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LINKS BETWEEN DEEP-SEA RESPIRATION AND COMMUNITY DYNAMICS

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Abstract

It has been challenging to establish the mechanisms that link ecosystem functioning to environmental and resource variation, as well as community structure, composition and compensatory dynamics. A compelling hypothesis of compensatory dynamics, known as 'zero-sum' dynamics, is framed in terms of energy resource and demand units, where there is an inverse link between the number of individuals in a community and the mean individual metabolic rate. However, body-size energy distributions that are non-uniform suggest a niche advantage at a particular size class, which suggests a limit to which metabolism can explain community structuring. Since 1989, the composition and structure of abyssal seafloor communities in the northeast Pacific and northeast Atlantic have varied inter-annually with links to climate and resource variation. Here, for the first time, class and mass-specific individual respiration rates were examined along with resource supply and time series of density and biomass data of the dominant abyssal megafauna, echinoderms. Both sites had inverse relationships between density and mean individual metabolic rate. We found fourfold variation in echinoderm respiration over inter-annual timescales at both sites, which were linked to shifts in species composition and structure. In the north-eastern Pacific, the respiration of mobile surface deposit feeding echinoderms was positively linked to climate-driven particulate organic carbon fluxes with a temporal lag of about one year, respiring about 1-6% of the annual particulate organic carbon flux.

Keywords: compensatory dynamics, zero-sum dynamics, respiration, biogeochemistry, carbon, benthic, deep sea, echinoderm

Introduction

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In recent decades, long-term trends in ocean environmental variables have been identified including warming, acidification, and productivity (Orr et al. 2005, Gehlen et al. 2007, Frölicher et al. 2009, Keeling et al. 2010, Steinacher et al. 2010). Understanding the relationships between environmental drivers and ecological variation over time in the deep sea comes from relatively few records (Glover et al. 2010, Ruhl et al. 2011). Links have been found between climate-driven shifts in sea surface productivity, sinking particulate organic carbon (POC) flux and deep-sea biomass, density, and community composition over periods as short as months (Ruhl et al. 2008, Smith et al. 2008, Billett et al. 2010, Moeseneder et al. 2012). Nevertheless, improving estimates of how the structural and functional attributes of benthic deep-sea systems will respond to a changing climate require improved understanding of ecological mechanisms and biogeochemical processes.

Assemblages of benthic megafauna at Station M (Sta. M) in the northeast Pacific and the Porcupine Abyssal Plain (PAP) in the northeast Atlantic have undergone substantial changes in their abundance and composition at the seafloor since 1989 (Billett et al. 2010, Ruhl 2008). Echinoderms dominate the mobile benthic megafauna (i.e. for marine benthic fauna this includes those with mass of about 1g wet weight or more) at these sites (Billett et al. 2010, Ruhl 2008). The marked dynamics provided an opportunity to investigate mechanisms that may relate to changes in composition and structure, and their connection to biogeochemical processes and ecosystem functions.

One of the key sets of mechanisms that are thought to control community dynamics are those relating to compensatory dynamics and resource limitation. The hypothesis of 'compensatory dynamics' posits that when resource levels are fixed, total abundance is constant, and increases in abundance of one taxon are compensated for by reductions in another (Hubbell

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2001, Ernest and Brown 2001, Houlahan et al. 2007). In real systems, however, evidence for such interspecific compensatory dynamics of abundances is limited. Specifically, little evidence exists for >50% negative covariance of abundance between various taxa expected from random interactions (e.g. Houlahan et al. 2007). Indeed, interspecific compensation can occur without negative density covariance, such as when all species might increase in abundance in response to a resource increase, but change their relative rank dominance because of differential resource use, or when taxa of different size change abundance relative to each other where there is an inverse relationship between density and mean individual metabolic rate during different parts of a timeseries.

'Zero-sum' dynamics posits a compensation hypothesis that directly examines energetic compensation (e.g. Ernest et al. 2008, 2009). Respiration is a key measure to frame ecological variations in a currency that accounts for the fact that resource use rates are dependent, in part, on body size, where larger fauna have lower mass-specific respiration rates than smaller fauna. A testable hypothesis of zero-sum theory is that given a fixed resource input and constant temperature, the total number of individuals (N) in a community is inversely related to the mean individual metabolic rate (B), where $N \alpha B^{-1}$(Fig. 1). Such an inverse relationship was observed in, for example, tropical forest data (Ernest et al. 2009). It follows from that hypothesis that if resources increase (i.e. $[R]/B \alpha N$, where R is available resource), that would allow an increase in density at a given mean individual respiration rate (or any combination of increased density and mean individual metabolic rate that equates to the increased resource). Fluctuations in resources over time could thus manifest as residuals from a best fit relationship of the whole time period where positive residuals relate to increased resource levels (Fig. 1).

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In a related thread of ecological theory, rank-abundance distributions (RADs) are believed to be an indicator of biodiversity that describes the abundance and dominance of each taxa relative to the others and is indicative of resource use by each rank (Motomura 1932, MacArthur 1957, Whittaker 1965, Sugihara et al. 2003, Thibault et al. 2004). Another consequence of zero-sum dynamics is that as communities shifted to lower mean individual respiration rates (more smaller individuals), there would tend to be an increase in relative dominance of the smaller individuals and decrease in evenness (Fig. 1). Thus, examination of rank-energy demand distributions provides a more direct measure of resource partitioning than abundance measures by also accounting for such allometric scaling.

Substantial challenges remain in reconciling such strictly size based theories with niche theories that necessitate other life history traits such as food selectivity differences at a given body size. A strictly energetic view of community structuring suggests a uniform relationship between mean individual size and the resources used at each size class. However, multimodal distributions have been found in body-size energy distributions suggesting a limit to which body size can explain community structuring (e.g. Ernest 2005), whereby some specific sizes may have niche advantages in a given habitat.

How variation in the structure of echinoderm assemblages influences their net functional role is poorly understood. One of the key ecosystem functions of benthic fauna is to remineralise POC that sinks to the seafloor (food supply) through the processes of respiration and nutrient regeneration. Dynamics of sediment community oxygen consumption (SCOC) is an indicator of the temporal variation in food demand. However, because of the nature of the respiration chambers typically used for studying SCOC, the respiratory demands of megafauna assemblages previously have not been systematically measured in examining food supply and demand.

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Here we present the first assessment of long-term variation in the respiration of echinoderm assemblages from deep-sea habitats to provide insights into the mechanisms driving their structure, dynamics and biogeochemical function. We examined if total respiration of the echinoderm assemblage is correlated with indicators of community composition and structure (CCS). We tested predictions of related hypotheses of compensatory dynamics (CD), zero-sum dynamics (ZSD), and multimodal distribution (MMD) in explaining patterns of assemblage structure, dynamics and functional role:

CD: With no long-term trend in food (resource) levels over time, the sign of covariance between pairs of taxon-specific respiration is, on average, more negative than positive among all pairwise combinations;

ZSD_1: Mean individual respiration rate is inversely related to total density while mean individual respiration rate is positively related to evenness of the echinoderm assemblage;

ZSD_2: Net respiration of the echinoderm assemblage is positively correlated with temporal variation in food supply;

ZSD_3: Residuals in a regression between mean individual respiration rate and total echinoderm density are positively related to resource availability; and

MMD: Multimodal distributions are present in distributions of energy use across body sizes.

