

Relationship between functional diversity and benthic secondary production in a disturbed estuary

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ABSTRACT: We investigated the relationship between functional diversity and secondary production in an estuarine system subjected to anthropogenic impacts and climate events. Data consisted of a 14 yr long study of benthic invertebrate production from a seagrass bed and a sandflat. We used generalized linear models to test whether secondary production was explained by a functional identity effect (dominant traits in the community), by a complementarity effect (dissimilarity in trait measurements) or by their combined effects. From *a priori* correlations among community-weighted means for all traits, we identified 3 main life-history groups in the estuarine communities, reflecting different strategies to cope with disturbance and resulting in different production levels: species with an opportunist strategy, large slow-growing species and species with attributes providing higher competitive advantages, such as high mobility and omnivore feeding. The functional identity effect, also known as mass ratio hypothesis, was tested with a model combining these life-history groups. Overall, the functional identity/mass ratio effect model best explained variability in secondary production compared to the complementarity and combined effects models. In general, species with an opportunist strategy had higher production. These species explained a higher proportion of the production changes during the study period than the other 2 life-history groups. Nevertheless, this type of production, sustained by large numbers of small opportunist species with a rapid completion of their life cycle, may contribute towards an impoverishment of overall ecosystem functioning. In addition, we discuss the variation of all functional diversity measurements for the sites along the study period and relative to the changes in production.

KEY WORDS: Secondary production · Functional diversity · Benthic community · Estuarine environments · Mass ratio hypothesis

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INTRODUCTION

The biodiversity and ecosystem functioning debate has focused on the role of diversity in ecosystem processes and the resulting services that sustain human societies (Stachowicz et al. 2007, Naeem et al. 2009, 2012). The quantification of ecosystem functioning is extremely complex as it involves the chemical, physical and biological components of the ecosystem and its processes (e.g. decomposition, nutrient cycling, production). Secondary production is a process

that links population characteristics (such as biomass, growth rate, survivorship, development time) to other ecosystem-level processes (Dolbeth et al. 2012). Moreover, secondary production is often a direct measure of food provision delivered by an ecosystem that is used to quantify ecosystem provisioning services (Haines-Young & Potschin 2013). In both terrestrial and marine environments, increasing biodiversity appears to positively affect secondary production (Duffy 2009, Naeem et al. 2009, Solan et al. 2012).

Estuarine systems are generally characterized by low species richness, as few species can cope with the environmental variability associated with the daily change in physical and chemical parameters. Benthic communities can reach considerably high production (Dolbeth et al. 2011, Elliott & Whitfield 2011) through inputs of organic matter, nutrient regeneration and habitat heterogeneity (McLusky & Elliott 2004). What characteristics enable a species to use available resources or whether the number of species—irrespective of their identity—may influence production has been debated (Duffy 2006, Worm et al. 2006). Functional diversity has been considered a key element in promoting ecosystem processes such as production (Mouillot et al. 2007, 2013). It refers to the functional component of biodiversity, usually measured using species traits, i.e. any morphological, physiological, phenological or demographic features measurable at the individual level (Violle et al. 2007, Mouillot et al. 2013). Functional diversity may be quantified using a community-weighted mean (CWM), which is a measure of the dominant traits in a community (Lepš et al. 2011), or by the degree of functional dissimilarity in the trait values using functional diversity indices (functional richness, functional evenness, among others; see Mouchet et al. 2010, Schleuter et al. 2010, Mouillot et al. 2013). These measurements and components of functional diversity may be used to assess ecosystem processes and services, as trait effects on the processes and services are mediated by the traits' kind, range and relative abundance in the communities (De Bello et al. 2010, Lavorel et al. 2013). Essentially, 2 hypotheses have been proposed to explain ecosystem functioning based on functional diversity: (1) the functional identity hypothesis or mass ratio hypothesis (Grime 1998), where the abundance/biomass of a dominant trait will determine the process/function; and (2) the functional complementarity hypothesis, which considers the dissimilarity indices that measure the presence or absence of traits (i.e. functional richness) or consider abundance of different traits in the community (i.e. weighted functional diversity indices such as functional evenness, divergence and dispersion) (De Bello et al. 2010, Gagic et al. 2015).

In this study, our aim was to assess the relationship between secondary production and functional diversity based on 2 hypotheses: (1) organisms and their traits respond to the environment, and, in turn, affect production levels; and (2) the level of production can be predicted by functional diversity, with its different facets having a greater influence on production than the dominant traits in the community. For this

purpose, we modelled secondary production as a function of relevant dominant life-history functional groups, as suggested by Verberk et al. (2008, 2013), and as a function of different multidimensional functional diversity indices, using macrobenthic intertidal communities of a disturbed estuary (Portugal) (Dolbeth et al. 2011, 2014). The life-history functional groups were defined *a priori* using the CWM of 6 traits (size, life span, living position, feeding, mobility and reproduction). The assessment based on life-history groups instead of single traits alone is founded on the idea that the adaptive value of a trait is context dependent (Verberk et al. 2008, 2013). As such, a combination of traits may be more important than a trait alone as a response to disturbance (Dolédec & Statzner 2008, Verberk et al. 2013). Overall, we expected to find a positive relationship between functional diversity and the estuarine production, and we tested whether production was explained by a functional identity effect (dominant traits in the community), by a complementarity effect (dissimilarity in trait measurements) or by a combination of both effects. Finally, we discuss how functional diversity changed spatially in an estuarine system that resembles other estuaries worldwide in terms of disturbance impact and species composition.

MATERIALS AND METHODS

Study area, sampling and data processing

We used data from the south arm of the Mondego estuary (8.6 km²), located in a warm temperate region on the Atlantic coast of Portugal (40° 08' N, 8° 50' S). The south arm is shallow (2 to 4 m during high tide, tidal range 1 to 3 m), characterized by large intertidal flats with several marshes and a seagrass bed. Samples of the intertidal benthic communities (both infauna and epifauna) were collected from January 1993 until December 2006 at 2 sites: (1) a seagrass bed, characterized by muddy sediments covered with *Zostera noltii*, high organic matter content (mean \pm SD, 6.2 \pm 1.7 %) and high water-flow velocity (1.2 to 1.4 m s⁻¹); and (2) a sandflat, characterized by sandy sediments, low organic matter content (mean 3.0 \pm 1.1 %), low water-flow velocity (0.8 to 1.2 m s⁻¹) and a seasonal cover of green opportunist macroalgae. Macrophytes used to grow in the sandflat but completely disappeared in the last 20 yr until present, where some patches have begun to appear.

