Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems

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Abstract

Global climate change will undoubtedly be a pressure on coastal marine ecosystems, affecting not only species distributions and physiology but also ecosystem functioning. In the coastal zone, the environmental variables that may drive ecological responses to climate change include temperature, wave energy, upwelling events and freshwater inputs, and all act and interact at a variety of spatial and temporal scales. To date, we have a poor understanding of how climate-related environmental changes may affect coastal marine ecosystems or which environmental variables are likely to produce priority effects. Here we use time series data (17 years) of coastal benthic macrofauna to investigate responses to a range of climate-influenced variables including sea-surface temperature, southern oscillation indices (SOI, Z4), wind-wave exposure, freshwater inputs and rainfall. We investigate responses from the abundances of individual species to abundances of functional traits and test whether species that are near the edge of their tolerance to another stressor (in this case sedimentation) may exhibit stronger responses. The responses we observed were all nonlinear and some exhibited thresholds. While temperature was most frequently an important predictor, wave exposure and ENSO-related variables were also frequently important and most ecological variables responded to interactions between environmental variables. There were also indications that species sensitive to another stressor responded more strongly to weaker climate-related environmental change at the stressed site than the unstressed site. The observed interactions between climate variables, effects on key species or functional traits, and synergistic effects of additional anthropogenic stressors have important implications for understanding and predicting the ecological consequences of climate change to coastal ecosystems.

Keywords: benthic macrofauna, freshwater discharge, interactions, key species, rainfall, regression trees, southern oscillation, species composition, temperature, wave exposure

Introduction

Anthropogenically induced global climate change has profound implications for marine ecosystems. Globally, the marine environment is changing rapidly (Hoegh-Guldberg & Bruno, 2010; Doney *et al.*, 2012) with unprecedented rates of change in sea water temperature throughout much of the globe occurring in the last decade (Philippart *et al.*, 2011). Changes also include the loss of sea ice cover in the Arctic and Antarctic, rising sea level, increased storm events, more variable precipitation with more frequent intense rainfall events and earlier occurrence of springtime phytoplankton blooms (IPCC, 2007; Solomon *et al.*, 2007; Hoegh-Guldberg & Bruno, 2010). Although marine species and ecosystems have responded to such variations in their environment throughout evolutionary history, a primary concern is the rapid rate of change currently observed (Root *et al.*, 2003; Philippart *et al.*, 2011).

Seminal reviews in the early 1990s (Fields *et al.*, 1993; Lubchenco *et al.*, 1993) summarised the understanding of climate change impacts on marine systems. At that time, research on the effects of rising temperatures focused on organismal and, to a lesser extent, population level processes, suggesting that the distribution and abundance of species would shift according to their thermal tolerance and ability to adapt. In 2006, Harley *et al.* (2006) suggested that for marine systems, it was time to move on from effects of temperature alone, and identified a number of other important aspects that deserved study, for example, ocean chemistry and circulation, UV and sea level rise. Despite this, many marine studies still focus on temperature predicting changes in distributional boundaries of species and replacement of cold-water taxa by others with warm-water affinities, over decades (Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999), associated with El Nino-Southern Oscillation events (Pearcy & Schoener, 1987; Dayton *et al.*, 1999), and extreme events (Wethey *et al.*, 2011; Smale & Wernberg, 2013; Boucek & Rehage, 2014).

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In coastal environments, the effects of waves and freshwater inputs on benthic processes can be expected to have important consequences. Moreover, coastal environments are frequently high-use areas by humans, impacted by multiple land- and sea-based human activities. In such cases, the potential for interaction between climate and other anthropogenic variables affecting responses exists (Harley *et al.*, 2006; Schindler, 2006; Walther, 2010) but these are not so frequently studied (Darling & Côté, 2008; Wernberg *et al.*, 2012).

Efforts to manage and conserve living coastal systems in the face of climate change require research that investigates community and functional attributes, synergistic effects with other anthropogenic variables and ecological thresholds. While laboratory experiments can generally be used to investigate organism responses/sensitivities to single (or at most a few) variables at small scales, field-based manipulative experiments at an appropriate scale are generally impossible. Time series data offer the opportunity to develop and test general hypotheses and to observe correlative patterns that may be used for large-scale predictions. Within this study, we use a time series of 17 years in the abundances of coastal benthic macrofauna to investigate biological responses. The 17 years covers a time period of strong southern oscillation, with winter water temperatures that varied from 13 to 16 °C (Fig. 1a–c). The following hypotheses were investigated:

1 The majority of responses will be nonlinear, and on occasion exhibit thresholds (i.e. a sudden drop in abundance or a change from increasing to decreasing abundance).

2 Responses to many variables, not just temperature, will be observed and interactions between variables will drive the responses.

3 Species that are near the edge of their tolerance to another stressor will exhibit responses with a lesser degree of change of climate-driven environmental variables.

4 Species replacement within functional trait groupings will result in shifted thresholds such that thresholds are only detected at more extreme conditions than those detected for individual species.