The assemblage was also quantified in terms of food supply and demand, feeding behavior, and the contribution to remineralisation of organic carbon on the deep seafloor.

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Methods

This study combined data from several previously published studies including data from benthic trawling, analyses of feeding guilds, photographic transects of the seafloor, relationships between individual body size and respiration rates and POC flux data from *in situ* sediment trap measurements. We calculated respiratory demand of the echinoderm assemblage for the two abyssal echinoderm communities by multiplying mass- and class-specific respiration rates by mean individual biomass and observed density (individuals per unit area) for each taxon during each observation time. We have built on a body of work that has examined relationships between individual taxa, their body size, and their respiration rates to make initial estimations of respiration for larger fauna at the seafloor (Smith 1983, Pipenburg and Schmid 1996, Ambrose et al. 2001, Rowe et al. 2008). The relationships between individual size and respiration were determined for each echinoderm class based on a meta-analysis of all available *in situ* respiration measurements of echinoderms (Hughes et al. 2011), which covered a range of depths to more than 4000 m depth. We applied a temperature correction for each site modifying the equations presented in Hughes et al. (2011) so that the PAP temperature correction was set to 2.6°C and Sta. M to 1.5°C, the measured ambient temperatures at each site. The mass-specific respiration rate equations take the following form: individual respiration rate = aM^b, where M is individual wet-weight mass, a is the class specific y-intercept and b is the related exponent.

Megafauna sampling

Methods varied according to the specific assemblage examined. Camera sled tows were conducted at Station M, which is located offshore of the California coastline in the north-eastern Pacific at 34°50'N, 123°00'W, at about 4100 m depth. Faunal density and body size estimates

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were determined using photogrammetric techniques on towed camera sled images. The camera was positioned about 82 cm above the seafloor and operated to create a roughly continuous set of seafloor images. Here we use a standard definition of megafauna, those fauna identifiable in these seafloor images (typically ≥ 1 cm in size *sensu* Grassle 1975). The top ten dominant mobile organisms were enumerated including the Holothuroids *Elpidia* sp., *Peniagone vitrea*, *P. diaphana*, *Scotoplanes globosa*, *Oneirophanta mutabilis*, *Psychropotes longicauda*, *Abyssocucumis abyssorum* and *Synallactes* sp., the echinoid *Echinocrepis rostata*, and the Ophiuroidea, all of which are echinoderms. Echinoderms make up more than 99% of the mobile individuals observed during the surveys (see Ruhl 2007 for more quantitative details). The species-specific density and body size data captured from the images was combined with length to wet weight conversions to calculate biomass. The length to weight conversions originated from PAP samples using the same species or closest congener in terms of body shape.

Benthic trawling was conducted at the Porcupine Abyssal Plain in the vicinity of 48°50'N, 16° 30'W in the north-eastern Atlantic at a depth of about 4850 m. Here megafauna are those caught in a semi-balloon otter trawl system with an 8.6 m opening and 13 mm stretch mesh liner in the cod end (Billett et al. 2001, Merrett and Marshall 1981). This system was typically trawled at about 0.75 m s^{-1} over the seafloor. Density and biomass data from multiple trawls during a single cruise were averaged to create monthly values. At this site we only examined the data for the echinoderms, which made up about 95% of the total trawled biomass (see Billett et al. 2010 for more quantitative details). We assigned the echinoderm taxa into feeding guilds based on results from a previous study that examined relative isotope quantities in tissues to establish the trophic position among a large proportion of the fauna collected in PAP trawls (Iken et al. 2001). The guilds were delineated as surface deposit feeders (SDF), sub-surface deposit

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feeders (SSDF), and suspension feeders (SF), and predators/scavengers (P/S). Here too the fauna were dominated by Holothuroidea including *Amperima rosea, O. mutabilis, Ellipinion molle, Ps. longicauda, P. diaphana (all SDFs) and Pseudostichopus spp. (SSDF)*, as well as Asteroidea including *Hyphalaster inermis* (SSDF) and *Dytaster grandis grandis* (P/S), Ophiuroidea (SDF), Echinodea (SDF), and Crinoidea (SF).

It is important to note key differences in the methods for density and biomass data for PAP and Station M. PAP results were based on trawl samples whereas Sta. M were determined photographically. The Sta. M wet weight biomass was estimated from taxon specific relationships for length to mass, and only the top ten most abundant mobile epibenthic megafauna were examined. PAP data quantified four echinoderm feeding guilds, whereas Sta. M photographic data only quantified animals feeding at the sediment surface. Thus, at Sta. M, obscured sub-surface deposit feeders are left out of any fauna/function calculations. The trawl used at PAP substantially under-samples the echinoderms with greater under-sampling likely at smaller body sizes, but can reproduce variation in key fauna (Bett et al. 2001). For that reason, only relative variation is considered in conclusions for PAP, rather than the specific values.

Community indicators

In order to examine relationships between energetic, biogeochemical and community variation we used monthly records to derive a series of uni- and multi-variate community descriptors. These descriptors included total echinoderm abundances in terms of density (TA_D) and biomass (TA_B), as well as total echinoderm respiration (TR). Also included were indices of species composition similarity based on density data (SC_D), biomass (SC_B), and energetic demand (SC_E). We also computed Pielou's evenness (*J'*) from density data, as well as a series of

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rank-abundance distribution similarity indices based on density (RAD_D), biomass (RAD_B), and energetic demand (RAD_E), where the taxon identity is replaced by rank during each sampling time. For the PAP dataset, we also calculated a feeding guild composition index based on energy use by each guild (FGC_E). These indices were created by log (x+1) transforming the relevant data and then calculating the Bray-Curtis similarity between all the pairwise sample times. Then, for each data type, we used the multidimensional scaling (MDS) x-ordinates plotted over time as indicators of community variation.

Biogeochemical fluxes

Food supply at both sites was quantified as POC flux using deep-sea sediment trap samples at each site using methods described previously (Baldwin et al. 1998, Lampitt et al. 2010). Each trap is conical in shape and collected material sinking through a baffled entrance with a 0.25 m^{-2} opening. Cups at the bottom of the trap move sequentially to capture samples in time-series with regular intervals. These samples are then returned to shore and analyzed for POC content (see Smith et al. 2008 for more quantitative details on Sta. M fluxes). The POC flux data used for Sta. M are a composite of 50 and 600 mab trap data where gaps in the 600 mab record are filled with 50 mab data that has had correction to account for the fact that the 50 mab trap can experience flux of resuspended particulates. This correction was made in the form of a linear regression between using 50 mab as the explanatory variable for the 600 mab data series. POC fluxes at PAP at 3000 m depth were measured using conical sediment traps (see Lampitt et al. 2010 for more quantitative details on fluxes at PAP). However, POC values for the time

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period October 2008 – July 2011 were estimated from volume flux measurements using an empirically derived linear relationship between the two variables ($r^2 = 0.75$, $p < 0.0001$).