On each occasion and at each site, sediment samples were randomly collected with a corer up to

20 cm deep (141 cm² core sectional area). Samples were collected in the morning during low tide, fortnightly for the first 18 mo (10 cores month⁻¹) and monthly until December 2006 (6 cores month⁻¹). Sampling did not occur from 1996 to 1998 in the seagrass site and in 1997 and 1998 in the sandflat, due to practical constraints. Each sample was sieved through a 500 µm mesh using estuarine water. Organisms were all sorted and identified to species level, counted and biomass evaluated as ash-free dry mass (AFDM) after combustion of organisms for 8 h at 450°C.

Impact of disturbance in the estuary and production data

In the last 3 decades, the Mondego estuary has been subjected to several anthropogenic impacts and climate events (summarised in Table 1). In the 1980s, anthropogenic activities triggered eutrophication in the south arm. By 1998, mitigation measures allowed a decrease in nutrient inputs and promoted the estuary recovery. However, from 2000 onwards, several unusual climate events such as floods, heat waves and droughts slowed down the recovery process in the estuary.

For this study, we used the annual production values estimated in Dolbeth et al. (2011) that combined cohort methods and empirical models to evaluate benthic community over the sampling period for the 2 sites (seagrass bed and sandflat; $n = 22$). Seagrass bed and benthic community production in the Mondego estuary suffered alternating decline and recovery periods during the 14 yr study period, which were caused by different sources of disturbance (detailed in Table 1). These periods are as follows: (1) a period before mitigation (Pre, 1993–1996), during which seagrass bed coverage declined from 1.6 ha in 1993 to a historical minimum of 0.02 ha in 1997, resulting in local effects on production levels (Dolbeth et al. 2011); (2) a first gradual recovery period (Post I, 1999–2002), which occurred after a management plan had been implemented in 1998 with an initial recovery of the seagrass and of the benthic production until a new decline occurred following a flood; and (3) a second recovery period (Post II, 2003–2006), which, however, was slowed down by the occurrence of heat waves and droughts. These climate events affected production similarly in both sites, resulting in a decrease, especially after the heat wave in 2003.

Trait selection

We chose 6 traits that are likely to have an influence on production levels: mean body mass (ADFM) measured from the field samples, life span (mo), considering the maximum known life span of the species, and the following categorical traits: feeding guilds, depth position on the sediment for epifauna and infauna, mobility, and reproduction frequency. Trait categories, rationale for trait selection and expected response according to disturbance are summarized in Table 2. Information on the traits (except for size, which was evaluated from our dataset) was obtained from established databases including BIOTIC (Biological Traits Information Catalogue, www.marlin.ac.uk/biotic/) and WoRMS (World Register of Marine Species, www.marinespecies.org) and supplemented with other published sources (e.g. Bremner 2005, Baeta et al. 2009, Queirós et al. 2013). Traits were assigned to the 25 species that accounted for more than 98 % of the density, biomass and secondary production in the intertidal flats of the Mondego estuary (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m539p033_supp.pdf).

Data analysis

Trait composition was quantified by calculating the CWM, which expresses the trait mean per sample weighted by species relative abundance or biomass (Lepš et al. 2011), therefore representing the dominant trait in the community. CWMs were used to test the mass ratio hypothesis.

To test the complementarity effect hypothesis, we computed functional richness (FRic), functional evenness (FEve), functional dispersion (FDis) and functional divergence (FDiv) (Villéger et al. 2008, Laliberté & Legendre 2010, Mouillot et al. 2013). As trait data was composed of both continuous (quantitative) and categorical (qualitative) data, we followed the procedure outlined by Laliberté & Legendre (2010), which enables computation of functional diversity indices using a mixture of qualitative and quantitative traits (Cailliez correction on a Gower distance matrix). FRic represents the amount of functional space filled by the community without considering species abundance. It has no upper limit and correlates positively with species diversity (Villéger et al. 2008). FEve, FDiv and FDis are weighted indices for which we used biomass. FEve describes how regular species biomass distributes in the functional space; it is independent of FRic and has a scale

Table 1. Summary of the main anthropogenic impacts and climate events occurring in the south arm of the Mondego estuary during the study period (1993–2006) with reference to the environmental and intertidal benthic community effects and with the possible reasons for the observed impacts in the community

Pressures/events	Time period	Environmental effects	Measured effects	Benthic intertidal invertebrate community: Possible causes
Pre-mitigation Eutrophication, upstream areas silted up	Ongoing since 1980s, culminating with macroalgal blooms in 1993	High nutrient discharges and high water residence time (wk); macroalgal blooms in spring 1993, sediment organic enrichment and sediment anoxia with the macroalgae crash by end of summer 1993 (Cardoso et al. 2010); contribution to long-term decline of seagrass beds, from 1.5 ha in the 1980s to 1.6 ha in 1993 (Dolbeth et al. 2007, 2011)	Overall decline in species number and production; increase production of small, r-strategist species during macroalgal blooms in the sandflat area (Dolbeth et al. 2011, 2014)	Habitat loss; during algal blooms, higher habitat heterogeneity, organic matter and food, favouring tolerant species; with algal crash, fauna mortality due to anoxia
Mitigation measures	1998	Re-establishment of the south arm riverhead connection (1 m ²) improving freshwater circulation, lower water residence time (d) and nutrient loading reduction (Cardoso et al. 2010); macroalgal blooms ceased and seagrass beds started to recover from a minimum area of 0.02 ha in 1997 (Cardoso et al. 2010, Neto et al. 2010)	Not measured in 1998, but from this year onwards tendency for gradual recovery: slight species number increase, but evenness values higher (Grilo et al. 2011), gradual increased production of K-strategists species (Dolbeth et al. 2011, 2014). This tendency was slowed down by occurrences of extreme weather events in 2000 and 2003–2005	
Post-recovery I Lowest seagrass bed biomass and extension	1999	Habitat loss, long-term decline of seagrass beds (Cardoso et al. 2010, Dolbeth et al. 2011)	Huge decrease in species number and benthic community production compared to pre-mitigation period (Dolbeth et al. 2007)	Habitat loss
Extreme floods	Winter 2000/2001	Sudden drastic decrease in salinity and higher freshwater runoff (Dolbeth et al. 2007)	Species number (Grilo et al. 2011) and benthic production (Dolbeth et al. 2007, 2011) decreased compared to 2000	Fauna displacement due to sudden high freshwater flow
Post-recovery II Heat waves in Portuguese territory	Summer 2003 and 2005	Huge and punctual increases of atmospheric temperature, translated into higher estuarine water temperature (Dolbeth et al. 2011, Grilo et al. 2011)	Species richness declined to lowest values during study (Grilo et al. 2011) and huge decreases in benthic community production compared to previous years (Dolbeth et al. 2011)	Increases in temperature beyond benthic species tolerance limits; higher desiccation risk for intertidal fauna
Drought and extreme drought	2004 and 2005	Lower freshwater flow and increases in salinity (Niyitrai et al. 2012); 2005 was the driest year in the last 60 yr (www.ipma.pt)	Decrease in benthic community production (Dolbeth et al. 2011)	Higher desiccation risk; may favour appearance of marine species
South arm riverhead connection; enlargement of the Gala Bridge	Spring 2006	Reduction of residence time and higher freshwater runoff (Neto et al. 2010); water confinement near the Gala Bridge, with decrease in water transparency (Verissimo et al. 2012a)	Decrease in total biomass and density (mainly <i>Cerastoderma edule</i> and <i>Peringia ulvae</i>) (Verissimo et al. 2012b)	Fauna displacement due to the differences in hydrodynamics and mortality due to possible lower O ₂ due to a decrease in transparency

