, Hawkins, & Jenkins 2006). With regard to their small-scale co-existence the latter classification is more informative and was employed in this study. More competition among species within functional groups is expected since those species display overlapping requirements. In this work, functional groups were determined according to 5 traits which we considered the most relevant with regard to competition in fouling communities (see Table 1, Wahl 2009) and which constitute a sub-sample of the traits suggested by Bremner, Rogers, and Frid (2006). Since our study focused only on sessile hard-bottom assemblages on suspended substrata, only the 'attached' type in the trait category 'motility' and all species recruited via water-born propagules were considered. After recruitment, the capacity for asexual reproduction ('modularity'), 'body size' and 'growth form' determined which part of this three-dimensional space is occupied by a given organism. Which energy resources are exploited within this physical space (and the water body passing through it) was identified by the trait 'trophic type'. Species were allocated to functional groups according to their properties at the adult stage regarding these five traits. We did not consider

Table 1. The five ecological dimensions used to determine the functional groups in this study (modified from Wahl 2009).

Trait 1 **Body size**	*Trait 2* **Growth form**	*Trait 3* **Trophic type**	*Trait 4* **Modularity**	*Trait 5* **Motility**
S	B	A	C	A
<1 mm	Bushy	Autotroph	Colonial	Attached
M	E	D	S	B
1 mm to <10 mm	Encrusting	deposit feeder	Solitary	Burrowing
L	F	G		C
10 mm to <100 mm	Filamentous	Grazers		Crawling
X	M	P		D
100 mm–1000 mm	Massive	Predator		Drifting
XX		S		S
>1000 mm		Suspension feeder		Swimming

ontogenetic shifts of functionalities since larvae and juveniles constituted a relatively small portion of the individuals. In the fouling communities of this study the following traits were observed: body size (small, medium, large, very large), growth form (encrusting, massive, bushy, filamentous), trophic type (autotroph, suspension feeder, deposit feeder), modularity (solitary, colonial) and motility (attached), which could in theory produce $4 \times 4 \times 3 \times 2 \times 1 = 96$ functional groups.

Spatial scales and data analysis

In each region, local species richness was calculated as the average species number present on five randomly selected panels (from the 20 panels designed for a given survey). Correspondingly, local functional richness was defined as the average number of FG colonizing the same five panels.

In the present study, we calculated taxonomic and functional regional richness based on the panels exclusively reserved for the evaluation of regional richness of all sampling events ($n = 3 \times 15 = 45$). In this way, we obtained the number of regional species colonizing the given substrata at the given depth at any time during the experimental duration. Regional diversity (taxonomic and functional) was estimated as the asymptote of the species and FG accumulation curves using the second-order Jackknife estimator (Jack2 – Smith & van Belle 1984). This non-parametric estimator takes into account the distribution of species amongst samples, i.e. considers both the number of species found in one sample only ('infrequent species') and in exactly two samples. For comparison, the cumulated number of species in the 45 replicates was also calculated (S_{obs} curve) in each region to test whether Jack2 under- or overestimates this value. Species accumulation curves were built from 999 permutations of the panels reserved for this estimation in each region using PRIMER software (Clarke & Gorley 2006). To avoid autocorrelation between spatial scales, panels used for local

diversity assessment were not considered for the regional pool.

Recently, we (Canning-Clode, Valdivia, Molis, Thomason, & Wahl 2008) developed a new statistical tool for estimating regional richness based on a limited number of replicates in order to optimize the quality of regional richness estimations. We used three data-sets with an exceptionally large number of replicates from different temperate shallow water habitats (including an identical study system as we use here, i.e., using the same substratum, size of experimental units and depth), and compared six common richness estimators against the asymptote of the species accumulation curve, which was used as a reference for 'true' regional richness. Subsequently, the estimation error was quantified as a function of sampling effort using the estimator with overall prime performance – Jack2. With 45 samples (the level of sampling effort used in this report to estimate regional richness), Jack2 performed best underestimating true richness by 3.5% only (Canning-Clode et al. 2008).