Analytical approach

Correlations between TR and the community indicators (CCS) described above were tested using the Spearman's rank correlation test (r_s), as well as a similarity matrix correlation test with randomization based significance testing (R, Clark 1993). Covariances of resource use (respiration) were also calculated between each taxon pair across sampling times (CD). The mean individual respiration rate (TR/TA_D) was tested for correlation to total density and evenness (*J'*) with an F-test used to determine significance for relationships between mean individual respiration rate and total density and r_s for correlating to evenness (ZSD_1). Correlation between TR and POC flux (ZSD_2) was tested via r_s. POC flux changes were allowed to precede TR in cross correlation revealing the time lag with a peak in correlation coefficient. The residuals of a least squares power function regression of mean individual respiration rate and total density were then similarly correlated with POC flux via r_s (ZSD_3). The Kolmogorov-Smirnov Test was used to determine if body size energy distributions were significantly different from a uniform distribution (MMD).

A ratio of food supply to demand was then examined. Here we considered respiration values in terms of mg C m^{-2} d^{-1} for direct comparison to POC flux units using a respiratory quotient of 0.85 (Smith 1978). The proportion of monthly TR in terms of food demand (TR_C) to POC flux (TR_C:POC flux) provided estimation of the proportion of food input used by the assemblage where TR_C was compared with the synoptic POC flux, as well as the mean POC flux from the preceding 12 months.

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Results

Station M

The Sta. M time series exhibited variations in TR of about a factor of four (Fig. 2A). The concentration of sampling with time at Sta. M provides a clear indication that variations in respiration of the assemblage can have significant shifts at inter-annual scales. For example, 1991 and 1994 have significantly different median respiration rates (Mann-Whitney U-test, $p = 0.02$). Respiration (TR) was significantly correlated with both TA_D and TA_B with respiration being more highly correlated to TA_B (CCS hypothesis, Table 1). TA_D and TA_B were not directly correlated. In addition, TR was correlated to the species composition descriptors SC_D, SC_B, and SC_E (Fig. 2, Table 1).

There were also significant correlations between TR and rank abundance indicators RAD_D, RAD_B, and RAD_E, which were based on density, biomass and energetic demand respectively (CCS hypothesis, Table 1). Each of these RAD types not only had changes in RAD shape (i.e. relative dominance and evenness), but there were also major shifts in terms of the relative ranks of several taxa (Fig 3A). Although RAD_D, RAD_B, and RAD_E variation had similarities, the taxonomic identity of the dominant taxon was frequently not the same from one RAD type to the next and many taxa exhibited substantial changes in relative dominance, in addition to density, biomass and resource use. For example, near the start of the time series in June 1991, density, biomass, and respiration were each dominated by a different taxon (Fig. 3A, B and C). There were also major shifts in rank over time at Sta. M, as shown notably by changes in the holothurian *Elpidia* spp., the urchin *Echinocrepis rostrata,* and the brittle stars

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Ophiuroidea dominated by *Ophiura bathybia.* Changes in SC_E were most closely correlated with density variation of these three taxa ($R = 0.58$-0.65, $p < 0.001$).

The covariance in TR between taxa over time was about ½ negative in sign considering all possible taxon-specific pairwise cases (CD hypothesis). There was a significant negative correlation between mean respiration per individual and total density, an expectation where increases in density are compensated by lower mean individual respiration rates (ZSD_1 hypothesis; $F = 23.2$, $p < 0.001$; Fig. 4). With no correlation between time and POC flux over the whole time series, there was no monotonic change in resources observed during the study period. Evenness was significantly lower when mean individual respiration rate was lower (ZSD_1 hypothesis; $r_s = 0.48$, $p = 0.002$; Fig. 4). A positive correlation was found between TR and POC flux with a time lag of 13 months (ZSD_2 hypothesis; $r_s = 0.45$, $p = 0.03$) with an intensity and time lag similar to results for correlations between SC_D and POC flux found previously (Ruhl 2008). The monthly echinoderm assemblage food demand was ~1-6% of the mean POC flux food supply of the preceding 12 months, and as much as 10% of the synoptic monthly supply (Fig. 6A). The residuals of the density-mean respiration rate relationship are positively correlated to monthly POC flux to the seafloor with a time lag of 12 months (ZSD_2 hypothesis; $r_s = 0.42$, $p = 0.03$; Fig. 4). When body- size energy distributions were examined across these two different parts of the time series, each period showed multimodal distributions (MMD hypothesis, $p < 0.001$, Fig. 5).

PAP

Here too we found approximately four fold variation in TR (Fig. 2B). The TR variation was significantly correlated with TA_D, TA_B, SC_D and SC_E, but not significantly to SC_B (CCS

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hypothesis, Table 1). Correlations were also found between TR and RAD descriptors matching results for Station M. Similarly, TA_D and TA_B were not correlated at PAP. The two major peaks in respiration at PAP were associated with a peak in TA_D in 1997 and TA_B in 1998 (Fig. 2D).

From the start of the PAP time series, the smaller holothurian *A. rosea* increased in relative density by several orders of magnitude, as well as rank to become most numerous by April 1997, but *A. rosea* declined again by the end of the time series (Fig. 3D). The increases in *A. rosea* were accompanied by a reduction in abundance and rank dominance of the holothurian *O. mutabilis*. It is notable that in April 1997 the dominant species in terms of biomass (*O. mutabilis*) was not so in terms of resource use. In another example, in April 1999 the most dominant in terms of density (*A. rosea*) was not so in terms of resource use (Fig. 3D, E and F). The relatively large holothurian *Psychropotes longicauda* had relatively high dominance in terms of energetic demand when compared to its dominance by density. *Psychropotes longicauda* also had the strongest correlation between any taxon-specific density and SC_E among the echinoderms at PAP ($R = 0.76$, $p < 0.001$).

Respiration (TR) variation was highly correlated to the feeding guild composition in terms of their energy demand (FGC_E, $R = 0.86$, $p < 0.001$), where variation in surface deposit feeder (SDF) explained the greatest proportion of variation in FGC_E. While PAP trawl samples spanned four feeding guilds described by Iken et al. (2001), variation in FGC_E was most related to SDF. The SDF guild made up ~87% of the individuals on average, followed in dominance by sub-surface deposit feeders (SSDF, Fig. 6B) with Fig. 3 indicating guild assignments of the dominant fauna during relatively contrasting community compositions. Together these two guilds made up an average of 95-99 % of the echinoderms in the trawl collections for each of the sampling times, with suspension feeders and predator/scavengers making up the remaining two

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guilds. The SDF respiration for the time series was more variable than that of the SSDF, which were relatively stable. However, the ratio of SDF to SSDF was not directly correlated to TR.

