ECOSYSTEMS AND SUSTAINABILITY

Functional diversity and species turnover of benthic invertebrates along a local environmental gradient induced by an aquaculture unit: the contribution of species dispersal ability and rarity

Charalampos Dimitriadis · Drosos Koutsoubas

Abstract The relation of macrobenthic species turnover (beta diversity) and species plylogenetic variation with functional diversity patterns, across an environmental gradient induced by an aquaculture unit, in a coastal area of the island of Lesvos (NE Aegean) has been investigated in this study. The contribution of rare species response and species dispersal ability in the variation of functional diversity patterns along the environmental gradient, on a spatio-temporal scale, has been also examined. Our results revealed that benthic functional diversity was decreasing monotonically with increasing species turnover rate and hence with increasing spatial variability along the environmental gradient. Increased environmental stress which was detected in the immediate vicinity of the fish cages resulted to low species functional redundancy, since different species didn't perform the same functional role at the most disturbed part of the established gradient. Functional diversity patterns were found to be correlated with species population size, whereas a strong linear relationship was also detected with phylogenetic diversity patterns, thus supporting the claim that wider local taxonomic trees can support a wider range of species functions even in small spatial scales. Rare species loss seemed to be one of the dominant factors ruling functional diversity variation. Species with the minimum possible dispersal ability, which were mostly rare, tend to diminish both in species number and population size faster than species with wider dispersal ability towards the most disturbed areas. The aforementioned results indicate that rare species variation and endemic species loss are critical factors in determining functional diversity loss across a human-induced environmental gradient in soft bottom benthic communities.

Keywords Functional diversity · Beta diversity · Aquaculture · Benthos

C. Dimitriadis · D. Koutsoubas (✉)
Department of Marine Sciences, Faculty of Environment, University of the Aegean, Lesvos Island 81100, Greece
e-mail: drosos@aegean.gr

Introduction

Biodiversity, as a multi-facet concept, can be distinguished in various sub-concepts such as beta or turnover diversity and functional diversity (Ricotta, 2007). Beta diversity represents the rate of species identities shift and measures species turnover rate along a given spatial scale (Whittaker, 1960, 1972) thus capturing differences in species composition either between two or more local assemblages or between local and regional assemblages (Koleff

et al., 2003). Despite the fact that it provides a fundamental tool in spatial diversity patterns decoding (Wilson & Shmida, 1984), it has received limited attention especially in the marine biome (Gray, 2000; Becking et al., 2006). However, a large variety of beta diversity indices have been proposed and used in the ecological literature, mainly concerning species presence/absence data rather than species abundance (Chao et al., 2005), while the original Whittaker's measure has been the most frequently employed (Koleff et al., 2003).

There is growing evidence that ecosystem functioning is primarily governed by species-specific functional traits rather than species richness per se (Loreau et al., 2001; Bolam et al., 2002; Giller et al., 2004; Hooper et al., 2005). The importance of species biological traits related to ecosystems functions have been highlighted in many biodiversity-function experiments, especially on small spatio-temporal scales, in a wide range of ecosystems (Cardinale et al., 2004). The value and range of species traits that influence ecosystem functioning in a given system have been used by Tilman (2001) in order to describe functional diversity. Species traits have been also used in several other definitions of functional diversity (e.g. Díaz & Cabido, 2001; Tesfaye et al., 2003; Petchey & Gaston, 2006). Therefore, functional diversity has progressively been used as a tool in exploring ecosystem mechanisms, such as resource use complementarity and facilitation (Díaz & Cabido, 2001; Petchey & Gaston, 2006), as well as in predicting functional consequences of human-induced pressure on the biota (Loreau et al., 2002). Since threats resulting to marine ecosystems degradation are rapidly increasing nowadays there is a great need to assess the impacts of man-made stress on marine ecosystems functioning (Gaston, 2000; Olsen et al., 2002; Pandolfi et al., 2003; Bremner 2008) and many indices that take into account functional differences between species have been proposed and reviewed in several studies (e.g. Petchey et al., 2004; Ricotta, 2005; Bremner et al., 2006; Petchey & Gaston, 2006; Podani & Schmera, 2006; Walker et al., 2008). However, investigation of functional diversity has been mostly focused in terrestrial ecosystems, while coastal areas have attracted less attention (e.g. Covich et al., 2004; Gessner et al., 2004). Furthermore, functional diversity patterns of benthic invertebrates and macroalgae in

aquatic habitats have been examined in rather few studies (e.g. Emmerson & Raffaelli, 2000; Emmerson et al., 2001; Biles et al., 2003; Raffaelli et al., 2003; Mermillod-Blondin et al., 2005; Griffin et al., 2009), while response of benthic invertebrates' functional diversity in coastal areas along a human-induced disturbance gradient is even less examined (Papageorgiou et al., 2009).