Space has frequently been confirmed as a limiting resource (Stachowicz, Fried, Osman, & Whitlatch 2002). In order to assess the potential importance of competition for attachment substratum in local assemblages, we calculated the average total percent cover of fouling species colonizing local panels ($n = 5$) through time presuming that the intensity of competition relates inversely with the availability of this resource.

The relation between local and regional richness (both taxonomic and functional) was determined at different stages of succession. This was done to test whether this relation is affected by the kind of the diversity considered.

The differentiation between 'type I' and 'type II' curves was examined by regressing log local diversity ('dependent') against log regional diversity ('independent') (in terms of both taxonomic and functional diversity). The slope (b) of this double-log representation indicates the degree of curvilinearity of this relationship. Linear plots (unsaturated relationships)

are represented by a slope of 1 while local saturation is represented by a slope significantly < 1 but > 0 (Griffiths 1997) . Complete independency of local richness from regional richness should result in a slope = 0. This method was reported advantageous when compared to the common linear and nonlinear regressions since estimates of the slope are not influenced by the errors present in the independent variable and thus the slope can be used for more consistent meta-analytical comparisons (Hillebrand & Blenckner 2002).

Results

Taxonomic RR was highest in the North Sea region, followed by the Mediterranean, NE Atlantic and Baltic
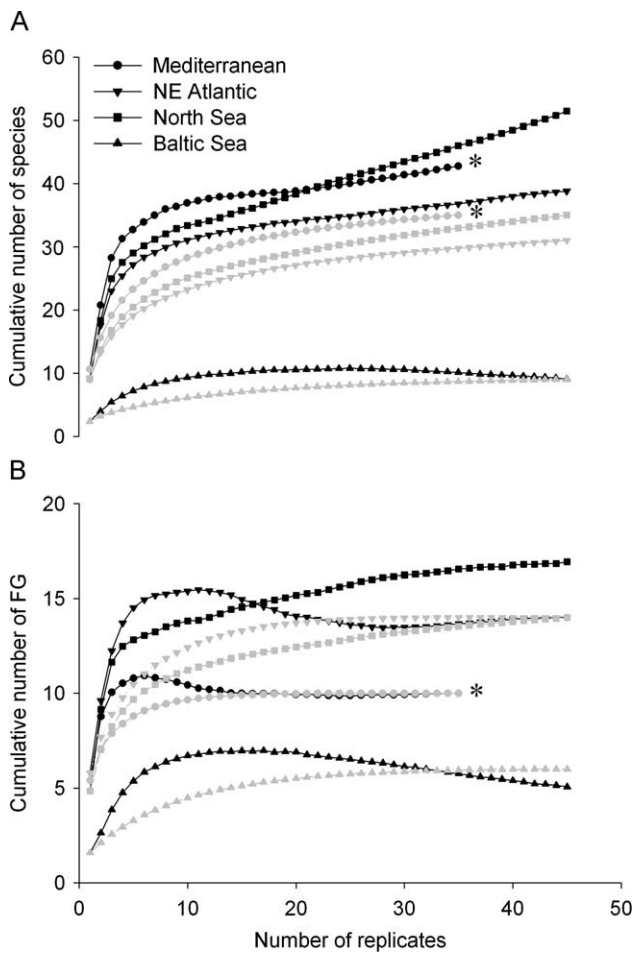

Fig. 1. Species (A) and functional groups (B) accumulation curves for 4 regions as a function of number of panels by using the Jack2 estimator of species richness (in black) and S_{obs} (in light gray). The endpoint of each curve (Jack2) was used as regional richness in the log–log regression of local–regional richness. * Jack2 and S_{obs} estimation at the Mediterranean region is based on 35 replicates due to the loss of replicates after 6 months of succession.

