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

Running header: Nonlinear responses of coastal macrofauna

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ABSTRACT

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25 Global climate change will undoubtedly be a pressure on coastal marine ecosystems, not only
26 affecting species distributions and physiology but also ecosystem functioning. In the coastal
27 zone, the environmental variables that may drive ecological responses to climate change
28 include temperature, wave energy, upwelling events and freshwater inputs, and all act and
29 interact at a variety of spatial and temporal scales). To date we have a poor understanding of
30 how climate-related environmental changes may affect coastal marine ecosystems or which
31 environmental variables are likely to produce priority effects. Here we use time series data
32 (17 years) of coastal benthic macrofauna to investigate responses to a range of climate
33 influenced variables including sea surface temperature, southern oscillation indices (SOI,
34 Z4), wind-wave exposure, freshwater inputs and rainfall. We investigate responses from the
35 abundances of individual species to abundances of functional traits and test whether species
36 that are near the edge of their tolerance to another stressor (in this case sedimentation) may
37 exhibit stronger responses. The responses we observed were all nonlinear and exhibited
38 thresholds. While temperature was most frequently an important predictor, wave exposure
39 and ENSO-related variables were also frequently important and most ecological variables
40 responded to interactions between environmental variables. There were also indications that
41 species sensitive to another stressor responded more strongly to weaker climate-related
42 environmental change at the stressed site than the unstressed site. The observed interactions
43 between climate variables, effects on key species or functional traits, and synergistic effects
44 of additional anthropogenic stressors have important implications for understanding and
45 predicting the ecological consequences of climate change to coastal ecosystems.

46

47 INTRODUCTION

48 Anthropogenically induced global climate change has profound implications for marine
49 ecosystems. Globally, the marine environment is changing rapidly (Hoegh-Guldberg &
50 Bruno, 2010; Doney *et al.*, 2012) with unprecedented rates of change in sea water
51 temperature throughout much of the globe occurring in the last decade (Philippart *et al.*,
52 2011). Changes also include the loss of sea ice cover in the Arctic and Antarctic, rising sea
53 level, increased storm events, more variable precipitation with more frequent intense rainfall
54 events and earlier occurrence of springtime phytoplankton blooms (IPCC, 2007; Solomon *et al.*,
55 2007; Hoegh-Guldberg & Bruno, 2010). Although marine species and ecosystems have
56 responded to such variations in their environment throughout evolutionary history, a primary

57 concern is the rapid rate of change currently observed (Root *et al.*, 2003; Philippart *et al.*,
58 2011).

59

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

73

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

80

81 Efforts to manage and conserve living coastal systems in the face of climate change requires
82 research that investigates community and functional attributes, synergistic effects with other
83 anthropogenic variables, and ecological thresholds. While laboratory experiments can
84 generally be used to investigate organism responses/sensitivities to single (or at most a few)
85 variables at small scales, field-based manipulative experiments at an appropriate scale are
86 generally impossible. Time series data offer the opportunity to develop and test general
87 hypotheses and to observe correlative patterns that may be used for large-scale predictions.

88 Within this study, we use a time series of 17 years in the abundances of coastal benthic
89 macrofauna to investigate biological responses. The 17 years covers a time period of strong
90 southern oscillation, with winter water temperatures that varied from 13 to 16 °C (Figure 1a-
91 c). The following hypotheses were investigated:

- 92 1. The majority of responses will be nonlinear, and on occasion exhibit thresholds (i.e., a
93 sudden drop in abundance or a change from increasing to decreasing abundance).
- 94 2. Responses to many variables, not just temperature, will be observed and interactions
95 between variables will drive the responses.
- 96 3. Species that are near the edge of their tolerance to another stressor will exhibit
97 responses with a lesser degree of change of climate- driven environmental variables.
- 98 4. Species replacement within functional trait groupings will result in shifted thresholds
99 such that thresholds are only detected at more extreme conditions, than those detected
100 for individual species.

101 We focus on benthic macrofauna as this group has been demonstrated to: affect benthic
102 microphyte communities and primary productivity (e.g., Thrush *et al.*, 2006; Colen *et al.*,
103 2008; Volkenborn *et al.*, 2009); modify hydrodynamics, nutrient recycling and benthic
104 pelagic coupling (e.g., Eckman *et al.*, 1981; Pilditch *et al.*, 1997; Nikora *et al.*, 2002; Lohrer
105 *et al.*, 2004; Newell, 2004); and provide food for fish and birds. Benthic macrofauna are
106 frequently used throughout the world in marine health and quality indices (e.g., Alden *et al.*,
107 2002; Borja & Dauer, 2008; Villnäs & Norkko, 2011; Rodil *et al.*, 2013). We move beyond
108 impacts to single species by considering effects on two key species which thus have the
109 potential to impact on the larger community (Harley *et al.*, 2006; Thrush *et al.*, 2009; Thrush
110 *et al.*, 2014). Finally, we use biological trait analysis to focus on some key functional traits
111 that would alter ecosystem function and, therefore, ecosystem services (Sara *et al.*, 2014).