Covariances between pairwise taxon-specific energy demand over time were also about ½ negative in sign (CD). Like Sta. M, there was also a significant negative correlation between mean individual respiration and total density (ZSD_1 hypothesis, $F = 81.5$, $p < 0.001$; Fig. 4), with higher evenness positively related to mean individual respiration rate ($r_s = 0.80$, $p < 0.001$). At PAP, TR was not found to increase relative to preceding POC flux by cross correlation analysis ($ZSD_{2 \text{ and } 3}$ hypotheses), as was done with Sta. M data, but this result could be related to the lower temporal resolution in data for PAP. Direct comparisons of POC flux quantity inputs (food supply) to TR (food demand) at PAP were not possible because of the known fishing efficiency issue with the otter trawl system.

Discussion

Total respiration (TR) of the echinoderm assemblage was related to community indicators with biomass based indicators at both sites being more correlated to TR than density indicators in most cases (CCS hypothesis, Fig. 2, Table 1). Changes in distribution shape are evident in the rank-abundance distributions (RADs Fig. 3), but also the ranks of the top ten dominant taxa over time with some taxa changing across ten or more ranks. Changes in taxon rank between density, biomass and respiration RADs were driven, in part, by the fact that smaller fauna have higher mass-specific respiration rates than larger fauna. As a result, the apparent dominance of a particular species in terms of density and/or biomass did not always translate to that species being dominant in terms of resource use (respiration).

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Compensatory dynamics in terms of >50% negative covariances were not found, even in terms of TR (CD hypothesis). Compensation in terms of zero-sum dynamics was, however, observed at both sites with links to evenness (ZSD_1 hypothesis, Fig. 4.). Here, when fewer individuals were present, there tended to be higher mean individual respiration rates at both sites. Differences between sites in density and mean individual respiration relate to the different sampling tools as discussed in the methods. Zero-sum dynamics have also been found in communities of desert rodents and in a tropical forest community (White et al. 2004, Ernest et al. 2008, 2009).

At Sta. M, where links between food supply and community dynamics are best understood, we found evidence of the interplay between zero-sum compensation and the non-steady state forcing of the system by changes in food supply. TR was correlated to POC flux (ZSD_2 hypothesis), and POC flux appeared to modulate zero-sum relationships between mean individual respiration rate and total density (ZSD_3 hypothesis). We found that although there were straightforward metabolism-based zero-sum compensation dynamics like those evident in Fig. 4, there was also a correlation of POC flux with the residual variation in density found in Fig 4A. Thus, as the density deviates from that expected by zero-sum compensation, food supply can explain some of this deviation in terms of more food supply relating to positive density residuals (Fig. 1).

Energetic theories of community structuring alone are not sufficient to explain the multimodal nature of the body size energy distribution at Sta. M (MMD hypothesis, Fig. 5). POC flux variation can be differentiated into temporal variance, as well as composition in terms of pigments, lipids and other nutrients. Both quantity and quality of food supply to the benthos vary over time. This temporal variation in a common set of resources to a community of differentially

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responding fauna likely provides the mechanism by which the abyssal echinoderms have exhibited substantial switches in rank abundance (e.g. FitzGeorge-Balfour et al. 2010). The habitat and its scale may also lend advantage to fauna of particular size classes (Ernest 2005). It will be informative to continue examination of suitable datasets for MMD patterns, particularly where there are data that span larger size ranges and assemblage types. However, care must be taken in considering potential biases from sampling gear (Bett 2013).

The degree to which taxon-specific niche vs. size-related mechanisms drive community dynamics is unclear, but indications of both were evident. Within a food limited system, we observed compensatory dynamics, rank switches, and non-random links between TR and measures of biodiversity such as SC_D and evenness. At PAP, where sampling included a broader range of feeding types, there were indications of correspondence between feeding guild variation and respiration. Links to resource availability and assemblage changes in terms of density have been linked to environmental conditions at Station M (Ruhl 2008, Ruhl et al. 2008) and there is evidence that these differences translate to changes in reproductive potential (Wigham et al. 2003, Ruhl 2007, FitzGeorge-Balfour et al. 2010). It is important to note, though, that swimming may provide another effective mechanism for abundance variation of some fauna at the study sites (Rogacheva et al. 2013). Several observed holothurians are capable of swimming and thus have potential ability for migration in terms of explaining observed variation, particularly *Peniagone* spp. and *A. rosea*, but the effectiveness of swimming as a migration mechanism is unknown.

The similarities in TR variation at both Sta. M and PAP suggest substantial variation in assemblage-related carbon cycle processes, at least on site specific and perhaps larger scales. The results from Sta. M suggest that food supply drives variation in respiration dynamics, in part. The

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383 results from Sta. M also suggest a modest increase in shortfall between the supply and demand of
384 incoming POC flux, as estimates now include data from the echinoderm assemblage. Because
385 the efficiency with which POC is assimilated into tissue is generally thought to be proportional
386 to respiration for these taxa (e.g. van Oevelen et al. 2012), the rates of secondary production
387 from these assemblages likely have similar variation, as would the rates of remineralisation.
388 Benthic echinoderms have been estimated to contribute to a substantial portion of inorganic C
389 production globally (up to about 1/4 that of pelagic inorganic C production, Lebrato et al. 2010).
390 Even though the echinoderm production rates peak at shallower depths than those studied here,
391 our results suggest the possibility of substantial temporal variation in those rates, which would
392 likely apply to any area experiencing similar climate-driven variation.

393 Total respiration rates at PAP have notable similarity to estimates from an inverse model
394 study. van Oevelen et al. (2012) estimated SDF and SSDF respiration as part of a comprehensive
395 inverse model budgeting of carbon stocks and flows at PAP. Both our study and the model study
396 use the trawl sampling as inputs to the estimates, but the linear inverse model approach estimates
397 these flows through balancing a series of equality and inequality equations where some, but not
398 all flows are known *a priori*, whereas the estimates presented here are relatively empirical. For
399 the period September 1996 to October 1998, the SDF respiration values measured here were
400 about 43 % less than those based on inverse methods for that period.

401 The methods here provide the best available estimates for resource use of the studied
402 fauna, which include empirical class specific rates that do not rely on *a priori* allometric scaling
403 relationships. A key limitation should be noted, though. The way we were able to apply size
404 specific respiration rates to density and body size data over time did not allow for the fact that
405 there could be variations in individual size-specific respiration over time within each taxon.