Table 2. Traits and their categories used in this study, with indication of the rationale for the selection and expectations with regard to disturbance impacts

Traits	Trait categories	Rationale
Size	Measured as the average body mass in mg ash-free-dry mass (AFDM) for each species	Size defines and correlates with other life-history traits and mediates structuring interactions. Small-bodied invertebrates may characterize environments with high instability, a consequence of environmental/anthropogenic pressures imposed on the organisms.
Life span	Here defined as the maximum life span for each species and measured in months	Previous studies showed shifts from large slow-growing species with longer life spans to less vulnerable faster-growing species, facing disturbance.
Living position on the substratum	Epifauna 0–2 cm depth 2–5 cm depth >5 cm depth	Important to determine vulnerability to hydrodynamic stress at the sediment–water interface, exposure to extreme temperatures and to risk of predation, as deeper-living species are potentially less subjected to those impacts related to hydrodynamics, temperature and predation
Mobility	Fixed tube dweller Limited movement Slow, free movement through the sediment matrix Free movement via burrow system	Here defined as the propensity to move through the sedimentary matrix (Queirós et al. 2013). Relates to resource dynamics (nutrients, sediment and space) and changes in their availability, capture and use, influencing the biogenic mixing depth
Feeding guild	Strictly deposit feeders Strictly herbivores Deposit/grazers Suspension/deposit Omnivores	Reflects the trophic structure, distribution of resources and how organisms adapt to the habitat
Reproduction frequency	Annual protracted (breeds over an extended or drawn out period ^a) Annual episodic (breeds in one or more discrete periods initiated by a trigger ^a) Semelparous (breeds once then dies ^a)	Reflects the investment in reproduction. Species with annual protracted frequency increase their chances of survival in unstable environments. In opposition, semelparous species concentrate their energy to produce the fittest offspring

^aMarLIN definition (www.marlin.ac.uk/biotic/)

between 0 and 1 (Villéger et al. 2008). FDiv indicates the degree of resource differentiation and predominance of species with extreme traits; it is also independent of species richness and FRic and also is scaled between 0 and 1 (Villéger et al. 2008, Mouchet et al. 2010). FDis measures the biomass-weighted deviation of species trait values from the centre of the functional space filled by the community; it has no upper limit and it is expected to decrease with disturbance (Laliberté & Legendre 2010, Mouillot et al. 2013).

To find the relation between annual secondary production and functional diversity, we first tested a linear regression. After detecting patterns in the residuals and inspection of data, we applied generalized linear model (GLM) with gamma distribution, which is adequate for continuous and positive values (Zuur et al. 2009). We performed 3 models to test whether benthic production was explained by the functional identity hypothesis, hereafter named mass ratio hypothesis (using CWM), by the complementarity

hypothesis (using FRic, FEve, FDis, FDiv), or by a combination of both hypotheses. For the mass ratio hypothesis, we first considered the Spearman correlations between the CWM for each trait category in order to define life-history groups as suggested by Verberk et al. (2013). First, we checked for trait combinations among all possible trait categories (positive correlation > 0.85); next we defined life-history groups with the dominant trait combinations in the community. The relative frequency of CWM from these life-history groups was used as the explanatory variable to test the mass ratio hypothesis. For the definition of the life-history groups with the quantitative variables size and life span, we also considered categories to provide an identity of the class with the best correlation among the other categories.

Prior to the analyses, collinear explanatory variables were removed after inspection of the correlation between predictor variables and the variation inflation factor (VIF > 3 was used to detect collinear variables; Zuur et al. 2009). For all models, we

included interactions between site and the other explanatory variables because all are expected to vary with site, except when site was a collinear variable. Model selection inference was based on the second-order corrected Akaike information criterion (AICc) to obtain the best combination of variables that explain the largest amount of variance taking into account the sample size (Barton 2014). Graphical validation was used to verify the underlying statistical assumptions of GLM (Zuur et al. 2009). The independence assumption was also verified with an autocorrelation function to check for patterns among residuals. Data analyses were conducted using the R libraries FD (Laliberté & Legendre 2010), Hmisc and MuMIn (<http://cran.r-project.org/authors/1332>) implemented in R freeware (R Development Core Team 2012).

In addition, the variation of the trait composition (both identity and complementarity) was analysed against site and the periods mentioned above, and their significance was tested with a 2-way ANOVA. Whenever the assumptions of ANOVA were not met (after graphical validation, Zuur et al. 2009), a 2-way ANOSIM with replicates was applied using a Bray-Curtis resemblance matrix (Clarke et al. 2014).