112

113 MATERIALS AND METHODS

114 *Macrofaunal Data*

115 Data on macrofaunal abundances were available from two study sites in Mahurangi Harbour
116 (174 degrees 45 minutes E, 36 degrees 30 minutes S), North Island, New Zealand. One near
117 where a major river enters the harbour (hereafter called mud) and one further out towards the
118 harbour entrance (called sand). The mud site had a sandy-mud substrate with up to 54% mud

119 (<63 μm). The sand site generally had little mud and a higher percentage (up to 88%) of fine
120 to medium sand (63 to 500 μm). Twelve replicate core samples (13 cm diam. by 15 cm
121 depth) were collected every three months at each site from July 1994 to April 2012. The
122 replicates were randomly allocated sample positions within 12 strata of equal size. Sites were
123 located in the low to mid intertidal (tidal range 2 – 3 m).

124

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

129

130 Taxa were allocated to the following four functional groups based on biological traits: (1)
131 suspension feeder; (2) bioturbators (subsurface or surface dwellers that move particles and
132 pore water); (3) sediment stabilisers (sedentary surface dwellers or infauna that produce
133 protruding tube mats); and (4) sediment destabilisers (mobile surface dwellers that produce
134 holes, pits or mounds in the sediment surface).

135

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

- 144 • *Macomona liliana* is a deposit-feeding bivalve that lives 5 – 10 cm below the
145 sediment surface as an adult and feeds on the surface, influencing the densities of
146 other species, nutrient recycling and sediment oxygenation (Thrush *et al.*, 1997;
147 Thrush *et al.*, 2006; Volkenborn *et al.*, 2013). For the functional group analyses it was
148 allocated to bioturbation and sediment destabilisation. *Macomona* prefers sandy
149 sediment and is sensitive to terrestrial sediment deposition and suspended sediment

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

- 154 • *Austrovenus stutchburyi*, the New Zealand cockle, is a suspension feeder living close
155 to the sediment surface, influencing primary productivity and nutrient cycling (Thrush
156 *et al.*, 2006; Sandwell *et al.*, 2009). For the functional group analyses it was allocated
157 to suspension feeding, bioturbation and sediment destabilisation. *Austrovenus* prefers
158 a sand to muddy sand substrate and is less sensitive to terrestrial sediment deposition
159 and suspended sediment (Thrush *et al.*, 2003; Thrush *et al.*, 2005) than *Macomona*.
- 160 • *Anthopleura aureoradiata* (Stuckey, 1909) is an anemone that lives on cockle shells.
161 For the functional group analyses, it was allocated to suspension feeding, as it filters
162 zooplankton from the water column. *Anthopleura* always occurred in higher densities
163 at the sand site.
- 164 • *Heteromastus filiformis* (Claparède, 1864) is a capitellid polychaete that feeds at
165 depth in the sediment and defecates on the surface. In New Zealand, it appears to be
166 one of the Capitellidae more sensitive to pollution (Hewitt unpub data). *Heteromastus*
167 is found across a wide range of sediment mud contents (Thrush *et al.*, 2003; Thrush *et*
168 *al.*, 2005) but in this study was found in higher densities at the mud site. For the
169 functional group analyses it was allocated to bioturbation and sediment
170 destabilisation.

171

172 For each replicate core sample, the number of taxa and abundance of organisms in the four
173 functional trait groups were calculated. Then for each site/time, the average number of taxa,
174 abundance of the four functional traits and abundance of the four species was calculated.

175 Plots over time of the variables are presented in Figures 1h, 2 and 3.

176

177 *Environmental Data*

178 Two indices of broad-scale temporal variability in climate were used (monthly estimates of
179 the southern oscillation index (SOI) and the mean sea level pressure difference between
180 Raoul and Chatham Islands (Z4, which represent the strength of westerly wind patterns).

181 Monthly sea-surface temperature (SST) records were available until April 2011 from the
182 nearby Leigh Marine Laboratory (University of Auckland). Monthly rainfall records were
183 available from NIWA's CliFlo website, for a site (-36°26'3.66", +174°40'3.58") south of
184 Warkworth, 10 km from the harbour. Daily discharge values for Mahurangi River were
185 obtained from Auckland Council. This data was used to calculate an average monthly
186 freshwater discharge volume. Wind exposure for both sites was calculated using input
187 records of wind measurements. The wind rose data was used for both sites (mud and sand),
188 assuming a constant wind field across the study domain. For each site the fetch was measured
189 from a map in eight cardinal directions. Wind speed in km.h⁻¹ was binned into these eight
190 classes, squared and multiplied by the fetch values to generate wave disturbance from eight
191 directions (Burrows *et al.*, 2008).