We focus on benthic macrofauna as this group has been demonstrated to affect benthic microphyte communities and primary productivity (e.g. Thrush *et al.*, 2006; Van Colen *et al.*, 2008; Volkenborn *et al.*, 2009); to modify hydrodynamics, nutrient recycling and benthic pelagic coupling (e.g. Eckman *et al.*, 1981; Pilditch *et al.*, 1997; Nikora *et al.*, 2002; Lohrer *et al.*, 2004; Newell, 2004); and to provide food for fish and birds. Benthic macrofauna are frequently used throughout the world in marine health and quality indices (e.g. Alden *et al.*,

2002; Borja & Dauer, 2008; Villnäs & Norkko, 2011; Rodil *et al.*, 2013). We move beyond impacts to single species by considering effects on two key species which thus have the potential to impact on the larger community (Harley *et al.*, 2006; Thrush *et al.*, 2009, 2014). Finally, we use biological trait analysis to focus on some key functional traits that would alter ecosystem function and, therefore, ecosystem services (Sara *et al.*, 2014).

Materials and methods

Macrofaunal data

Data on macrofaunal abundances were available from two study sites in Mahurangi Harbour (174° 45 min E, 36° 30 min S), North Island, New Zealand. One near where a major river enters the harbour (hereafter called mud) and one further out towards the harbour entrance (called sand). The mud site had a sandy-mud substrate with up to 54% mud (<63 μm). The sand site generally had little mud and a higher percentage (up to 88%) of fine to medium sand (63 to 500 μm). Twelve replicate core samples (13 cm diam. by 15 cm depth) were collected every three months at each site from July 1994 to April 2012. The replicates were randomly allocated the sample positions within 12 strata of equal size. Sites were located in the low- to mid-intertidal (tidal range 2–3 m).

Samples were sieved on a 0.5-mm mesh sieve and preserved in 50% IPA before being sorted to remove macrofauna. Macrofauna were identified to the lowest practical level (generally species, but at least to family level, with the exception of nemerteans and oligochaetes) and then counted.

Taxa were allocated to the following four functional groups based on biological traits: (i) suspension feeder; (ii) bioturbators (subsurface or surface dwellers that move particles and pore water); (iii) sediment stabilisers (sedentary surface dwellers or infauna that produce protruding tube mats); and (iv) sediment destabilisers (mobile surface dwellers that produce holes, pits or mounds in the sediment surface).

To identify the individual responses of species that are often numerically dominant, four species that were present at both sites were selected for analysis. When selecting these four, we also used criteria that ensured they covered a range of responses to mud content; from a preference for sand, through neutral, to a preference for high mud content. Unfortunately, we were unable to find a species with a preference for high mud content that occurred at both sites. Two of these species [*Macomona liliana* (Iredale, 1915) and *Austrovenus stutchburyi* (W. Wood 1828)] have been identified as key species on New Zealand's estuarine intertidal flats.