RESULTS

CWMs and life-history strategies

The dominant CWMs for the trait categories over the study period were: species living up to 2 cm depth and below 5 cm for the trait living position; species that can behave both as deposit feeders and grazers, and species that can behave both as suspension and deposit feeders and omnivores for feeding guilds; limited movement and slow, free movement in the sediment for mobility; and annual protracted (breeds over an extended period) for reproduction frequency. Regarding the quantitative traits, the CWM for size varied between (mean \pm SD) 9.8 ± 2.3 and 5.6 ± 1.7 mg AFDM for the sandflat and seagrass sites, respectively; and for life span, between 43.1 ± 7.2 and 32.4 ± 5.0 mo, respectively. Size and life span correlated positively with at least one of the dominant categories (Table S2 in Supplement 1 at www.int-res.com/articles/suppl/m539p033_supp.pdf). For definition of the life-history groups based on positive Spearman correlations (>0.85), we also considered categories for the size and life span to identify the best correlation with the other trait categories. First, we checked and defined

the trait category combinations among all CWMs (Fig. 1, Table S2). From these combinations, we selected the dominant trait categories and defined 3 distinct life-history groups (Fig. 1). The first group (LH1) combined small individuals, with a short life span, mostly epifauna that could move slowly in the sediment and could behave either as grazer or deposit feeder. The second group (LH2) was composed of large individuals, with a long life span, behaving as suspension or deposit feeders, limited in their movement, which could be buried into the sediment below 5 cm depth (Fig. 1). Finally, intermediate-sized omnivores with a 2 to 5 yr life span composed the third group (LH3). Some of these species moved freely into the sediment and had semelparous reproduction; however, these characteristics were not dominant and therefore not included in the life-history group. We used the relative frequency of the CWM from these life-history groups to test the mass ratio hypothesis for production.

Considering the spatial and temporal trends, LH1 was dominant in the seagrass bed (ANOSIM, $R = 0.89$, $p < 0.05$), especially in the Pre period relative to Post I (Fig. 2a, see ANOSIM pairwise comparison in Supplement 2 at www.int-res.com/articles/suppl/m539p033_supp.pdf). A positive relation occurred between production and LH1 (Fig. 2b). LH2 was dominant in the sandflat (ANOSIM, $R = 1$, $p < 0.05$). In the seagrass bed, LH2 showed an increasing tendency in latest years (Post I and II, Fig. 2c), although this tendency was not statistically significant (Supplement 2). The relationship with production was negative up to a frequency threshold (around the median), with a slight tendency to increase afterwards (Fig. 2d). LH3 had higher biomass frequency in the sandflat and limited occurrence in the seagrass site (Fig. 2e, ANOSIM, $R = 0.667$, $p < 0.05$). Its relationship with production differed between sites, although there was tendency for a decrease with time at both sites (Fig. 2f).

Functional diversity indices

FRic was highest in the Pre period for seagrass, it decreased in the Post I and Post II periods (ANOVA: $p < 0.001$, Supplement 2), with high variability in Post II (from 1999 to 2002). FRic was lower in the sandflat than in seagrass in Pre (ANOVA: $p < 0.001$), but with a tendency to increase during the study period, particularly in the Post II period (Fig. 3a). FRic increased with increasing benthic production, but the trend was not linear (Fig. 3b), nor was it statistically sig-

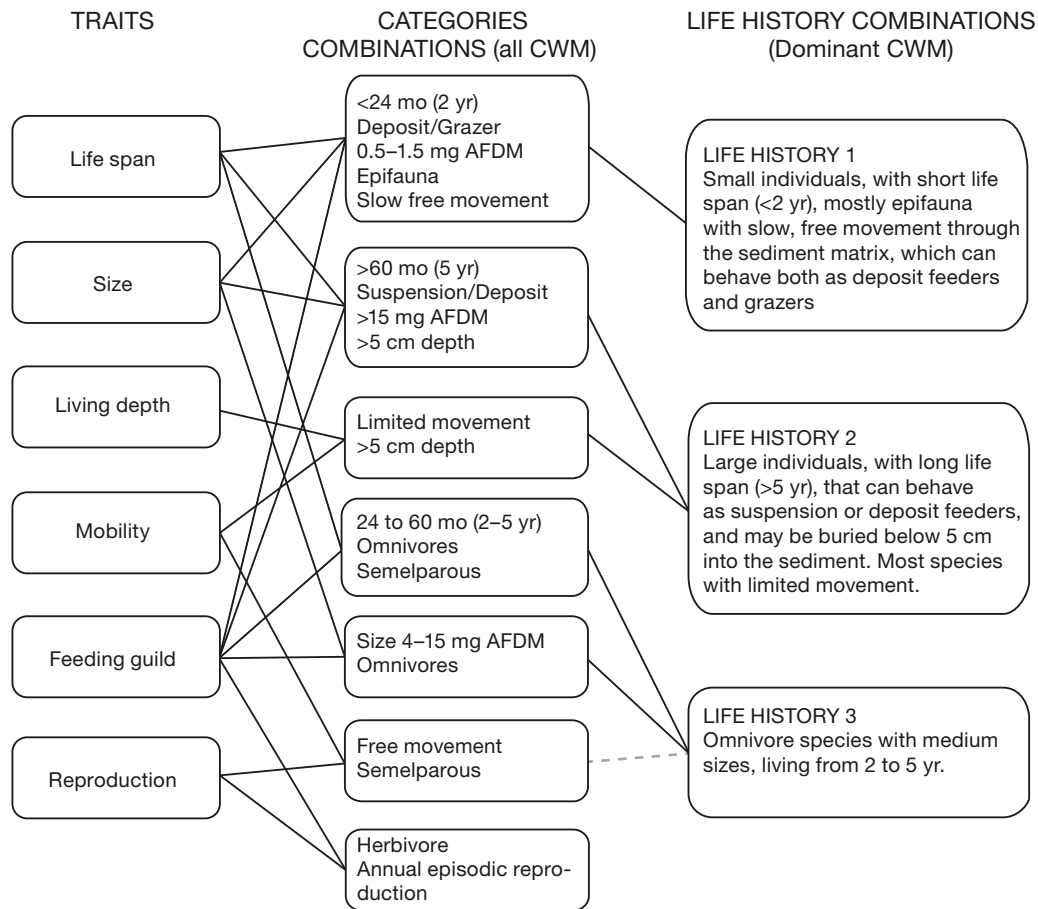


Fig. 1. Trait combinations based on the correlations of the community weighted means (CWMs) for the traits categories. Category combinations were based on positive Spearman correlations (>0.85) between the CWMs for all trait categories; life-history combinations were defined based on the trait combinations for the dominant CWM trait categories. AFDM: ash-free dry mass

nificant, according to the best model inference (Table 3).