The present study aims to address marine benthic functional diversity levels, on a small spatial scale, along an environmental gradient caused by the presence of an aquaculture unit in a coastal area of the NE Mediterranean. In addition, we present the relation of species turnover (beta diversity) and species plylogenetic variation with functional diversity patterns across this gradient. Finally, we examined the hypothesis whether a decline in rare species number and species geographic range size contributes in the variation of functional diversity patterns along the environmental gradient.

Materials and methods

Study area

The study area is located at NE Aegean Sea (Eastern Mediterranean Sea) and particularly at the entrance of the semi-enclosed Bay of Gera in Lesvos Island (Fig. 1). The presence of an aquaculture unit (with an average annual production of 150 tones of sea-bream and sea-bass) in the study area has proven to cause a series of modifications in the environmental conditions across a gradient (stations N, M, F—Fig. 1) which subsequently have an effect on the structure and dynamics of benthic fauna (Dimitriadis & Koutsoubas, 2008).

Data analysis

The Molluscan taxocoenosis data set (Dimitriadis & Koutsoubas, 2008) has been used in the analysis of the present study. This analysis involved the calculation of beta and functional diversity along the environmental transect (Fig. 1) and between the different sampling seasons. Beta diversity measurement involved the use of two quantitative and two qualitative indices based on species presence–absence and species abundance data correspondingly.
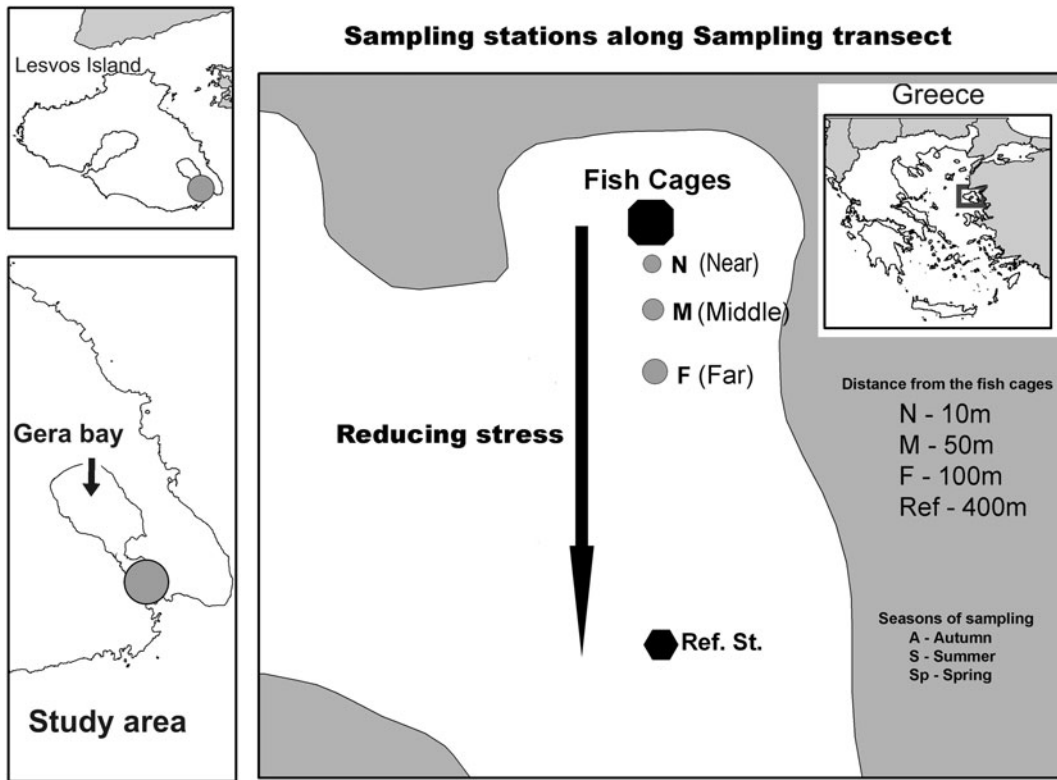
Fig. 1 Study area and sampling design for macrofauna samples (after Dimitriadis & Koutsoubas, 2008, slightly modified)

Considering the qualitative beta diversity measures Whittaker's (1960) index β_w of species continuity and index β_{gl} (Lennon et al., 2001), which is specially designed for species richness gradients (Koleff et al., 2003), have been used. Quantitative beta diversity CJE and CSE indices involved the use of the modified Jaccard and Sørensen indices correspondingly for species abundance data (Chao et al., 2005). The later have been also corrected for the effect of unseen shared species (i.e. species that are likely to be present in a theoretical larger sample of the assemblage, but that are missing from actual sample data) (Chao et al., 2005). According to Chao et al. (2005), higher values of CJE and CSE index correspond to lower beta diversity levels, whereas lower values of CJE and CSE correspond to higher beta diversity levels. Beta diversity indices were calculated between adjacent pairs of sampling sites along the sampling transect as it is proposed and discussed by Wilson & Shmida (1984). Quantitative beta diversity indices have been calculated by means of the ESTIMATES v8 software package (Colwell, 2005).