1 *Macomona liliana* is a deposit-feeding bivalve that lives 5 – 10 cm below the sediment surface as an adult and feeds on the surface, influencing the densities of other species, nutrient recycling and sediment oxygenation (Thrush *et al.*, 1997, 2006; Volkenborn *et al.*, 2013). For the functional group analyses, it was allocated to bioturbation and sediment destabilisation. *Macomona* prefers sandy sediment and is sensitive
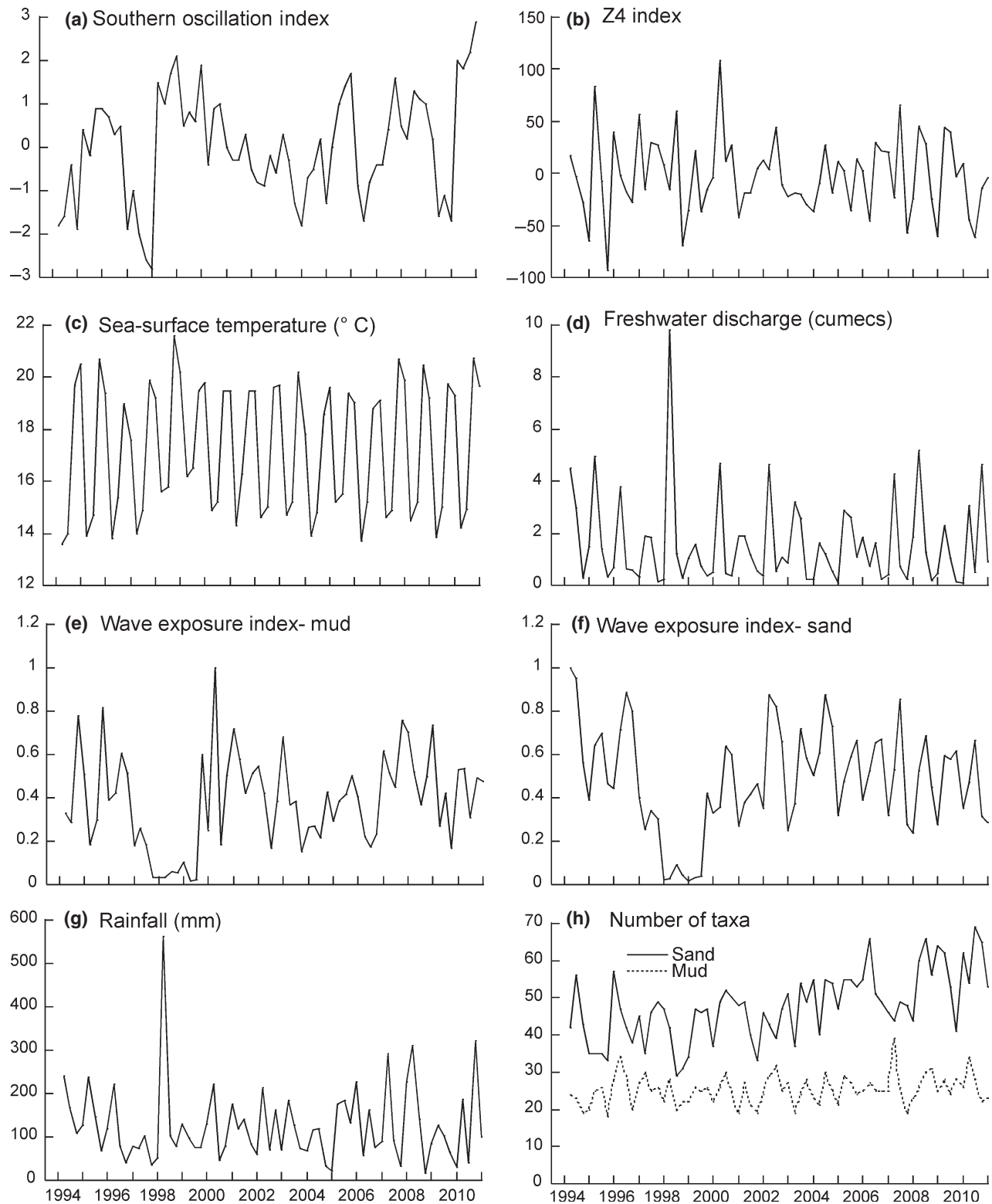
Fig. 1 Time series plots of environmental variables and number of taxa at both sites. Number of taxa is given as average per 12 cores (13 cm diam × 15 cm deep).

to terrestrial sediment deposition and suspended sediment (Thrush *et al.*, 2003, 2005; Ellis *et al.*, 2006; Anderson, 2008). It was found in higher numbers at the sand site and its abundance at the mud site decreased markedly over part of the time series, possibly as a response to increased sediment deposition at this site.

2 *Austrovenus stutchburyi*, the New Zealand cockle, is a suspension feeder living close to the sediment surface, influencing primary productivity and nutrient cycling (Thrush *et al.*, 2006; Sandwell *et al.*, 2009). For the functional group analyses, it was allocated to suspension feeding, bioturbation and sediment destabilisation. *Austrovenus* prefers a sand substrate to muddy sand substrate and is less sensitive to terrestrial sediment deposition and suspended sediment (Thrush *et al.*, 2003, 2005) than *Macomona*.

3 *Anthopleura aureoradiata* (Stuckey, 1909) is an anemone that lives on cockle shells. For the functional group analyses, it was allocated to suspension feeding, as it filters zooplankton from the water column. *Anthopleura* always occurred in higher densities at the sand site.

4 *Heteromastus filiformis* (Claparède, 1864) is a capitellid polychaete that feeds at depth in the sediment and defecates on the surface. In New Zealand, it appears to be one of the Capitellidae more sensitive to pollution (Hewitt unpub data). *Heteromastus* is found across a wide range of sediment mud contents (Thrush *et al.*, 2003, 2005) but in this study was found in higher densities at the mud site. For the functional group analyses, it was allocated to bioturbation and sediment destabilisation.

For each replicate core sample, the number of taxa and the abundance of organisms in the four functional trait groups were calculated. Then for each site/time, the average number of taxa, the abundance of the four functional traits and the abundance of the four species were calculated. Plots over time of the variables are presented in Figs 1h, 2 and 3.

Environmental data

Two indices of broad-scale temporal variability in climate were used [monthly estimates of the southern oscillation index (SOI) and the mean sea level pressure difference between Raoul and Chatham Islands (Z4, which represent the strength of westerly wind patterns)]. Monthly sea-surface temperature (SST) records were available until April 2011 from the nearby Leigh Marine Laboratory (University of Auckland). Monthly rainfall records were available from NIWA's CliFlo website, for a site (−36°26′3.66″, +174°40′3.58″) south of Warkworth, 10 km from the harbour. Daily discharge values for Mahurangi River were obtained from Auckland Council. This data was used to calculate an average monthly freshwater discharge volume. Wind exposure for both sites was calculated using input records of wind measurements. The wind rose data were used for both sites (mud and sand), assuming a constant wind field across the study domain. For each site, the fetch was measured from a map in eight cardinal directions. Wind speed in km.h^{-1} was binned into these eight classes, squared and multiplied by the fetch values to generate wave disturbance from eight directions (Burrows *et al.*, 2008).