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406 During periods of higher fluxes, when activity is known to be higher from time lapse
407 photography (Bett et al. 2001, Vardaro et al. 2009), individuals may have elevated respiration
408 rates not accounted for here. Such changes in individual respiration in response to food input
409 would likely increase correlation between POC flux and respiration fundamentally. However,
410 increased respiration related to activity may also shorten the observed time lag in correlations
411 between POC flux and respiration. Or it might introduce a multi peaked distribution where a
412 correlation with little or no time lag might be associated with individual metabolic change and
413 longer-term lagged correlation such as the one found here, which is driven by density and mass
414 variations in the community.

415 The significant correlations found here have important unexplained variation, for
416 example between TR and POC flux. Higher-resolution datasets with greater statistical power to
417 discern food quantity and quality, as well as demand, will likely be needed to make progress in
418 explaining a greater portion of variation (e.g. Sherman and Smith 2009). Further consideration of
419 lateral flux of carbon, the flux of larger detrital aggregates and carrion, irregular pulsed POC flux
420 delivery contributing to a 'food bank', is also warranted in helping to constrain food supply
421 estimates, as well as the local production of biomass via background microbial chemosynthesis
422 (Robison et a. 2005, Smith et al. 2006, Company et al. 2008, Drazen et al. 2012).

423 The extensive changes in respiration, resource use, remineralisation, and community
424 structure and composition meet specific assumptions of climate-driven community variation via
425 niche-based and energetic abundance mechanisms. Climatic variations such as El Niño or the
426 North Atlantic Oscillation can relate to ocean circulation, surface production, POC fluxes and
427 ultimately deep-sea assemblages (reviewed in Smith et al. 2009). The observed changes in rank
428 abundance of the studied assemblage appear to be related to the availability of a multivariate

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niche space that includes quantity and quality of food supplies. Moreover, the quantitative relationships identified between respiration and feeding guild have quantitative links to each other providing evidence that multiple functional changes can be tied to basic changes in resources. If projected changes in ocean productivity occur (e.g. Steinacher et al. 2010), we expect that such changes would translate through to pervasive changes in benthic community structure and function.

As presented here, more long-term synoptic studies of the dynamics of resource availability, taxon specific resource use and ecosystem function over wider ranges of body size and taxa could help reconcile size- and energy-based theories of community structuring with niche theories (Issac et al. 2012**)**, as well as resolve imbalances in biogeochemical dynamics. An improved understanding of these relationships has implications not only for understanding climate related impacts on the seafloor and other ecosystems, but also for disentangling climate from other forcing factors such as natural resource extraction.

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457 Institution of Oceanography Benthic Invertebrate Collection, the Smithsonian Institution, and the
458 Discovery Collections, a joint effort of the National Oceanography Centre and Natural History
459 Museum, London.

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596 Table 1. Statistical correlation results comparing total echinoderm megafauna respiration (TR,
597 i.e, energy or food demand) from the Sta. M photographic data and PAP trawl data to various
598 other uni- and multi-variate community descriptors.

Community descriptor	Sta. M (n=37)		PAP (n=15)	
	TR		TR	
univariate	r_s	*p*	r_s	*p*
Total abundance as density - TA_D	***0.64***	***<0.001***	**0.61**	**0.02**
Total abundance as biomass - TA_B	***0.82***	***<0.001***	***0.94***	***<0.001***
multivariate	R	*p*	R	*p*
Species composition similarity from density - SC_D	**0.11**	**0.032**	**0.34**	**0.007**
Species composition similarity from biomass - SC_B	***0.35***	***<0.001***	0.20	0.07
Species composition similarity from energetic demand - SC_E	***0.35***	***<0.001***	**0.42**	**0.02**
Rank-abundance distribution similarity from density - RAD_D	***0.23***	***<0.001***	**0.37**	**0.004**
Rank-abundance distribution similarity from biomass - RAD_B	***0.58***	***<0.001***	***0.49***	***<0.001***
Rank-abundance distribution similarity from energetic demand - RAD_E	***0.76***	***<0.001***	***0.78***	***<0.001***

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Figure Legends

Figure 1. Conceptual model illustrating relationships between mean individual respiration rates and total density (blue line), as well as and Pielou's evenness index (*j'*, black line) with arrows indicating increases in variable quantity. Thus, this theoretical formulation, including residuals, allows for analysis of data from a temporally dynamic study area.

Figure 2. Time series (by month) of echinoderm megafauna community dynamics for the Sta. M and PAP with: A and B) total respiration of the echnioderm megafauna (●, TR) and an index of echinoderm species composition similarity based on energetic demand (○, SC_E); and C and D) total density (●, TA_D), total biomass (○, TA_B); E and F) Monthly POC flux to 4050 and 3000 m depth at Sta. M and PAP, respectively. The figure illustrates, in part, that TR varies by up to 4-fold for each site with some synchrony to community composition.

Figure 3. Rank distribution plots for Sta. M data for selected times during the time series based on A) density; B) biomass; and C) energetic demand (respiration). PAP data are similarly shown in D) for density; E) biomass; and F) energetic demand (respiration). The surface deposit feeders (SDF) are open bars, sub-surface deposit feeders (SSDF) diagonally hatched bars, suspension feeders (SF) have horizontally hatched bars, and predators/scavengers (P/S) are cross hatched. The figure illustrates differences between density, biomass and resource use by species, as well as how various taxon rank in these factors at specific times, as well as changes in the shape and magnitude of the RADs.

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Figure 4. Relationship between total density (TA_D), mean individual respiration rates and Pielou's index of evenness (*J'*) at Sta. M (A) and PAP (B). Points are monthly estimates. This figure provides data supporting hypothetical relationships presented in Fig. 1. The color in the points is indicates corresponding evenness with the values provided in the legend to the right of panel B.

Figure 5. Multimodal distributions of total respiration rates in 0.2 log unit size classes at Sta. M for the two periods with the most different species composition. The total respiration is corrected for the number of months with data for each period (n = 29 for 1989-1998, n = 8 for 2001-2004). This figure illustrates that the assemblage does not have a uniform body-size energy distribution.

Figure 6. Indicators of ecosystem function variation including A) Sta. M time series of monthly ratio between total echinoderm assemblage respiration in terms of respired C (TR_C) and mean POC food supplies both for synoptic fluxes (○TR_C:POC flux) and for the mean of the 12 months leading up to and including the monthly TR value (●); and B) Monthly energetic demand estimates for PAP surface deposit feeders (●, SDF) and subsurface deposit feeders (○, SSDF), as well as an index of feeding guild composition over time based on energetic respiratory demand (×, FGC_E).