Considering species functional traits nine different functional characteristics of benthic molluscs related to resource use requirements (i.e. detritus feeders, suspension feeders, deposit feeders, herbivores, parasitic), life mode (positioning in the sediment—i.e., sub-surface infauna, epifauna) and movement in the sediment (i.e. mobile, sessile) (Norling et al., 2007; Papageorgiou et al., 2009) have been incorporated in the analysis. Functional diversity was calculated based on functional attribute diversity index (FAD) which reflects the sum of the pair-wise functional dissimilarities of species (Walker et al., 1999). The properties and performance of FAD index are discussed by Ricotta (2005) and Schmera et al. (2009). According to Walker et al. (2008), FAD is probably more appropriate index in revealing the resilience of a community in the face of an environmental change and this has been the reason to select this index instead of other functional diversity indices (see Petchey & Gaston, 2006). All pair-wise distances between species in functional trait space were calculated with the use of Euclidean distance in SPSS v12 (SPSS, 2002).

Correlation of functional diversity with species richness, total taxonomic distinctness $s\Delta^+$, variation of taxonomic distinctness Λ^+ (Warwick & Clarke, 2001), species abundance and rare species number was carried out with the use of Spearman's correlation index (ρ) provided by SPSS v12 software. A regression model was also used in order to describe the relationship between the aforementioned variables. Finally, significant differences among measurements were detected with the non-parametric Mann–Whitney test (Zar, 1984).

Results

Species turnover

Calculation of beta diversity indices β_w and β_{gl} based on species presence/absence data revealed a pattern of gradual decrease in species turnover towards the environmental gradient with decreasing disturbance levels. Maximum species turnover rate was detected close to the areas of the immediate vicinity of the fish-cages during summer and autumn, while minimum rate was noticed at the less impacted sampling sites further away from the fish-cages during spring. However, significant alterations in beta diversity levels were noticed only between the pairs of stations N-M and F-Ref (Mann–Whitney test results, $P <$ 0.05), indicating that the area located at the middle of the environmental gradient consists a transitional point in species turnover (Fig. 2). An alteration in species turnover rate was also detected from the

quantitative indices CJE and CSE along the environmental gradient. Hence, maxima of species turnover (minimum values of CJE and CSE index) were recorded to the pair of stations close to the cages while minima (maximum values of CJE and CSE index) were obtained further away. Significant modifications in the values of CJE and CSE indices were obtained for the pairs of stations N-M and F-Ref between all sampling seasons denoting an important shift in species turnover rate therein (Mann–Whitney test results, $P < 0.05$; Fig. 3). Increased turnover rates between the most impacted sites were found to be driven by both quantitative and qualitative changes in species composition since those areas were only sharing a few species, whereas common species populations were roughly decreasing from intermediate to highly impacted sites. In addition, rare species number seemed to strongly affect beta diversity levels rather than the fluctuations of common species abundance. On the contrary, seasonal modifications of beta diversity were not statistically significant for the pooled abundance data in the study area (Mann–Whitney test results, $P > 0.05$) implying that seasonal variation was not a major factor governing species turnover rate.

Functional diversity

Regarding functional diversity, maxima were recorded to the area of low environmental stress (station SpF) during spring sampling period, while minima were obtained to the area of the immediate vicinity of the fish cages during summer (station SN).