As macrofaunal core data were collected every three months, corresponding physical data for each month were extracted for all physical variables (SOI, Z4, SST, wind exposure, freshwater input and rainfall). Plots of the information are available in Fig. 1a–g.

While a 17-year time period is not long, the variables we use are likely to exhibit extremes in a short time series. For example, although the Pacific Decadal Oscillation occurs over 60 – 70 years, NZ has undergone a shift within our time series. Moreover, changes in the intensity and strength of El Nino/La Nina events (one of the strongest climate oscillations on earth) occur around New Zealand at much shorter timescales and control wind, rainfall and ocean upwelling and thus influence coastal ecosystems. A very intense El Nino event occurred in 1998/1999 and annual mean sea level pressure for 1996, 1998, 2007, 2010 and 2012 differed from the average over the 1961–1990 periods by 2 standard deviations. A series of data sets were searched to provide evidence that the time period of our data did encompass environmental fluctuations that were similar to longer time periods. Air temperature and rainfall were available from a nearby site from 1972, SOI was available from 1876, and Z4 was available from 1938. Maxima, 90th percentiles, 10th percentiles and minima were calculated for each time period (Appendix S1). While the monitored time period did not encompass the maximum or minimum of the longer SOI or Z4 time series, the 90th and 10th percentiles were similar, and the maximum and minimum found for the SOI and Z4 data from 1972 (40 years) were similar to those observed in our shorter time period. The monitored time period also encompassed the daily rainfall and the daily minimum and maximum temperatures from 1972–2012.

Statistical analysis

Regression trees were used to investigate responses to environmental drivers (Breiman *et al.*, 1984; De'ath & Fabricius, 2000). Initially slow to be used in ecology, their ability to deal with nonlinear relationships and interactions has seen their use increase markedly since 2000. Trees explain variation in a single response variable by repeatedly splitting the data into two more homogeneous groups, using the best explanatory variable in each case. Regression tree analyses were conducted for each site separately, using the RPART package (Therneau *et al.*, 2014 available in R (R Core Team, 2013)). Tree growth was constrained to have a minimum of 20 observations in a node (group) before attempting a split; the split had to increase the fit (represented by the R^2) by ≥0.03 and each terminal node (final most homogeneous group) had to contain at least 6 observations. Tenfold cross validation was used to prune and produce the optimum tree.