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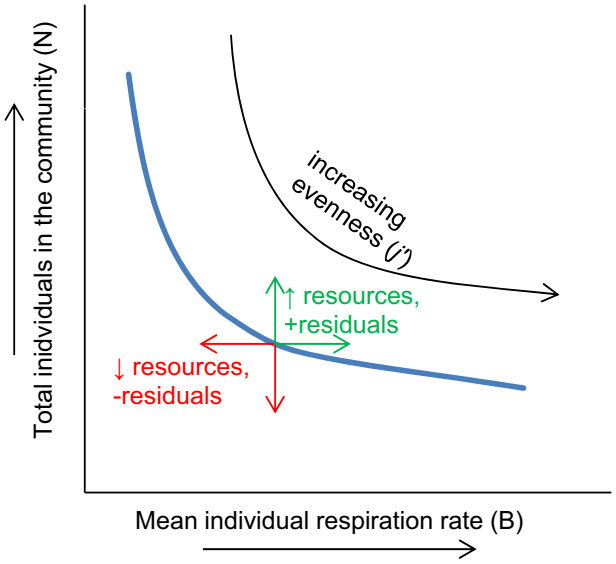

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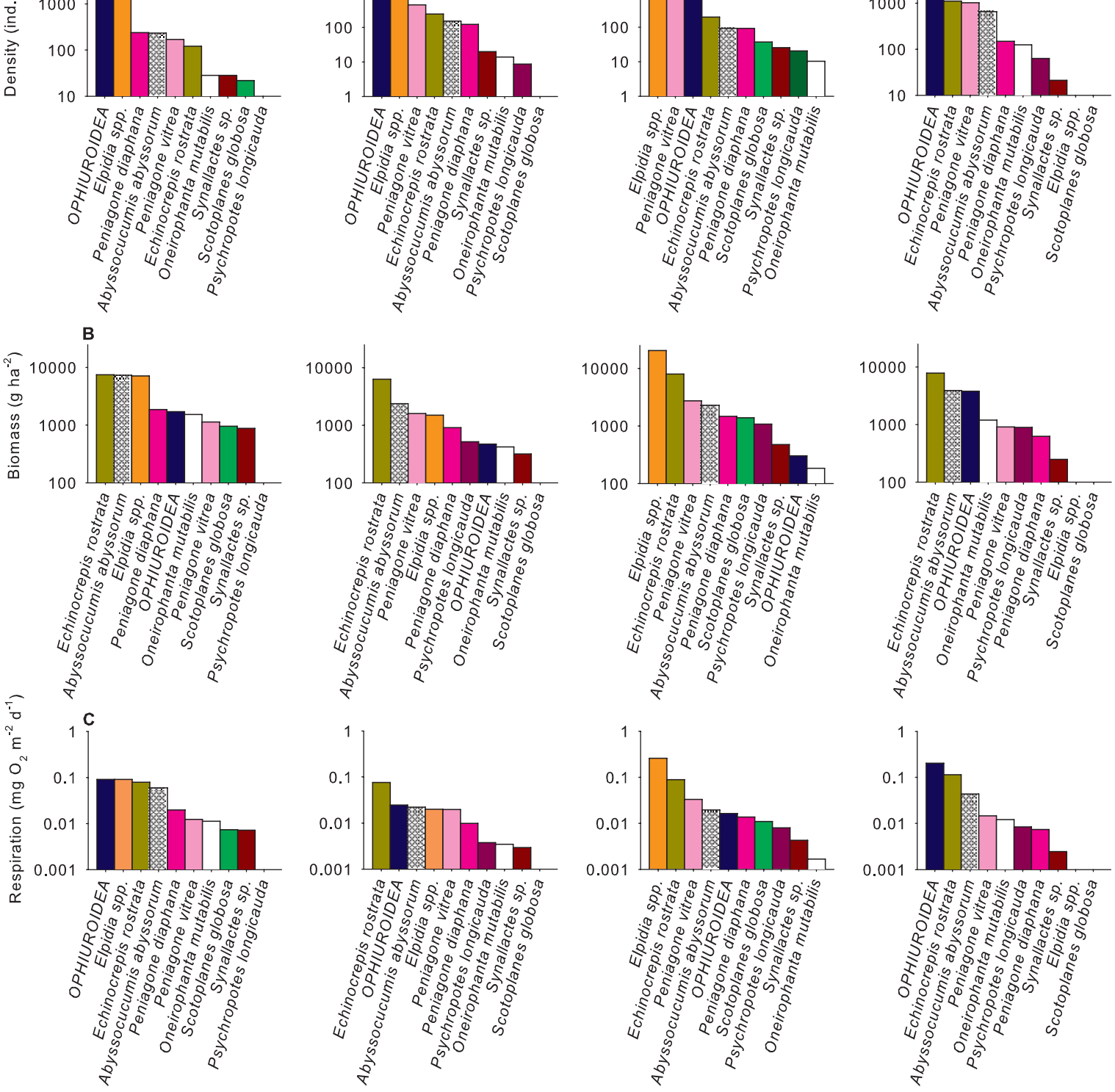
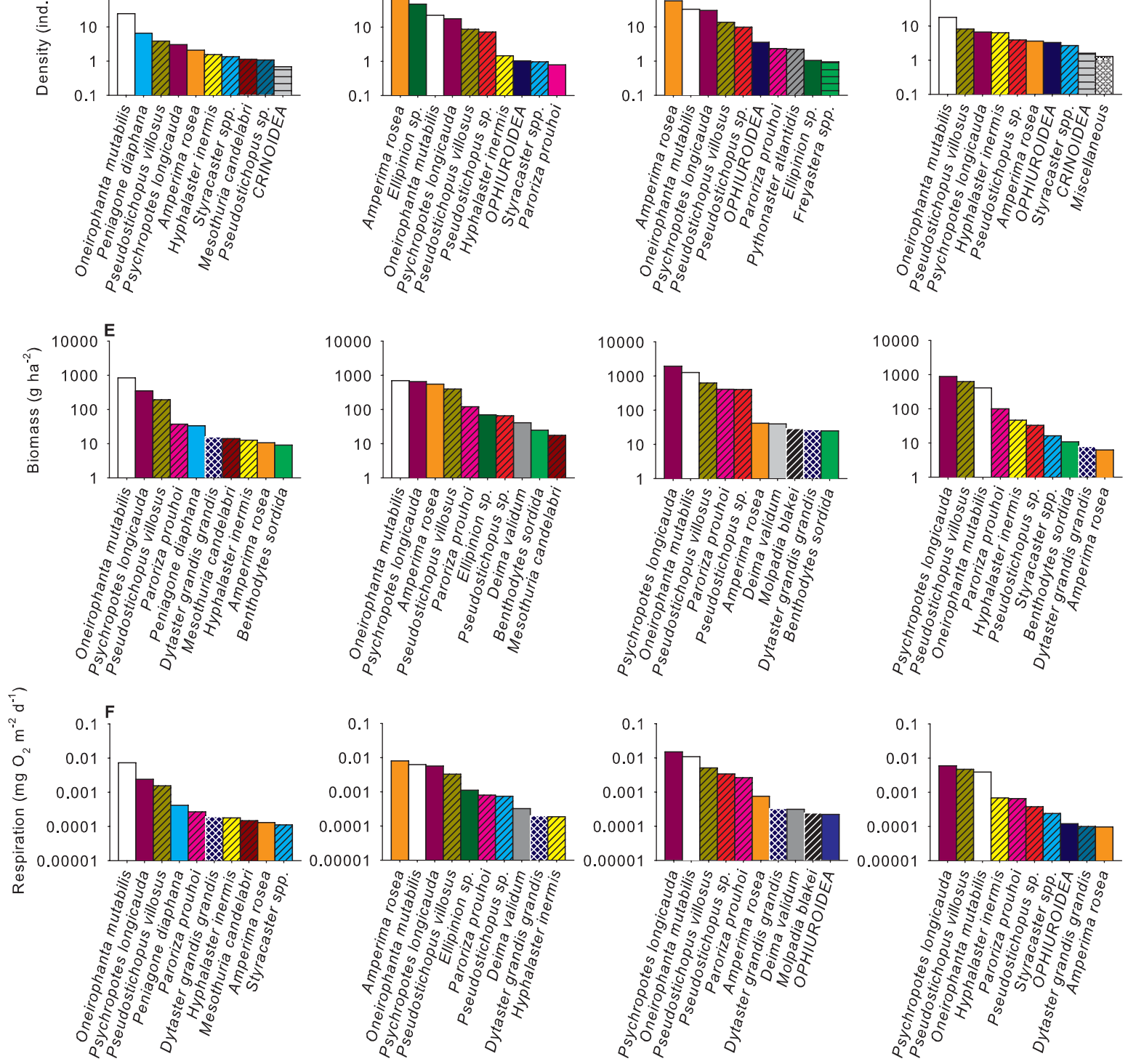
A
B
C
D
E
F
Total echinoderm respiration (TR, mg O2 m-2 d-1)
Community composition (SCE, O2 demand)
Total Density (TAD, ind. ha-1)
Total Biomass (TAB, g ha-1)
POC flux (mg C m-2 d-1)
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012