Fig. 2 Beta diversity variation according to a β_{gl} index and b β_w index along the environmental gradient for the pooled species presence–absence data of Molluscan fauna (error bars represent standard error of mean)
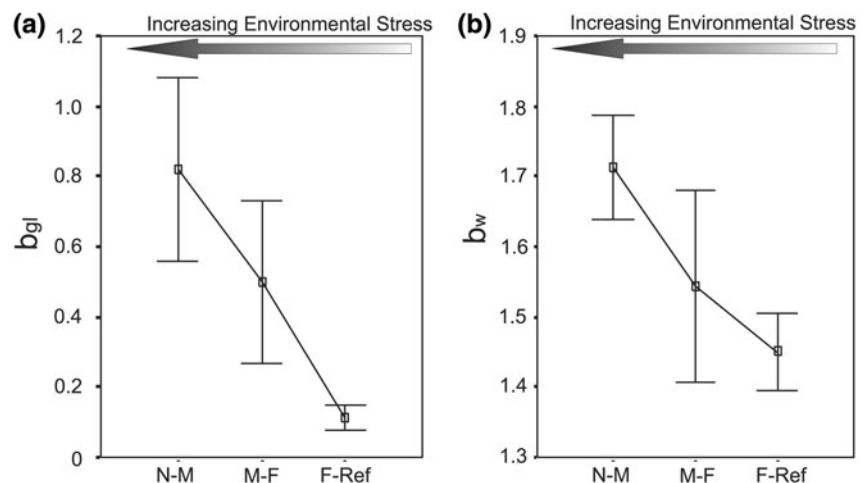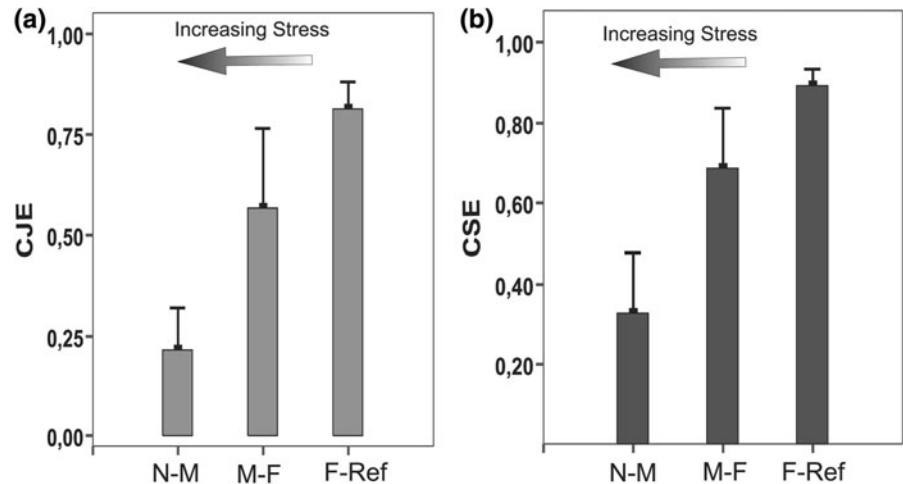
Fig. 3 Beta diversity variation according to **a** CJE index and **b** CSE index along the environmental gradient for the pooled species abundance data of Molluscan fauna (*error bars* represent standard error of mean)