Due to correlations between SOI and Z4, the regression trees were constrained to only use whichever of these appeared first in the tree. Lagged variables were included, but once the lag of a variable was chosen, subsequent tree structure was constrained to using that lag (full tree structures are given in Appendix S2). As regression tree analysis does not have any distributional assumptions, no transformations were used.
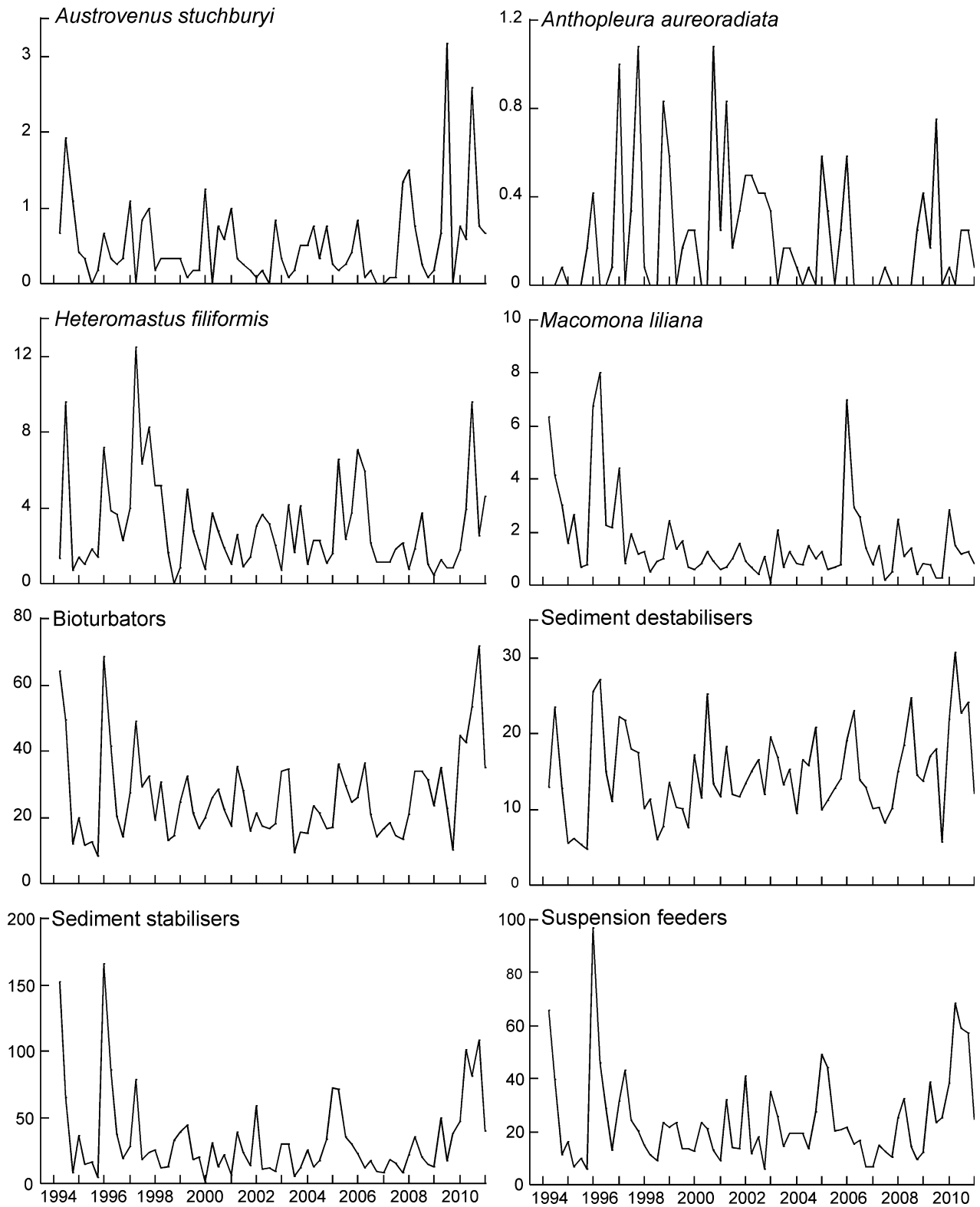
Fig. 2 Time series plots of abundance of biological response variables at the sand site. Abundance is average abundance of 12 cores (13 cm diam × 15 cm deep).
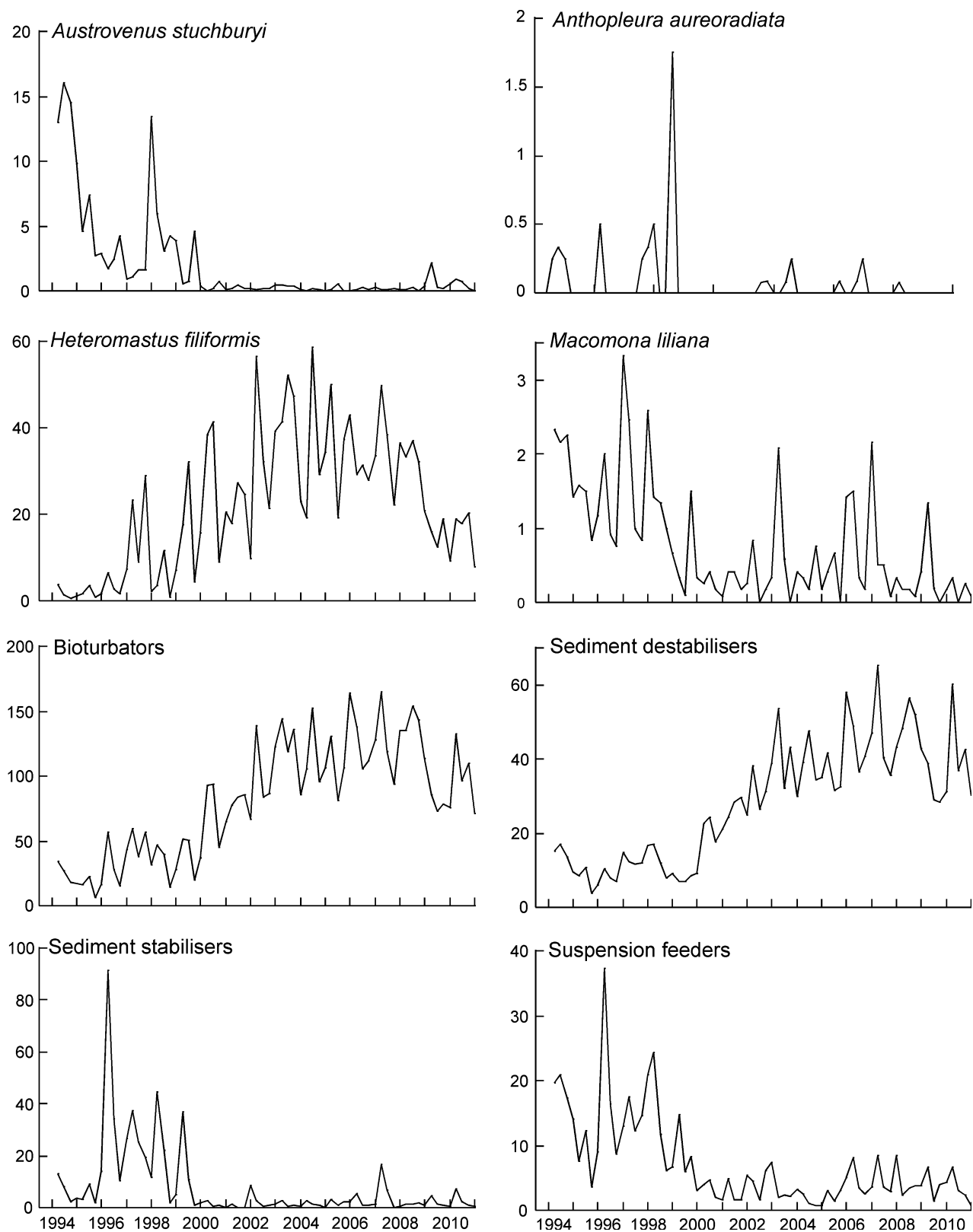
Fig. 3 Time series plots of abundance of biological response variables at the mud site. Abundance is average abundance of 12 cores (13 cm diam × 15 cm deep).