FEve values were all lower than 0.5 and slightly higher for seagrass (Fig. 3c). In the Post I period there was high variation in seagrass, due to the extremely low FEve observed in 2001 (FEve = 0.093). Nevertheless, no statistical differences were found between sites and periods (Supplement 2). A positive relationship with benthic production seemed to occur (Fig. 3d), although this was not significant.

Both FDis and FDiv were lowest for seagrass in the Pre period, increasing afterwards (Fig. 3e,g). However, statistical differences were found for both sites and when comparing Pre with the remaining Post I and Post II (FDis: ANOVA, $p < 0.05$; FDiv: ANOSIM, $R \approx 0.36$, $p < 0.05$, Supplement 2). FDiv values were high in both sites (>0.8) and higher in the sandflat than in the seagrass. FDiv increase was related with decreasing production (Fig. 3f), but, again, was not significant (Table 3).

Production and functional diversity models

For the mass ratio hypothesis, after removing collinear variables and model selection, we found a single significant predictor of benthic production: LH1 (small epifauna with a short life span, free movement, grazers or/and deposit feeders), explaining 73.7% of total variation (Table 3). For the complementarity effect hypothesis, both FDis and site were significant predictors. Together, these predictors explained 68.2% of total variation, yet most of the variability was explained by site (51.3%, Table 3). A fitted line was added to the significant predictors of both models to clarify the variation trends (Fig. 4). Production increased with LH1 frequency increase, and this relation was not linear (Fig. 4a). The relationship of FDis with benthic production seemed negative (Fig. 4b). A different pattern seemed to emerge depending on the site (Fig. 3h); however, the interaction FDis \times Site was not significant (Table 3). A fitted line

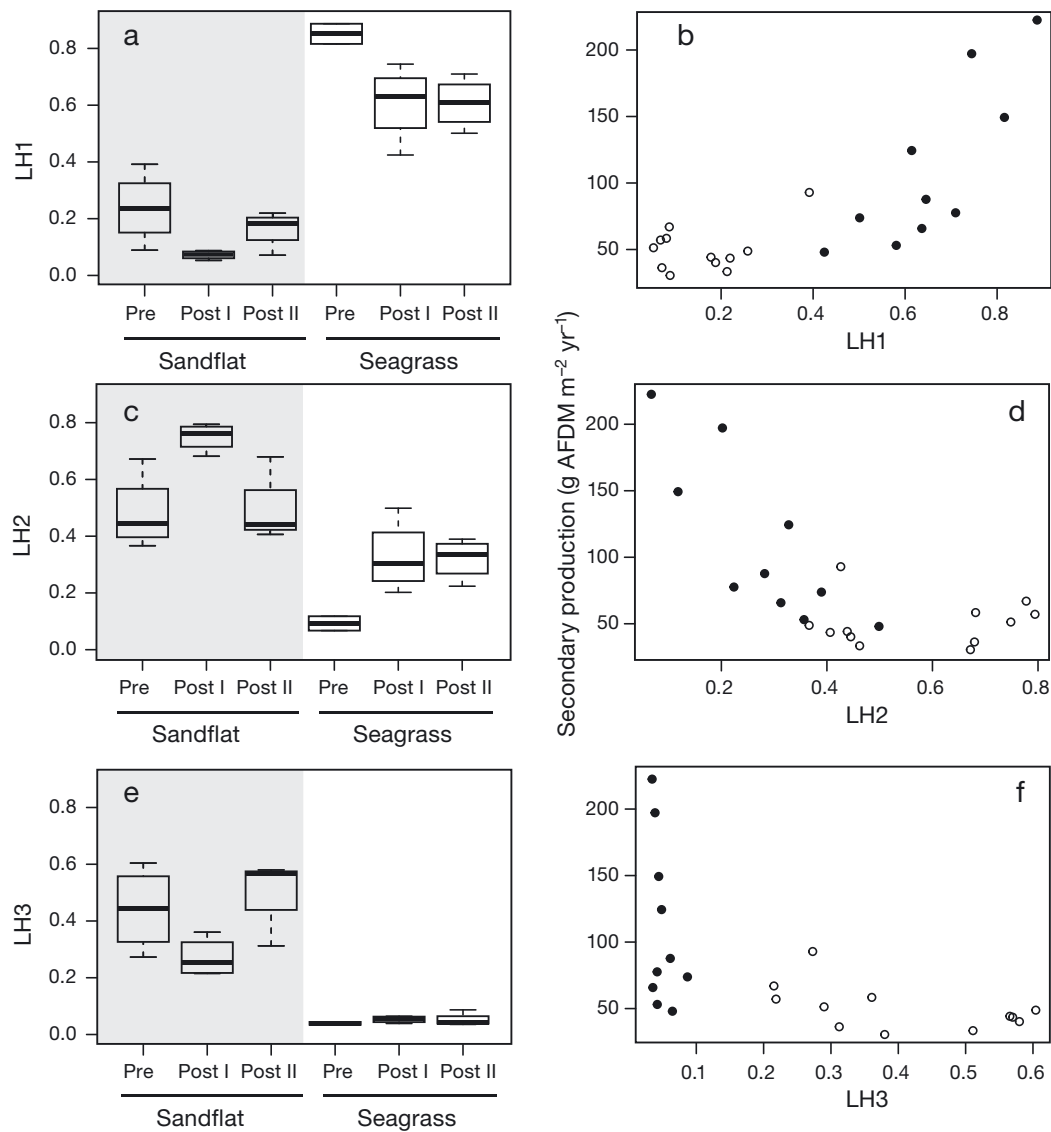


Fig. 2. Boxplots of the variation of CWMs for the 3 life-history (LH) groups defined in Fig. 1 in the seagrass and sandflat sites during the study period (Pre: 1993–1996, Post I: 1999–2002, Post II: 2003 to 2006) and variation in secondary production as a function of the respective LH group (frequency). The middle line of the boxplots indicates the 50th percentile; extremities of the box are the 25th and 75th percentiles; the maximum length of each whisker represents 5th and 95th percentiles; outliers are shown individually. Filled circle: seagrass; open circles: sandflat

clarified the negative non-linear (Fig. 4b) and weak relation between FDis and production (only 17% of variation explained, Table 3). Regarding site—also a significant predictor in the complementarity model—production was higher in seagrass than in the sandflat (Fig. 4c).