Sea regions. In all regions Jack2 overestimated S_{obs} (Fig. 1A). Functional RR ranked in a slightly different order: North Sea, NE Atlantic, Mediterranean and Baltic Sea. In this case and at maximum sampling effort, Jack2 and S_{obs} yielded comparable estimates (Fig. 1B). Total species and functional groups accumulation curves for the Mediterranean region were constructed based on only 35 replicates because 10 panels were lost during the second sampling. Using almost identical conditions as we use here (substratum, panel size and depth), Canning-Clode et al. (2008) quantified the error by Jack2 in estimating regional richness. At this level of sampling effort ($n = 35$), Jack2 underestimated true richness by 6.8% only (Canning-Clode et al. 2008). Therefore, we do not expect severe implications in the local–regional richness analysis.

With the exception of the Mediterranean region after 3 months and North Sea after 6 months, average percent cover of local fouling species always exceeded 100% (Fig. 2) suggesting a large potential for competition for space even at all stages of succession. During the entire duration of the experiment, however, the communities expanded along the third dimension in space ('thickened') presumably leading to an intensification of competition for resources along this axis.

Local taxonomic and functional diversity in the course of succession related similarly to regional richness in all regions (Fig. 3). For both dimensions of diversity, the portion of RR species coexisting at the local scale increased during succession (Fig. 3A–B). However, for taxonomic diversity all ratios were below 0.4, which indicates that the regional pool of species colonizing these substrata at this depth was at least 2 times higher than the average number of species found on a given panel (Fig. 3A). In general, the number of locally found FG was closer to the regionally available
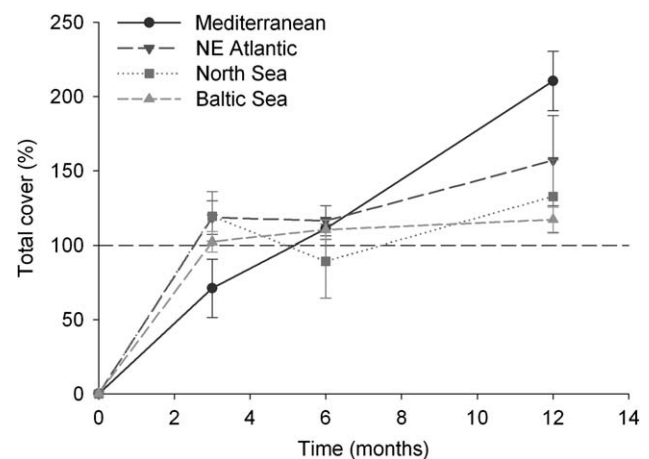