As regression trees will split the data into trees even if a linear model would fit the data (Breiman *et al.*, 1984), models were checked to determine whether the regression tree approach was valid by the following: (i) comparing the % explained by the regression tree (1 – relative error) with a linear multiple regression (model deviance/total deviance); (ii) visual inspection of residuals from a linear multiple regression and (iii) scatter plots highlighting the regression tree splits. Multiple regression models were derived using generalised linear modelling techniques (normal or poisson error structures) with backward selection. If these models explained as much variation as did the regression tree, we would assume that no nonlinearities, thresholds or interactions occurred.

Results

Hypothesis 1 – were responses to environmental variables linear?

No. Multiple linear regression models explained less of the variability than the regression trees for all but *Anthopleura* at the mud site, which had very low abundances and was not well explained by either method (Table 1). *Anthopleura* at this site was thus dropped from further analysis and discussion. The increase in % explained by the regression tree approach ranged from 4% (sediment stabilisers at the mud site) to 41% (sediment destabilisers at the mud site) with an average increase of 25%. The magnitude of change in densities (highest group – lowest group as a % of the average, Table 1), predicted by the first three tree levels, varied from 30.1–171.8% at the mud site and 29.8–173.1% at the sand site.

Hypothesis 2 – which variables were most important and did interactions occur?

Similar results were found at both sites. SST was the environmental variable most likely to form the first split, followed by SOI or wave exposure (Table 2). These first splits explained % magnitude changes from 15 to 123 (Table 1), leaving between 18 and 54% of the changes still to be explained. SOI was also most likely to form the second split. Wave exposure was the next most likely variable overall, whereas freshwater input was never identified as a driver within the first two nodes of a tree.

There were no models that used all five environmental variables (i.e. waves, rainfall, freshwater, SST and either SOI or Z4). However, interactions between four environmental variables did occur for bioturbators and *Macomona* at both sites and number of taxa and *Heteromastus* at the sand site (Table 3). For example, wave exposure provided a first-level split for bioturbators at the mud site, followed by SOI at the second level, freshwater at the third level and SST at the fourth. Interactions between a single pair of environmental variables only occurred for *Austrovenus* (SOI and rain) at the mud site and for suspension feeders and *Austrovenus* (SST and SOI) at the sand site. Pairwise interactions generally involved SST with either SOI or rain,

Table 2 Variables driving the first two nodes in the regression trees summed over all response variables at each site. Appendix S2 shows the complete tree for each variable at both sites

	SST	SOI	Waves	Rain	Z4	Freshwater
Mud site						
1st split	4	2	2			
2nd split		5	2	2	1	
Total	4	7	4	2	1	0
Sand site						
1st split	5	2	1	1		
2nd split	1	5	2	1	1	
Total	6	7	3	2	1	0

Table 1 Percentage explained by multiple linear regression verses regression tree models at each site. Blank cells are where final models explained < 10% of the variance. Also given is the magnitude of the difference between the highest value and the lowest value group (as a % of the average) predicted by the tree down to three split levels (3S) and the first level only (1S)

	Mud site				Sand site			
	Linear	Tree	3S	1S	Linear	Tree	3S	1S
Austrovenus	13	23	172	123		30	173	79
Heteromastus		30	94	69	14	23	105	63
Macomona	19	41	146	88		27	107	86
Anthopleura					16	33	168	99
Stabilisers	17	21	146	111		23	126	76
Destabilisers		41	116	93		38	58	34
Suspension feeders	16	40	108	85		22	94	52
Bioturbators		39	96	79		30	65	46
No. of taxa	24	42	30	15		39	30	17

Table 3 Environmental variables important for the regression tree models at each site

	T SOI	T W	T F	T R	T Z4	SOI W	SOI F	SOI R	F R	R Z4
Mud site										
Austrovenus								y		
Heteromastus			y					y		
Macomona	y							y	y	
Stabilisers		y				y				
Destabilisers						y		y		
Suspension feeders		y				y				
Bioturbators		y			y	y				
No. of taxa			y	y						y
Sand site										
Anthopleura		y			y					
Austrovenus	y									
Heteromastus	y		y					y		
Macomona	y		y					y		
Stabilisers	y	y				y				
Destabilisers		y				y				
Suspension feeders	y									
Bioturbators	y						y		y	
No. of taxa						y		y	y	

The presence of two-way interactions is indicated by 'y', blank cells indicate no two-way interactions. T = SST, W = wave exposure, R = rainfall, F = freshwater.