Finally, we combined the significant predictors from the previous models into a third model, testing both identity and complementarity. After removing collinear variables and model selection, the final best model is composed of a single variable, LH1, i.e. the same as in the mass ratio hypothesis model (Table 3).

DISCUSSION

Benthic production versus functional diversity

The Mondego estuary resembles other transitional ecosystems regarding the type of anthropogenic disturbance (e.g. eutrophication, hydro-morphological changes due to river embankment) and weather extremes (e.g. floods, heat waves, droughts) occurring during the study period. The community production data allowed testing hypotheses about the effect of environmental disturbance for the functioning of

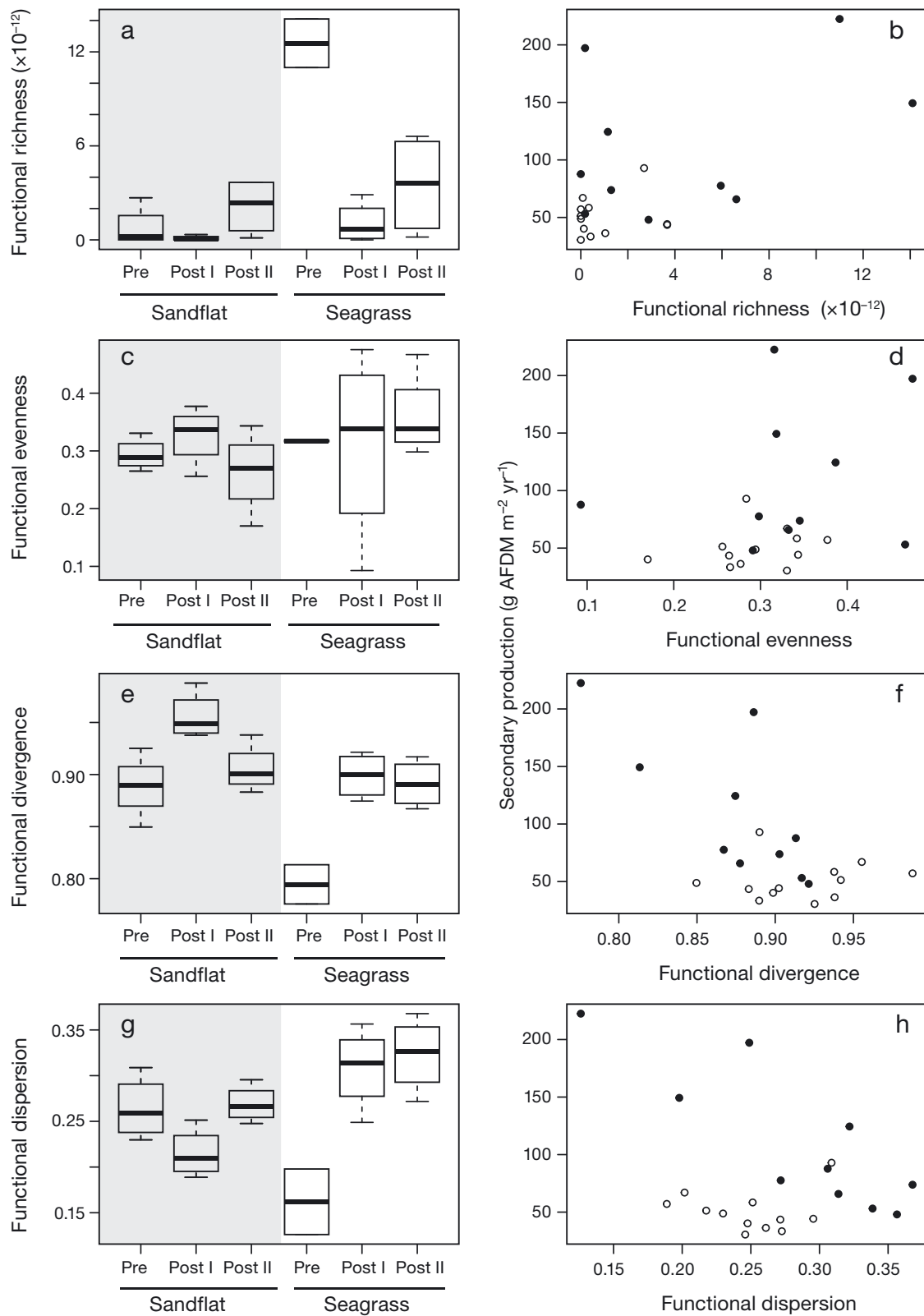


Fig. 3. Boxplots of the variation of functional richness, functional evenness, functional divergence and functional dispersion in the seagrass and sandflat sites during the study period (Pre: 1993–1996; Post I: 1999–2002; Post II: 2003–2006) and variation in secondary production as a function of the respective functional diversity indices. The middle line of the boxplots indicates the 50th percentile; extremities of the box are the 25th and 75th percentiles; the maximum length of each whisker represents 5th and 95th percentiles; outliers are shown individually. Filled circles: seagrass; open circles: sandflat

Table 3. Significant results for generalized linear models of benthic secondary production and functional diversity, with indication of the tested model and final significant model. LH: life history group; LH1: small epifauna with short life span, free movement, grazers and/or deposit feeders; LH2: large long-lived burrowing species with limited movement, suspension and/or deposit feeders; FRic: functional richness, FEve: functional evenness; FDis: functional dispersion; FDiv: functional divergence. Initial model tested after removing collinear variables

	p	% variance explained
Mass ratio hypothesis		
Initial tested model:		
<i>Benthic production</i> = $f(LH1 + LH2)$		
LH1	<0.001	73.7
Significant final model: <i>Benthic production</i> = $f(LH1)$		
		73.7
Complementarity effect hypothesis		
Initial tested model:		
<i>Benthic production</i> = $f(FRic \times Site + FEve \times Site + FDis \times Site + FDiv \times Site)$		
FDis	0.002	16.9
Site	<0.001	51.3
Significant final model: <i>Benthic production</i> = $f(FDis + Site)$		
		68.2
Combining mass ratio and complementarity		
Initial tested model:		
<i>Benthic production</i> = $f(LH1 + FDis)$		
LH1	<0.001	73.7
Significant final model: <i>Benthic production</i> = $f(LH1)$		
		73.7