Fig. 2. Total percent cover of fouling species colonizing local panels ($n = 5$) at all regions throughout succession. Means and 95% confidence intervals are indicated.
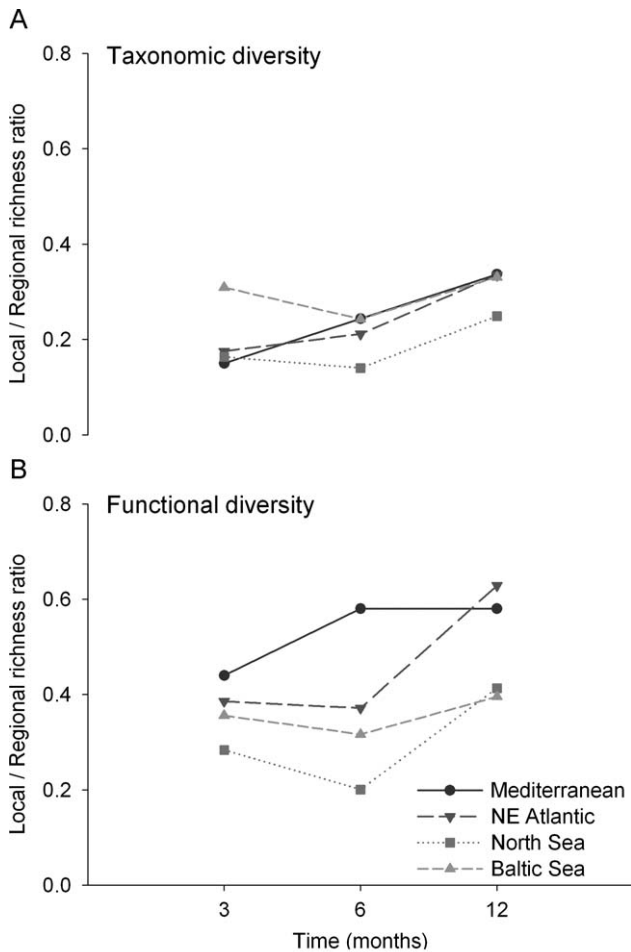
Fig. 3. Local/regional richness ratios at three stages of succession for taxonomic diversity (A) and functional diversity (B).
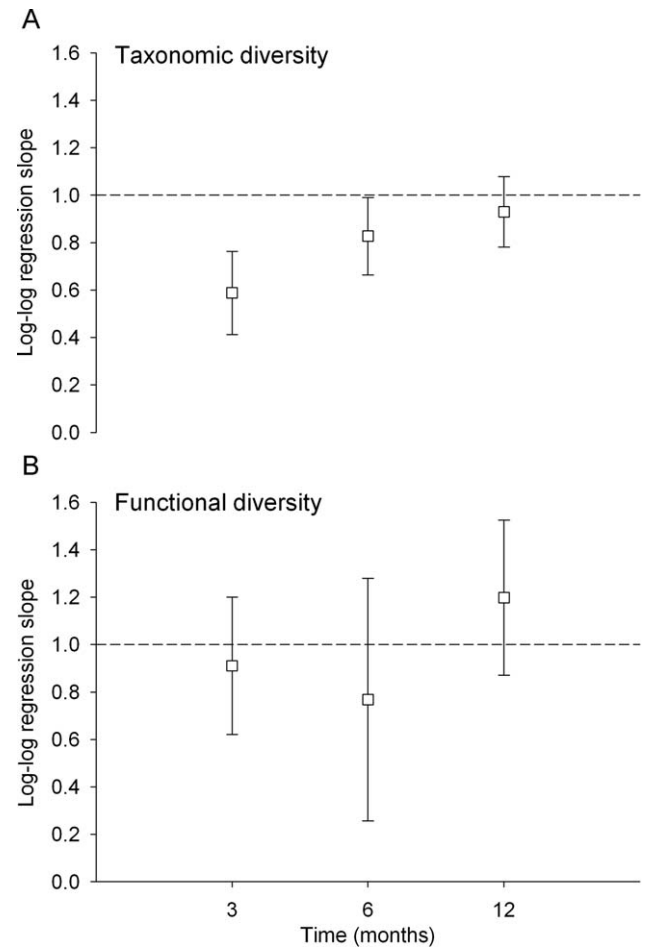

Fig. 4. Slopes of the double log regression analysis over time for taxonomic diversity (A) and functional diversity (B). Slopes and 95% confidence intervals are indicated. The dashed line indicates a slope of 1. A slope that does not differ from 1 is indicative of unsaturation, while local saturation is represented by a slope significantly smaller than 1. $n = 4$ for each sampling date.

functional richness, particularly after 12 months, when ratios exceeded 0.5 in the Mediterranean and Baltic Sea regions (Fig. 3B).

The slope of the log–log regression tends to increase with time for taxonomic richness (Fig. 4A) indicating that a larger portion of the RR species coexists in more mature communities. In addition to the general trend, at the successional ages of 3 and 6 months local species richness increased with taxonomic RR ($b > 0$) but reached saturation ($b < 1$). After 12 months of colonization, local richness increased with regional richness ($b > 0$) but did not reach saturation ($b \sim 1$) (Fig. 4A). For functional diversity, the slope was not significantly different from 1 (due to large variance) at all stages of succession. In this case, 95% confidence intervals included values > 1 and in some cases close to 0, which may suggest a more pronounced independency of local functional diversity from functional RR (Fig. 4B).