Functional diversity presented a linear decrease ($R^2 = 0.61$, $P < 0.05$) with increasing environmental stress across the sampling transect revealing a pattern of seriation in functional diversity variation (Fig. 4), since functional diversity was gradually decreasing towards the most disturbed end of the gradient. Significant modifications of FAD index values were obvious between the group of areas of high and moderate disturbance effects with the rest of the study area where higher functional diversity values were present during all sampling seasons (Mann–Whitney test results, $P < 0.05$). Though, in seasonal basis, FAD values didn't show any significant alterations in functional diversity levels between the three sampling seasons (Mann–Whitney test results, $P > 0.05$) a fact that should be mainly attributed to the effect of the increased functional diversity levels during spring throughout the whole length of the sampling transect. Correlation of functional diversity with species richness of benthic molluscs revealed a strong linear relationship between them (Spearman's $\rho = 0.876$, $P < 0.05$) suggesting that increasing species diversity leads to species assemblages of higher functional complexity along the environmental gradient towards the undisturbed areas. In addition, a positive linear relationship was also detected when functional diversity index FAD and taxonomic distinctness index $s\Delta^+$ are considered (Spearman's $\rho = 0.867$, $P < 0.05$).
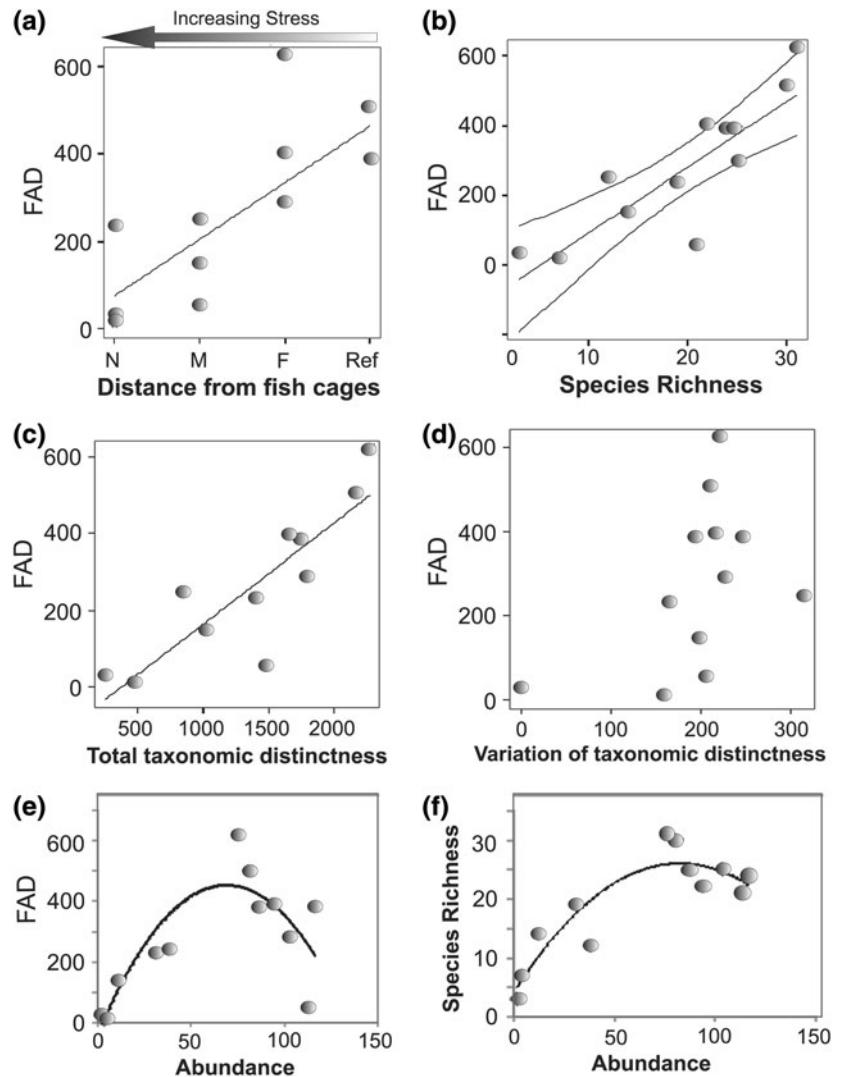
The latter denotes that wider phylogenetic trees can support a greater number of species functions. On the other hand, variation of taxonomic distinctness $L+$ seemed to be more or less constant with increasing values of functional attribute diversity index. Correlation of functional diversity with species abundance across the environmental gradient showed a hump-shaped relationship between these two variables (Fig. 4). A hump-shaped relationship was also detected in the correlation of species richness and species abundance. Functional diversity was highly correlated with rare species number variation along the environmental gradient. Thus, loss of rare species seemed to be linearly correlated with functional diversity loss across the environmental gradient ($R^2 = 0.92$, $P < 0.05$; Fig. 5).

Discussion

According to the P–R (Pearson–Rosenberg) model (Pearson & Rosenberg, 1978), marine benthic community succeeds in several progressive stages towards a disturbance gradient in space and time from diverse community fauna to a transitional community structure where opportunistic species are proliferating in terms of abundance and species number and eventually to an azoic area at the most disturbed end of the gradient. Changes in benthic species composition, species diversity patterns (Pearson & Rosenberg, 1978; Gray, 1981), life history traits (Diaz & Rosenberg, 1995; Cheung et al., 2008), feeding guilds (Pagliosa, 2005; Dimitriadis & Koutsoubas, 2008) and species range size representation (Dimitriadis & Koutsoubas, 2008) along environmental gradients are well documented in contrast with benthic functional diversity patterns

Fig. 4 Scatter plots of
a FAD index and distance
from the fish cages (linear
regression, $R^2 = 0.61$,
$P < 0.05$), **b** FAD index
and species richness (linear
regression, $R^2 = 0.72$,
$P < 0.05$), **c** FAD index and
total taxonomic distinctness
(linear regression,
$R^2 = 0.75$, $P < 0.05$),
d FAD index and variation
of taxonomic distinctness
(linear regression,
$R^2 = 0.02$, $P > 0.05$),
e FAD index and species
abundance (polynomial
regression of second order,
$R^2 = 0.70$, $P < 0.05$) and
f species richness and
species abundance
(polynomial regression of
second order, $R^2 = 0.83$,
$P < 0.05$)