coastal/transitional waters, which is among the most challenging topic within integrated coastal zone management. In this respect, trait-based measurements are generally better predictors of ecosystem functions/processes than species richness and abundance (Díaz et al. 2007, Griffin et al. 2009, Gagic et al. 2015). Indeed, species are not equal in their effects on ecosystem functioning (Haddad et al. 2008, Mouchet et al. 2010, Mouillot et al. 2013), and processes/functions may be chiefly determined by the trait identity of a dominant species (i.e. the mass ratio hypothesis, Grime 1998), by the trait dissimilarity in the community (i.e. complementarity hypothesis) or by a combination of both (e.g. Díaz et al. 2007, Griffin et al. 2009). We found evidence that both hypotheses explained part of the benthic invertebrate community production. However, the mass ratio effect model, tested with the dominant life-history groups, explained a higher amount of the production variability than the complementarity effect model. In support of this hypothesis, when we tested the combined effect of mass ratio/identity and complementarity in a third model, the final significant model was the same as the mass ratio/identity hypothesis. Other studies comparing the relationship between functional diversity and ecosystem processes also found the mass ratio/functional identity to have a greater effect (i.e. terrestrial plants and fauna; Díaz et al. 2007, Roscher et al. 2012, Gagic et al. 2015).

The mass ratio model had a single life-history group predicting 74% of production, composed of small epifauna with a short life span, free movement, grazers and/or deposit feeders, i.e. LH1. These functional characteristics, generally associated with an opportunist strategy (discussed below), made the largest contribution to the ecosystem biomass, therefore exerting a major effect on ecosystem secondary production. In addition, secondary production was clearly higher in the seagrass site, making the site also an important determinant for estuarine production in the complementarity hypothesis model. This was expected if taking into consideration the natural productivity of vegetated environments compared to non-vegetated ones (Duffy 2006, McArthur 2006, Dolbeth et al. 2012) and the observed differences in functional diversity among sites. Below, we expand on these findings, reflecting on the system's life-history functional groups, functional dissimilarity and how these have changed among sites and with disturbance.

Functional identity characterization of benthic communities

The intertidal communities of the Mondego estuary resemble those of other intertidal systems in terms of species composition and abundance pat-

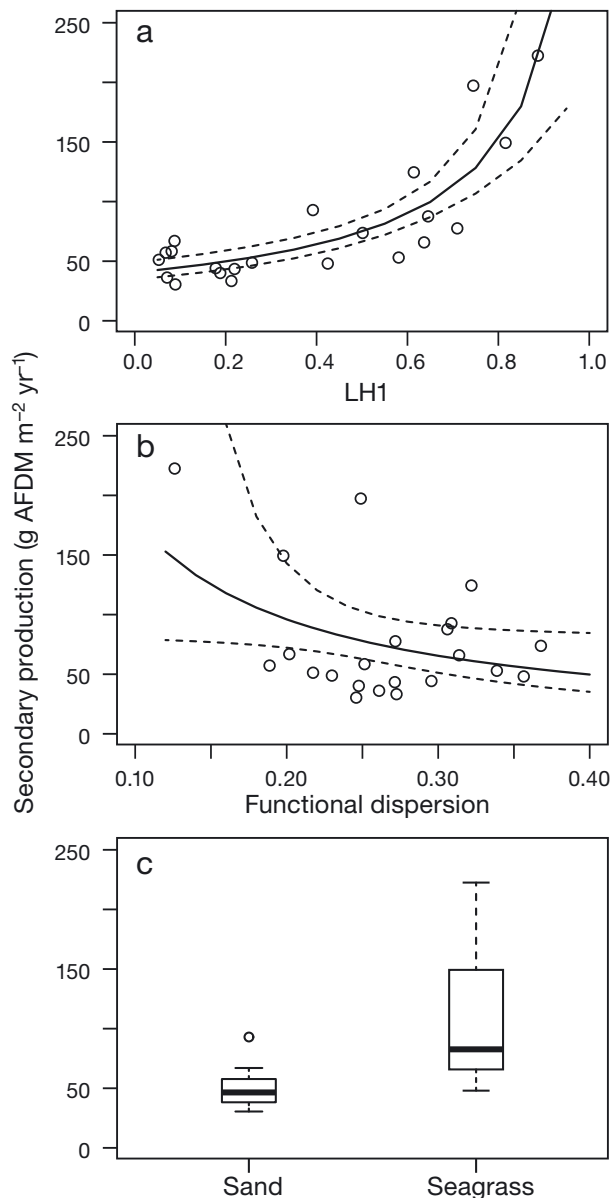


Fig. 4. Benthic community secondary production (g AFDM m⁻² yr⁻¹) variation in relation to the significant predictors in the mass ratio and complementarity effect models. Fitted lines from the GLM model were added to the data plot to clarify variation patterns of the explanatory variable with benthic production. LH1: life-history group 1 (small epifauna with short life span, free movement, grazers and/or deposit feeders). The middle line of the boxplots in (c) indicates the 50th percentile; extremities of the box are the 25th and 75th percentiles; the maximum length of each whisker represents 5th and 95th percentiles; outliers are shown individually

terns (e.g. long-lived bivalves, epibenthic gastropods and amphipods, several burrowing polychaetes, McLusky & Elliott 2004). Habitat filtering is the dominant process determining species coexistence, with biotic interactions presumably important

within a subset species with specific traits (Dolbeth et al. 2013). However, in communities, traits are often inter-correlated due to ecological and evolutionary linkages (e.g. trade-offs, synergies), which reflect different strategies to cope with habitat filters (Winemiller 2005, Dolédec & Statzner 2008, Verberk et al. 2013). The adaptive value of a trait may only be expressed in combination with other traits, as a response to disturbance, highlighting the importance of considering 'life-history groups' in trait-based analyses (Verberk et al. 2013). These life-history groups and strategies have been traditionally explored with life-history theories, such the r-K continuum, Grime's CRS plant strategies or the universal adaptive strategy theory as a progression of CRS for other forms of life (Grime & Pierce 2012), the adversity selection (Greenslade 1983) and the Winemiller and Rose model (Winemiller 2005).