Table 4 Environmental variables with splits occurring more than once in the tree. Where the lowest or highest densities of the response variable show a unimodal response, the range of the environmental variable is given

Response variable	Environmental variable	Range
Mud site		
Austrovenus	SOI	Lowest 0.15 to −1.35
Heteromastus	SOI	Highest −0.25 to −1.45
Macomona	Freshwater	
Stabilisers	Waves	Lowest 0.16 to 0.72
Destabilisers	SOI	
Suspension feeders	SOI	Lowest −0.7 to −1.65
Bioturbators	Freshwater	Lowest 0.69 to 0.31
No. of taxa	Rain	
Sand site		
Anthopleura	Z4	Lowest 53 to 19
Austrovenus	SOI	Lowest −0.75 to −1.45
Heteromastus	SOI	Lowest 0.45 to −1.15
Macomona	SST	
Stabilisers	SST	Lowest 19.3 to 14.3
Destabilisers	Waves	Highest 0.40 to 0.14
Suspension feeders	SST	Lowest 19.3 to 14.5
No. of taxa	SOI	Lowest 0.25 to 0.95

followed by SOI and wave exposure. No pairwise interactions between waves and Z4, freshwater or rain were observed, nor between Z4 and freshwater.

Occasionally, a tree would reuse a variable in another split further down the tree. Examination of the mean densities associated with these splits revealed that none of these was coincident with a monotonic change in the response variable (Table 4). For example, the number of destabilisers at the mud site had three splits associated with SOI, occurring at SOI values of −1.45, 0.55 and 1.05. The lowest mean abundances occurred between SOI values of 0.55–1.05, and the highest with SOI values >1.05.

Hypothesis 3 – comparison of sensitive species responses between sites

Macomona at the mud site had highest densities when SST <14.1 °C (low winter temperatures), while at the sand site, high densities did not appear to be affected by SST at all. Rainfall had an influence on lowest densities at both sites for *Macomona*, with lower splitting values at the mud site (<77 m^3 s^{-1}) than the sand site (<223 m^3 s^{-1}). Highest densities of *Austrovenus* were found with a strongly negative SOI in the previous

month at the mud site but at an even stronger negative SOI at the sand site.

Hypothesis 4 – functional trait responses and number of taxa vs. individual species

Functional trait groups did not produce less complex trees, interactions or nonmonotonic responses than individual species (Tables 3 and 4), although the variables selected as good predictors did vary. Functional trait groups were more likely to have wave exposure as an important factor than individual species (eight nodes across all traits *cf.* zero at the mud site and six vs. one at the sand site). There was also no consistent difference between functional traits and individual species in the magnitude of the change between highest and lowest values predicted by the trees. For the sand site, the % magnitude change was greater for individual species than for functional traits (one-sided *t*-test with equal variance, $P = 0.0375$), but there was no significant difference for the mud site (one-sided *t*-test with equal variance, $P = 0.2032$).

Number of taxa was the response variable best predicted at both sites (Table 1), with wave exposure, temperature, ENSO and rainfall all important predictors of variation (Table 3). At the sand site, wave exposure

was the most important factor, with the highest number of taxa found with more waves in years with a positive SOI (Table 5). Lowest numbers of taxa were observed in years with a low numbers of waves. At the mud site, where waves were low, SST was the most important factor. Highest numbers of taxa were observed with lower SST when rainfall was high, and lowest numbers were observed with higher SST and a strongly negative Z4.

Discussion

Our results have important implications for how we should consider ecological responses to climate change. We observed responses to climate change at all levels from individual species to community level responses such as species richness and functional traits. Interestingly, the number of taxa was the response variable best predicted at both sites, suggesting that species richness has the potential to be strongly affected by climate change. We observed indications that species that are near the edge of their tolerance to another stressor may have a lower threshold. Thus, intact communities

may be more resilient to climatic disturbances and may minimise the risk of population collapses and biodiversity loss due to climate change (Hughes *et al.*, 2003). Although the magnitude of these effects we observed was weak, they do imply that this is an important avenue for future research on how communities respond to change.

Our fourth hypothesis was related to the potential for ecosystem level responses to be smoother than species-level responses, with fewer nonlinear, threshold responses and interactions between variables. We found no evidence of this, which does not bode well for the resilience of function in the face of climate change. This may have been a result of the timescales we were analysing over, only 17 years. Longer timescales may allow dispersal and recruitment of other species to build resilience in functional traits.