which are not widely understood yet along gradients (e.g. Norling et al., 2007; Papageorgiou et al., 2009). The results of the present study revealed that benthic functional diversity was decreasing monotonically with increasing species turnover rate and hence with increasing spatial variability of macrofauna along the established environmental gradient. Furthermore, beta diversity patterns were strongly governed by the loss rate of rare species across the environmental gradient, a fact which has also been reported in several studies for other major taxonomic groups (e.g. Gaston, 1994). Functional diversity was strongly correlated to rare species number denoting that the loss of rare species leads to the gradual loss of functional complexity of benthic communities across

the environmental gradient. It was also evident that increased environmental stress resulted to low species functional redundancy (Lawton & Brown, 1993; Loreau, 2004) since different species didn't perform the same functional role across the gradient. Low functional redundancy across the environmental gradient can be possibly attributed to the fact that the smothering of the habitats towards the disturbance source acts as selective mechanism resulting in the reduction of species with similar functional traits. Hence, the gradual loss of certain species' functional traits with increasing environmental stress led to a strong and successive decline in benthic functional diversity suggesting that species diversity (i.e. species richness) changes can trigger shifts in benthic

community functional stability. The latter has also been reported in several studies which have also shown a strong correlation between species diversity and functional diversity in marine sediments (Papageorgiou et al., 2009). However, low functional redundancy levels which were observed in the study area do not necessarily imply that functional redundancy were not present among some of the species since, for example, the bivalve *Nucula nitidosa* was replaced by the functionally similar bivalve *Nuculana pella* at the area of the immediate vicinity of the fish cages. Similar results have also been recorded when species functional redundancy was investigated within functional groups (Loreau et al., 2001).

Benthic functional diversity patterns across the environmental gradient were found to be strongly correlated with species population size. The hump-shaped relation between functional diversity and species abundance denotes that functional diversity increases when low and intermediate levels of species abundance are involved. However, when species abundance is reaching its maximum values, functional diversity is decreasing. This pattern was also the case for species richness and species abundance correlation which was also described from a hump-shaped relationship. Hence, species richness was decreasing when abundance was reaching intermediate and maximum values in species communities. These results suggest that the most populated communities do not necessarily encompass increased functional complexity since there was an upper limit in species abundance from which functional diversity was starting to decline.

A strong linear relationship was detected between functional and phylogenetic diversity patterns thus supporting the claim that wider local taxonomic trees can support a wider range of species functions even in small spatial scales. However, the proliferation of disturbance regimes results to narrower taxonomic trees with a smaller range of species functions. This narrow range of species functions is maintained by certain species which were also present in the wider taxonomic trees. Therefore, the results of this study confirm the hypothesis that some species are more important than other in ecosystem functioning (Tilman et al., 1997). Rare species loss seemed to be one of the dominant factors ruling functional diversity variation at different disturbance levels in space since it is well known that these species are characterized by high
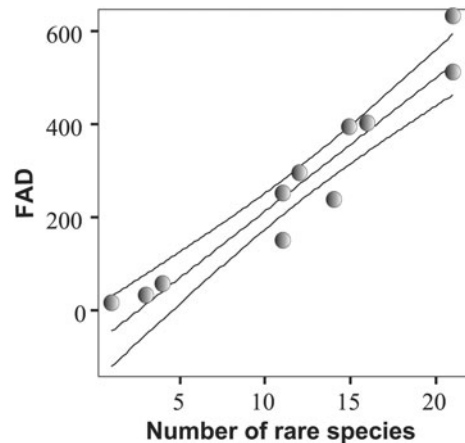

Fig. 5 Functional attribute diversity index plotted against rare species number in the study area (linear regression, $R^2 = 0.92$, $P < 0.05$)

niche differentiation and are usually intolerant in disturbance regimes (Smith & Knapp, 2003). Therefore, it seems that rare species are important in maintaining the stability of ecosystem functioning in changing environments (Walker et al., 1999; Loreau et al., 2001). Rare species included a broad range of functional traits which were comparable to the ones noticed for the total species pool, a fact which was also observed by Ellingsen et al. (2007) for soft bottom macrofauna. According to Naeem & Li (1997) and Ellingsen et al. (2007), the latter pattern demonstrates that species with restricted geographic dispersal ability can have an impact on stability and resilience of soft bottom communities. Earlier publications concerning species geographic range size in the study area revealed that endemic species (i.e. species with the minimum possible dispersal ability) which were mostly rare tend to diminish their species number and population size faster than species with wider dispersal ability with increasing environmental stress (Dimitriadis & Koutsoubas, 2008). Hence, benthic rare species do not invest in functional resilience but they can still have an important influence in community and ecosystem functioning (Ellingsen et al., 2007). Although it is widely acknowledged that species dispersal ability consist a primary factor governing biodiversity distribution patterns in nature (Tilman, 1999), relatively less attention has been paid in the influence of species dispersal ability on the variation of functional diversity (Giller et al., 2004; France & Duffy, 2006) and especially in cases of environmental gradients.