Discussion

In recent years, for a variety of statistical and theoretical issues, regressions of local against regional richness have been criticized (e.g. Hillebrand 2005; Shurin & Srivastava 2005).

In this study we avoided a number of these drawbacks by following several recommendations (Harrison & Cornell 2008; Hillebrand & Blenckner 2002). First, we collected separate samples for both spatial scales to avoid circularity between local and regional scales. Second, *pseudosaturation* caused by overestimation of regional richness was avoided by using only those species or FG capable of colonizing the local habitat at a given depth and time to estimate the regional species or functional pools. Third, a possible underestimation of

true regional richness was corrected by using the non-parametric estimator Jack2 which is based on the presence/absence of infrequent species. Moreover, Jack2 was found to have prime performance among five other estimators in a study performed at almost identical circumstances as we use here (Canning-Clode et al. 2008). Finally, we used the double-log regression to distinguish between 'type I' and 'type II' curves.

To the best of our knowledge, this is the first contribution on the local–regional richness relationship that incorporates simultaneously different successional stages and two dimensions of diversity. We demonstrate that the relevant regional richness, i.e. the number of regionally available colonizers varies in time. In contrast to the common use of species inventories, our method of estimating the relevant regional species or functional groups pools, avoids the danger of including species which were not available during the assembly of a community or which for ecological reasons would not establish in the habitat under consideration.

This study showed that for taxonomic richness, the 'degree of unsaturation', i.e. the mean slope of the log–log relationship, tends to increase in the course of succession. However, saturation is significant at the first successional stage (3 months). In contrast, local communities with regard to functional diversity displayed an unsaturated pattern at all successional ages.

For taxonomic diversity, our findings partially corroborate the theoretical approach developed by Mouquet et al. (2003). According to their model we would have expected to find (pseudo-) saturation early in succession, followed by transient unsaturation and possibly merging into saturation at a more mature stage of community assemblage. Indeed, in our study 3-month-old communities were saturated changing to unsaturated in the 2 subsequent surveys. We cannot exclude that the second saturated pattern was not obtained because communities were still immature. However, space was limited from a community age of 3 months onward and competitive exclusion should have had sufficient time to produce saturation. Disturbances can limit competitive exclusion and, consequently, the appearance of a saturated relationship. However, our method of suspending fouling panels from floats limited benthic predation or mechanical damage and, indeed, disturbance marks were only rarely observed.

The model by Mouquet et al. (2003) should be used just as a general qualitative trend since the time scales depend on the dynamics of colonization and the competition mode of the communities under investigation. There was no prediction in Mouquet's model for the development of the local–regional relationship regarding functional diversity.

Recent studies have suggested considering also neutral processes (equilibrium between immigration and extinction processes) as significant determinants in addition to e.g. competition as a driver (Fox & Srivastava 2006; He, Gaston, Connor, & Srivastava 2005). Therefore, local–regional richness plots should be used only as a starting point in the theoretical interpretation on the influence of local and regional processes in local communities (Cornell, Karlson, & Hughes 2008; Russell et al. 2006).

Finally, the present study on the local–regional richness relationship may also be influenced by the number of regions and the range of regional richness values. While more regions and a wider richness range are undoubtedly advantageous, some previous studies used even fewer regions (e.g. Hugueny, Cornell, & Harrison 2007). We consider that there are no simple rules concerning the number of regions one needs to examine the pattern on the condition that more than two regions are included and appropriate spatial scales and theoretical inferences are used.

The core conclusion of this study is that the shape of the relationship between local and regional diversity in fouling communities is sensitive to succession. Here we show that the mean slope of the log–log relationship tends to increase in the course of succession. Therefore, we emphasize the need to incorporate this aspect in future analyses of the pattern.

Acknowledgments

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