Definite nonlinear responses to environmental variables were observed (hypothesis 1), with all but one of our ecological response variables being better explained by regression tree models than multiple linear regression. These nonlinearities usually involved thresholds, with highest or lowest densities of biological response

Table 5 Summary of the key environmental variables and split values identified at the mud and sand sites for which highest and lowest values of response variables occurred

Response variable	Mud site		Sand site	
	Highest abundance	Lowest abundance	Highest abundance	Lowest abundance
Anthopleura			SST lag≥ 17.2 Waves<0.41	SST lag<17.2 Z4 lag 53 to −19
Austrovenus	SOI lag ≤−1.35	SOI lag > 0.15 Rain <222.6	SOI< −1.45	SOI −1.45 to −0.75 SST<19.8
Heteromastus	SOI 1.45 to −0.25	SOI >−0.25 Rain < 131.6 SST lag > 18.3	SOI lag <1.15	SOI lag≥1.15 Rain<176.6 SST ≥19.5
Macomona	SST <14.1	SST ≥14.1 SOI lag ≥−1.15 Rain≤76.5	Rain ≥223	Rain <223 SOI lag ≥ −1.15 SST lag<18.1
Stabilisers	SST <14.1	SST ≥14.1 Waves 0.72 to 0.17 SOI lag ≥1.65	SST<14.3	SST ≥14.3 SOI <1.65 Waves >0.49
Destabilisers	Waves ≥0.17 SOI ≥1.05	Waves <0.17	SST ≥14.5 Waves 0.13 to 0.40 SOI lag≥0.4	SST ≥14.5 Waves<0.13
Suspension feeders	SST <14.1	SST ≥14.1 Waves ≥0.17 SOI −0.7 to −1.65	SST<14.5	SST ≥14.5 SOI 0.95 to 1.65
Bioturbators	Waves ≥0.17 SOI ≥−1.45 FW ≥0.69 SST lag ≥15.9	Waves <0.17	SST <14.5	SST ≥14.5 SOI lag <1.25 FW <0.64 Rain <61.6
No. of taxa	SST <15.7 Rain ≥185.7	SST ≥15.7 Z4 lag <−26.5	Waves <0.14 SOI ≥0.95	Waves >0.14

variables found nearer to the centre of the observed environmental range, rather than occurring at either end. Importantly, our results suggest that responses are a result of interactions occurring between climate change-related variables and highlight the potential for sudden changes. There is a body of marine literature that suggest that interactive and nonindependent effects may be important (Hoffman *et al.*, 2003; Reynaud *et al.*, 2003; Pörtner *et al.*, 2005).

As per our second hypothesis, all trees had more than one level, demonstrating that interactions occurred. While temperature was the most likely predictor forming the primary split at both sites, ENSO variables and wave exposure were also frequently important. In coastal zones, wave disturbance is an important driver of species distributions (e.g. Hewitt & Thrush, 2009; Pedersen *et al.*, 2012; Tam & Scrosati, 2014). In particular, estuarine and near-shore species may be exposed to synergistic effects where wave disturbance increased by increasing storm frequency/intensity is further increased by changing water depth as sea levels rise. Further, changes in broad-scale processes such as wave climate can have important implications for local ecological interactions. For example, field experiments have demonstrated that wave climate influenced the strength of negative ecological interactions among adult and juvenile bivalves (Thrush *et al.*, 2000).

Changes in the abundance of key species may result in far-reaching effects, as frequently such species perform more than a single function. For both sites, lower densities of *Macomona* (up to 140% of average) were predicted to occur with increasing temperatures, in combination with lower rainfalls and low SOI values. Similarly, low SOI values in combination with lower rainfall were predicted to decrease densities of *Austrovenus* at the sand site, but at the mud site, increasing temperatures would result in increasing densities. These changes would result in differences in the way nutrients are processed and exchanged between the sediment and the water column and the degree of primary productivity. Adult *Macomona* control macrofaunal community composition, pore water pressure gradients, the presence of anoxic water at the sediment – water interface and nutrient fluxes (Thrush *et al.*, 2000, 2006, 2014; Volkenborn *et al.*, 2013). *Austrovenus*, while a lesser driver of macrofaunal community composition, does control primary productivity, nutrient fluxes and sedimentation rates (Thrush *et al.*, 2001, 2006; Sandwell *et al.*, 2009; Hewitt & Cummings, 2013). A positive feedback loop has been demonstrated to exist between mud content, sediment chlorophyll *a* and *Austrovenus* density in clear water that is broken when light levels are decreased (Thrush *et al.*, 2014). Thus,

changes in these key dominants may control the potential for threshold responses and regime shifts in ecosystem functioning in response to land-use change induced sediment inputs into the coastal zone.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Maxima, 90th and 10th percentiles and minima of selected environmental variables for different time periods.

Appendix S2 Regression trees structure for each response variable at the two sites separately.