Conclusions

Understanding the relationship between benthic diversity loss and functional diversity modifications can increase our knowledge in predicting the functional consequences of human induced pressure on the marine environment. From the above, it was evident that human activities such as fish farming can modify benthic biodiversity which in return can alter functional diversity of sediment communities and affect ecosystem functioning in coastal areas. However, functional diversity loss was restricted to the immediate vicinity of the fish cages, a fact that clearly demonstrates that impacts of aquaculture on benthic communities functioning had a strictly local character. The results from the present study have also revealed that species dispersal ability increment (i.e. loss of species with narrow geographic range size—endemic species) and rare species number decrement influenced the magnitude of functional diversity loss with increasing levels of stress on soft bottom benthic communities.

References

Becking, L. E., D. F. R. Cleary, N. J. De Voogd, W. Renema, M. De Beer, R. W. M. Van Soest & B. W. Hoeksema, 2006. Beta diversity of tropical marine benthic assemblages in the Spermonde Archipelago, Indonesia. Marine Ecology 27: 76–88.

Biles, C. L., M. Solan, I. Isaksson, D. M. Paterson, C. Emes & D. G. Raffaelli, 2003. Flow modifies the effect of biodiversity on ecosystem functioning: an in situ study of estuarine sediments. Journal of Experimental Marine Biology and Ecology 286: 165–177.

Bolam, S. G., T. F. Fernandes & M. Huxham, 2002. Diversity, biomass, and ecosystem processes in the marine benthos. Ecological Monographs 72: 599–615.

Bremner, J., 2008. Species traits and ecological functioning in marine conservation and management. Journal of Experimental Marine Biology and Ecology 366: 37–47.

Bremner, J., S. I. Rogers & C. L. J. Frid, 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecological Indicators 6: 609–622.

Cardinale, B. J., A. R. Ives & P. Inchausti, 2004. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos 104: 437–450.

Chao, A., R. L. Chazdon, R. K. Colwell & T. J. Shen, 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8: 148–159.

Cheung, S. G., N. W. Y. Lam, R. S. S. Wu & P. K. S. Shin, 2008. Spatio-temporal changes of marine macrobenthic community in sub-tropical waters upon recovery from eutrophication. II. Life-history traits and feeding guilds of polychaete community. Marine Pollution Bulletin 56: 297–307.

Colwell, R. K., 2005. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8. User's Guide and Application, http://purl.oclc.org/estimates.

Covich, A. P., M. C. Austen, F. Barlocher, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner & B. Moss, 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. Bioscience 54: 767–775.

Díaz, S. & M. Cabido, 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16: 646–655.

Diaz, R. J. & R. Rosenberg, 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology Annual Review 33: 245–303.

Dimitriadis, C. & D. Koutsoubas, 2008. Community properties of benthic molluscs as indicators of environmental stress induced by organic enrichment. Journal of Natural History 42: 559–574.

Ellingsen, K. E., J. E. Hewitt & S. F. Thrush, 2007. Rare species, habitat diversity and functional redundancy in marine benthos. Journal of Sea Research 58: 291–301.

Emmerson, M. C. & D. G. Raffaelli, 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. Oikos 91: 195–203.

Emmerson, M. C., M. Solan, C. Emes, D. M. Paterson & D. G. Raffaelli, 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature 411: 73–77.

France, K. E. & J. E. Duffy, 2006. Diversity and dispersal interactively affect predictability of ecosystem function. Nature 441: 1139–1143.

Gaston, K. J., 1994. Rarity. Chapman and Hall, London.

Gaston, K. J., 2000. Global patterns in biodiversity. Nature 405: 220–228.

Gessner, M., P. Inchausti, L. Persson, D. G. Raffaelli & P. S. Giller, 2004. Biodiversity effects on ecosystem functioning: insights from aquatic systems. Oikos 104: 419–422.

Giller, S. P., H. Hillebrand, U. G. Berninger, O. M. Gessner, S. Hawkins, P. Inchausti, C. Inglis, H. Leslie, B. Malmqvist, T. M. Monaghan, J. P. Morin & G. O'Mullan, 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. Oikos 104: 423–436.

Gray, J. S., 1981. The Ecology of Marine Sediments. Cambridge University Press, Cambridge.

Gray, J. S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. Journal of Experimental Marine Biology and Ecology 250: 23–49.

Griffin, J. N., V. Méndez, A. F. Johnson, S. R. Jenkins & A. Foggo, 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. Oikos 118: 37–44.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3–35.