Density (ind. m-2)
1000
100
10
OPHIUROIDEA
Elpidia spp.
Peniagone diaphana
Abyssocucumis abyssorum
Peniagone vitrea
Echinocrepis rostrata
Oneirophanta mutabilis
Synallactes sp.
Scotoplanes globosa
Psychropotes longicauda
100
10
1
OPHIUROIDEA
Elpidia spp.
Peniagone vitrea
Echinocrepis rostrata
Abyssocucumis abyssorum
Peniagone diaphana
Synallactes sp.
Oneirophanta mutabilis
Psychropotes longicauda
Scotoplanes globosa
100
10
1
Elpidia spp.
Peniagone vitrea
OPHIUROIDEA
Echinocrepis rostrata
Abyssocucumis abyssorum
Peniagone diaphana
Scotoplanes globosa
Synallactes sp.
Psychropotes longicauda
Oneirophanta mutabilis
1000
100
10
OPHIUROIDEA
Echinocrepis rostrata
Peniagone vitrea
Abyssocucumis abyssorum
Peniagone diaphana
Oneirophanta mutabilis
Psychropotes longicauda
Synallactes sp.
Elpidia spp.
Scotoplanes globosa
B
Biomass (g ha-2)
10000
1000
100
Echinocrepis rostrata
Abyssocucumis abyssorum
Elpidia spp.
Peniagone diaphana
OPHIUROIDEA
Oneirophanta mutabilis
Peniagone vitrea
Scotoplanes globosa
Synallactes sp.
Psychropotes longicauda
10000
1000
100
Echinocrepis rostrata
Abyssocucumis abyssorum
Peniagone vitrea
Elpidia spp.
Peniagone diaphana
Psychropotes longicauda
OPHIUROIDEA
Oneirophanta mutabilis
Synallactes sp.
Scotoplanes globosa
10000
1000
100
Elpidia spp.
Echinocrepis rostrata
Peniagone vitrea
Abyssocucumis abyssorum
Peniagone diaphana
Scotoplanes globosa
Psychropotes longicauda
Synallactes sp.
OPHIUROIDEA
Oneirophanta mutabilis
10000
1000
100
Echinocrepis rostrata
Abyssocucumis abyssorum
OPHIUROIDEA
Oneirophanta mutabilis
Peniagone vitrea
Psychropotes longicauda
Peniagone diaphana
Synallactes sp.
Elpidia spp.
Scotoplanes globosa
C
Respiration (mg O2 m-2 d-1)
1
0.1
0.01
0.001
OPHIUROIDEA
Elpidia spp.
Echinocrepis rostrata
Abyssocucumis abyssorum
Peniagone diaphana
Peniagone vitrea
Oneirophanta mutabilis
Scotoplanes globosa
Synallactes sp.
Psychropotes longicauda
1
0.1
0.01
0.001
Echinocrepis rostrata
OPHIUROIDEA
Abyssocucumis abyssorum
Elpidia spp.
Peniagone vitrea
Peniagone diaphana
Psychropotes longicauda
Oneirophanta mutabilis
Synallactes sp.
Scotoplanes globosa
1
0.1
0.01
0.001
Elpidia spp.
Echinocrepis rostrata
Peniagone vitrea
Abyssocucumis abyssorum
OPHIUROIDEA
Peniagone diaphana
Scotoplanes globosa
Psychropotes longicauda
Synallactes sp.
Oneirophanta mutabilis
1
0.1
0.01
0.001
OPHIUROIDEA
Echinocrepis rostrata
Abyssocucumis abyssorum
Peniagone vitrea
Oneirophanta mutabilis
Psychropotes longicauda
Peniagone diaphana
Synallactes sp.
Elpidia spp.
Scotoplanes globosa