In the present study, we inspected the functional composition of the Mondego intertidal invertebrate communities, aiming to understand how disturbance or habitat influence benthic production by selecting species with the best fitness for the environmental changes in the estuary (response traits). Other studies relating marine invertebrate production to traits have not identified a clear effect between a single or a group of traits and production (Bolam & Eggleton 2014). With the present approach we identified the best combination of traits to cope with disturbance and associated production levels, i.e. LH1. Most of the benthic community belonged to 3 functional life-history groups, suggesting 3 primary strategies to cope with disturbance as debated by Grime & Pierce (2012) in another context. These strategies, reflecting a higher resilience to disturbance, were associated with different production levels. Generally, the life-history strategy group of small, short-lived epifauna species, behaving either as grazers or deposit feeders and moving slowly through the sediment (LH1) was associated with higher production levels, which generally occurred in the Pre period and at the seagrass site. These species also had annual protracted reproduction, as did most of the Mondego community (the dominant trait category in the estuary). Small size, short life span, protracted reproduction, relative mobility in the sediment and deposit feeding reflect high opportunism (McLusky & Elliott 2004). The combination of these traits with epifauna and grazers probably reflected the particular characteristics of the seagrass area, which conveys protection to predators and epiphytic algae. In addition, this opportunist behaviour would thrive in environments where additional resources are provided, which occurred in

both seagrass and sandflat for a short period during the eutrophication phase (in 1993, Pre), provided by the additional habitat patches and food resources from the macroalgae blooms. Generally, these traits would be highly successful for an unpredictable environment, subjected to a disturbance source that provides additional, but ephemeral, food resources. This strategy translated into large populations of small-size individuals, reflecting the higher production.

As an opposite strategy, the large, long life-span species, with limited movement, and that can bury deep into the sediment and behave as suspension or deposit feeders (LH2) were generally associated with low production. This strategy occurred mainly in the sandflat, but with increasing frequency for both sites after the mitigation measures in the estuary. Species with this strategy also had annual protracted reproduction. The bare sandflat is naturally more exposed to predation. As a result, a strategy of burying deep into the sediment and the possibility of suspension feeding to acquire food seems highly advantageous to cope with the potential higher predation pressure. Over the long term, species with this strategy concentrate efforts in increasing their body mass and live longer, although their reproduction frequency yet denotes opportunistic behaviour. Such functional attributes are generally associated with an increasing predictability in the spatial–temporal variability of the available resources (Winemiller 2005).

In the third functional life-history group (LH3), the species had an intermediate size and life span and were omnivores, suggesting greater possibilities for using the available food resources. In addition, some species could move freely in the sediment, reflecting greater possibilities for using available resources, and had semelparous reproduction, denoting a higher energy investment in the offspring. Such characteristics provide a higher competitive advantage in stable environments. This life-history group occurred mainly in the sandflat with a slight tendency to increase in the seagrass site with the estuary recovery, after 1998.

Overall, the distribution frequency of the 3 life-history groups through time suggests a shift from highly opportunist, mostly density-independent driven populations, which would thrive in unstable environments via a rapid completion of their life cycle, towards more stable K-strategist populations and species with higher competition advantage, which maximize resource acquisition. In terms of production, this shift translated into a decrease in production, due to a higher investment in body mass, repro-

duction and life span. However, over the long term, this type of production from the large, long-lived species may be more sustained, potentially fuelling a richer trophic chain (e.g. Emmerson 2012), and contributing to improve ecosystem functioning (via other functions, such as nutrient dynamics as a result of increased bioturbation, e.g. Queirós et al. 2013).

Functional dissimilarity trends

Functional richness (FRic) was higher in the seagrass beds, particularly during the Pre period, and tended to change positively with production. This result may be seen as an indirect effect of the seagrass bed, which provides habitat heterogeneity, food and shelter for the benthic fauna and therefore, higher functional diversity (Boström et al. 2006, Duffy 2006). However, the majority of species belonged to the opportunist life-history group, translating into lower functional dispersion (FDis) and divergence (FDiv) during the Pre period. Species shared similar functional characteristics and could compete for the same resources during that period (Mouchet et al. 2010). Nevertheless, the abundance of resources available in the system, probably propagated by the algal blooms, resulted in an increase in population and secondary production during that period. FRic showed an increasing trend in the sandflat after the mitigation measures in the estuary, also suggesting a richer community. This result is consistent with the recovery of the environmental condition of the estuary from the anthropogenic impacts (Cardoso et al. 2010, Neto et al. 2010, Dolbeth et al. 2011).

Functional evenness (FEve) was slightly higher in the seagrass beds, suggesting a more even distribution of species and their biomass in the functional space (Mouchet et al. 2010, Mouillot et al. 2013). The flood in 2001 led to uneven biomass distribution among traits and to the lowest FEve of the study period. This negative effect of the flood was only detected with FEve. We also found a tendency for a positive relation between FEve and production, probably resulting from a more efficient utilization of the available resources (Mason et al. 2005). In contrast, a lower FEve would mean that some parts of niche space are not used, resulting in decreased production (Mason et al. 2005).

Functional divergence (FDiv) was generally high, suggesting a high degree of niche differentiation and low resource competition (Mason et al. 2005), a result already outlined by Dolbeth et al. (2013). FDiv was slightly higher in the sandflat, as most species be-

longed to 2 distinct life-history groups and therefore fused the available resources in different ways (i.e. different functional space). Regarding secondary production, there seems to be a negative relation with increasing FDiv, which for our case study does not represent a decrease in the efficiency of resource use, as suggested by Mason et al. (2005), because the highest production was due to a single and highly opportunist life history group, i.e. LH1.

Finally, FDis was negatively correlated with production in the seagrass beds, which might be associated with a disturbance effect (Mouillot et al. 2013). In the sandflat, FDis was slightly lower than in the seagrass, but the relationship with production was not clear (except for during the Pre period). This may be because there is less variety of functions and associated biomass, translating in to low dispersion (Laliberté & Legendre 2010).

CONCLUSIONS

We found evidence that functional diversity explained a major part of the secondary production variation (74 %) in an estuarine system subjected to different sources of disturbance. The functional identity/mass ratio explained production better than the complementarity effect, implying that the production levels were dependent on the biomass from a particular group of functional characteristics. This group was essentially characterized by an opportunist strategy, which included small species, with a rapid completion of their life cycle, potentially able to use additional resources in a quick and effective way. This life-history group was associated with high production levels. Nevertheless, this sort of production sustained by large numbers of opportunist species may harm the functioning of the ecosystem, because functional diversity also decreases. Over the long term, with the estuarine recovery from anthropogenic disturbance, functional diversity seems to be increasing in the estuary due to a more even biomass distribution among different functional groups.

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