Koleff, P., K. J. Gaston & J. J. Lennon, 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72: 367–382.

Lawton, J. H. & V. K. Brown, 1993. Redundancy in ecosystems. In Schulze, E. D. & H. A. Mooney (eds), Biodiversity and Ecosystem Function. Springer, Berlin: 255–270.

Lennon, J. J., P. Koleff, J. J. D. Greenwood & K. J. Gaston, 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology 70: 966–979.

Loreau, M., 2004. Does functional redundancy exist? Oikos 104: 3.

Loreau, M., S. Naeem, P. Inchausti, J. Nengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman & D. A. Wardle, 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804–808.

Loreau, M., S. Naeem & P. Inchausti, 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.

Mermillod-Blondin, F., F. François-Carcaillet & R. Rosenberg, 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. Journal of Experimental Marine Biology and Ecology 315: 187–209.

Naeem, S. & S. Li, 1997. Biodiversity enhances ecosystem reliability. Nature 390: 507–509.

Norling, K., R. Rosenberg, S. Hulth, A. Grémare & E. Bonsdorff, 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Marine Ecology Progress Series 332: 11–23.

Olsen, D. M., E. Dinerstein, G. V. N. Powell & E. D. Wikramanayake, 2002. Conservation biology for the biodiversity crisis. Conservation Biology 16: 1–3.

Pagliosa, P. R., 2005. Another diet of worms: the applicability of polychaete feeding guilds as a useful conceptual framework and biological variable. Marine Ecology 26: 246–254.

Pandolfi, J. M. R. H., E. Bradbury, T. P. Sala, K. A. Hughes, R. G. Bjorndal, D. Cooke, L. McArdle, M. J. H. McClenachan, G. Newman, R. R. Paredes, J. B. C. Warner & Jackson, 2003. Global trajectories of long-term decline of coral reef ecosystems. Science 301: 955–958.

Papageorgiou, N., K. Sigala & I. Karakassis, 2009. Changes of macrofaunal functional composition at sedimentary habitats in the vicinity of fish farms. Estuarine, Coastal and Shelf Science 83: 561–568.

Pearson, T. H. & R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16: 229–311.

Petchey, O. L. & K. J. Gaston, 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9: 741–758.

Petchey, O. L., A. Hector & K. J. Gaston, 2004. How do different measures of functional diversity perform? Ecology 85: 847–857.

Podani, J. & D. Schmera, 2006. On dendrogram-based measures of functional diversity. Oikos 115: 179–185.

Raffaelli, D., M. Emmerson, M. Solan, C. Biles & D. Paterson, 2003. Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. Journal of Sea Research 49: 133–141.

Ricotta, C., 2005. A note on functional diversity measures. Basic and Applied Ecology 6: 479–486.

Ricotta, C., 2007. A semantic taxonomy for diversity measures. Acta Biotheoretica 55: 23–33.

Schmera, D., T. Erős & J. Podani, 2009. A measure for assessing functional diversity in ecological communities. Aquatic Ecology 43: 157–167.

Smith, M. D. & A. K. Knapp, 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6: 509–517.

SPSS Inc, 2002. SPSS Base 11.5. User's guide: 613 pp.

Tesfaye, M., N. S. Dufault, M. R. Dornbusch, D. L. Allan, C. P. Vance & D. A. Samac, 2003. Influence of enhanced malate dehydrogenase expression by alfalfa on diversity of rhizobacteria and soil nutrient availability. Soil Biology and Biochemistry 35: 1103–1113.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. The Robert H. MacArthur Award Lecture. Ecology 80: 1455–1474.

Tilman, D., 2001. Functional diversity. In Levin, S. A. (ed.), Encyclopedia of Biodiversity. Academic Press, San Diego, CA.

Tilman, D., J. Knopps, D. Wedin, P. Reich, M. Ritchie & E. Siemann, 1997. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300–1302.

Walker, B., A. Kinzig & J. Langridge, 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2: 95–113.

Walker, S. C., M. S. Poos & D. A. Jackson, 2008. Functional rarefaction: estimating functional diversity from field data. Oikos 117: 286–296.

Warwick, R. M. & K. R. Clarke, 2001. Practical measures of marine biodiversity based on relatedness of species. Oceanography and Marine Biology 39: 207–231.

Whittaker, R. H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279–338.

Whittaker, R. H., 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.

Wilson, M. V. & A. Shmida, 1984. Measuring beta diversity with presence–absence data. Journal of Ecology 72: 1055–1064.

Zar, J. H., 1984. Biostatistical Analysis. Prentice-Hall Inc, Englewood Cliffs, NJ.