Density (ind. m-2)
10
1
0.1
Oneirophanta mutabilis
Peniagone diaphana
Pseudostichopus villosus
Psychropotes longicauda
Amperima rosea
Hyphalaster inermis
Styracaster spp.
Mesothuria candelabri
Pseudostichopus sp.
CRINOIDEA
Amperima rosea
Ellipinion sp.
Oneirophanta mutabilis
Psychropotes longicauda
Pseudostichopus villosus
Pseudostichopus sp.
Hyphalaster inermis
OPHIUROIDEA
Styracaster spp.
Paroriza prouhoi
Amperima rosea
Oneirophanta mutabilis
Psychropotes longicauda
Pseudostichopus villosus
Pseudostichopus sp.
OPHIUROIDEA
Paroriza prouhoi
Pythonaster atlantidis
Ellipinion sp.
Freyastera spp.
Oneirophanta mutabilis
Pseudostichopus villosus
Psychropotes longicauda
Hyphalaster inermis
Pseudostichopus sp.
Amperima rosea
OPHIUROIDEA
Styracaster spp.
CRINOIDEA
Miscellaneous
E
Biomass (g ha-2)
10000
1000
100
10
1
Oneirophanta mutabilis
Psychropotes longicauda
Pseudostichopus villosus
Paroriza prouhoi
Peniagone diaphana
Dytaster grandis grandis
Mesothuria candelabri
Hyphalaster inermis
Amperima rosea
Benthodytes sordida
Oneirophanta mutabilis
Psychropotes longicauda
Amperima rosea
Pseudostichopus villosus
Paroriza prouhoi
Ellipinion sp.
Pseudostichopus sp.
Deima validum
Benthodytes sordida
Mesothuria candelabri
Psychropotes longicauda
Oneirophanta mutabilis
Pseudostichopus villosus
Paroriza prouhoi
Pseudostichopus sp.
Amperima rosea
Deima validum
Molpadia blakei
Dytaster grandis grandis
Benthodytes sordida
Psychropotes longicauda
Pseudostichopus villosus
Oneirophanta mutabilis
Paroriza prouhoi
Hyphalaster inermis
Pseudostichopus sp.
Styracaster spp.
Benthodytes sordida
Dytaster grandis grandis
Amperima rosea
F
Respiration (mg O2 m-2 d-1)
0.1
0.01
0.001
0.0001
0.00001
Oneirophanta mutabilis
Psychropotes longicauda
Pseudostichopus villosus
Peniagone diaphana
Paroriza prouhoi
Dytaster grandis grandis
Hyphalaster inermis
Mesothuria candelabri
Amperima rosea
Styracaster spp.
Amperima rosea
Oneirophanta mutabilis
Psychropotes longicauda
Pseudostichopus villosus
Ellipinion sp.
Paroriza prouhoi
Pseudostichopus sp.
Deima validum
Dytaster grandis grandis
Hyphalaster inermis
Psychropotes longicauda
Oneirophanta mutabilis
Pseudostichopus villosus
Paroriza prouhoi
Amperima rosea
Dytaster grandis grandis
Deima validum
Molpadia blakei
OPHIUROIDEA
Psychropotes longicauda
Pseudostichopus villosus
Oneirophanta mutabilis
Hyphalaster inermis
Paroriza prouhoi
Pseudostichopus sp.
Styracaster spp.
OPHIUROIDEA
Dytaster grandis grandis
Amperima rosea

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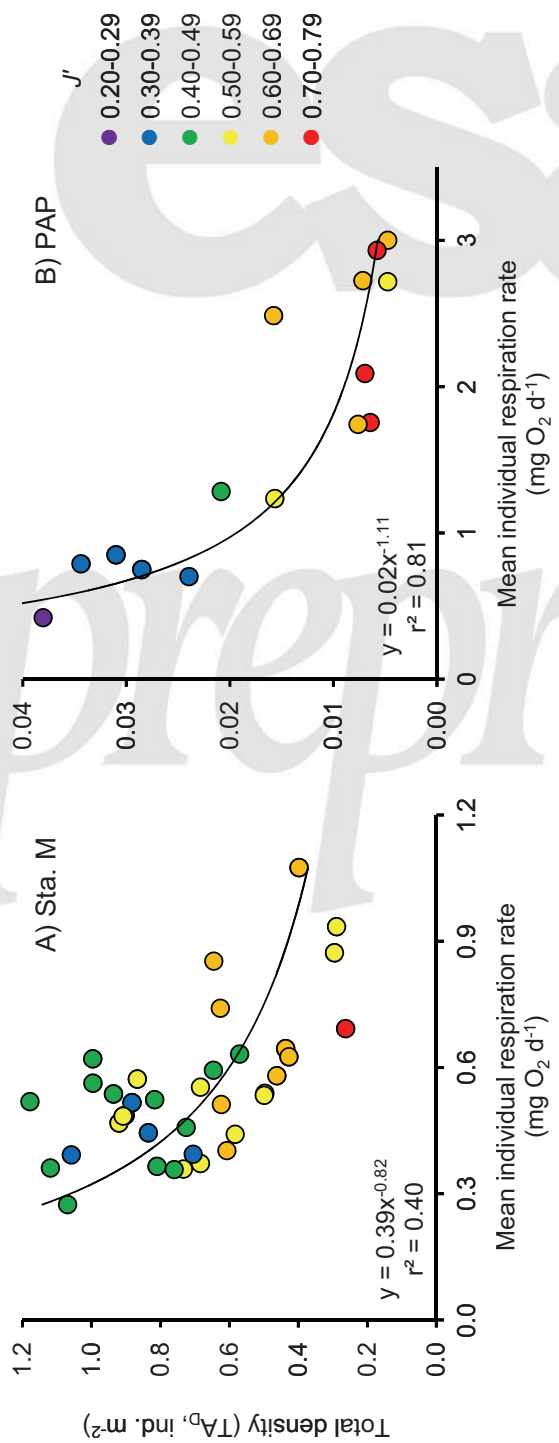

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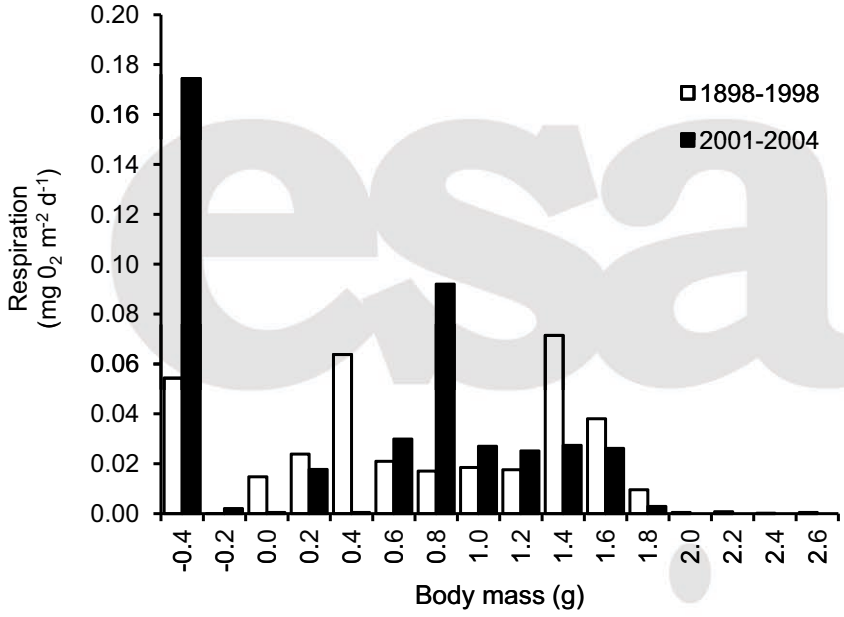

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A
TR$_C$:POC flux
0.10
0.08
0.06
0.04
0.02
0.00
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005

B
SDF & SSDF respiration
(mg O$_2$ m^{-2} d^{-1})
0.03
0.02
0.01
0.00
Feeding guild composition
index (FGC$_E$, O^2 demand)
3
2
1
0
-1
-2
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012