192

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

196

197 While a 17 year time period is not long, the variables we use are likely to exhibit extremes in
198 a short time series. For example, although the Pacific Decadal Oscillation occurs over 60 –
199 70 years, NZ has undergone a shift within our time series. Moreover, changes in the intensity
200 and strength of El Nino/La Nina, events (one of the strongest climate oscillations on earth)
201 occur around New Zealand at much shorter time scales and control wind, rainfall and ocean
202 upwelling and thus influence coastal ecosystems. A very intense El Nino event occurred in
203 1998/1999 and annual mean sea level pressure for 1996, 1998, 2007, 2010 and 2012 differed
204 from the average over the 1961 – 1990 period by 2 standard deviations. A series of datasets
205 were searched to provide evidence that the time period of our data did encompass
206 environmental fluctuations that were similar to longer time periods. Air temperature and
207 rainfall were available from a nearby site from 1972, SOI was available from 1876 and Z4
208 was available from 1938. Maxima, 90th percentiles, 10th percentiles and minima were
209 calculated for each time period (Supporting information S1). While the monitored time
210 period did not encompass the maximum or minimum of the longer SOI or Z4 time series, the
211 90th and 10th percentiles were similar, and the maximum and minimum found for the SOI and
212 Z4 data from 1972 (40years) were similar to those observed in our shorter time period. The

213 monitored time period also encompassed the daily rainfall and the daily minimum and
214 maximum temperatures from 1972- 2012.

215 *Statistical Analysis*

216 Regression trees were used to investigate responses to environmental drivers (Breiman *et al.*,
217 1984; De' Ath *et al.*, 2000). Initially slow to be used in ecology, their ability to deal with non-
218 linear relationships and interactions has seen their use increase markedly since 2000. Trees
219 explain variation in a single response variable by repeatedly splitting the data into two more
220 homogeneous groups, using the best explanatory variable in each case. Regression tree
221 analyses were conducted for each site separately, using the rpart package (Therneau *et al.*,
222 2014 available in R (R Core Team, 2013)). Tree growth was constrained to have a minimum
223 of 20 observations in a node (group) before attempting a split; the split had to increase the fit
224 (represented by the R^2) by ≥ 0.03 and each terminal node (final most homogeneous group)
225 had to contain at least 6 observations. Tenfold cross validation was used to prune and
226 produce the optimum tree.

227

228 Due to correlations between SOI and Z4, the regression trees were constrained to only use
229 whichever of these appeared first in the tree. Lagged variables were included, but once the
230 lag of a variable was chosen, subsequent tree structure was constrained to using that lag (full
231 tree structures are given in S1). As regression tree analysis does not have any distributional
232 assumptions, no transformations were used.

233

234 As regression trees will split the data into trees even if a linear model would fit the data
235 (Breiman *et al.*, 1984), models were checked to determine whether the regression tree
236 approach was valid by: (1) comparing the % explained by the regression tree (1 – relative
237 error) with a linear multiple regression (model deviance/total deviance); (2) visual inspection
238 of residuals from a linear multiple regression and (3) scatter plots highlighting the regression
239 tree splits. Multiple regression models were derived using generalised linear modelling
240 techniques (normal or poisson error structures) with backwards selection. If these models
241 explained as much variation as did the regression tree, we would assume that no
242 nonlinearities, thresholds or interactions occurred.

243

244 RESULTS

245 *Hypothesis 1- were responses to environmental variables linear?*

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

254 *Hypothesis 2- which variables were most important and did interactions occur?*

255 Similar results were found at both sites. SST was the environmental variable most likely to
256 form the first split, followed by SOI or wave exposure (Table 2). These first splits explained
257 % magnitude changes from 15 to 123 (Table 1), leaving between 18 to 54% of the changes
258 still to be explained. SOI was also most likely to form the second split. Wave exposure was
259 the next most likely variable overall, whereas freshwater input was never identified as a
260 driver within the first two nodes of a tree.

261

262 There were no models that used all five environmental variables (i.e., waves, rainfall,
263 freshwater, SST and either SOI or Z4). However, interactions between 4 environmental
264 variables did occur for bioturbators and *Macomona* at both sites and number of taxa and
265 *Heteromastus* at the sand site (Table 3). For example, wave exposure provided a first level
266 split for bioturbators at the mud site, followed by SOI at the second level, freshwater at the
267 third level and SST at the fourth. Interactions between a single pair of environmental
268 variables only occurred for *Austrovenus* (SOI and rain) at the mud site and for suspension
269 feeders and *Austrovenus* (SST and SOI) at the sand site. Pairwise interactions generally
270 involved SST with either SOI or rain, followed by SOI and wave exposure. No pairwise
271 interactions between waves and Z4, freshwater or rain were observed, nor between Z4 and
272 freshwater.

273

274 Occasionally a tree would reuse a variable in another split further down the tree. Examination
275 of the mean densities associated with these splits revealed that none of these were coincident
276 with a monotonic change in the response variable (Table 4). For example, the number of
277 destabilisers at the mud site had three splits associated with SOI, occurring at SOI values of -
278 1.45, 0.55 and 1.05. The lowest mean abundances occurred between SOI values of 0.55 –
279 1.05, and the highest with SOI values >1.05.

280 *Hypothesis 3- comparison of sensitive species responses between sites*

281 *Macomona* at the mud site had highest densities when SST <14.1 °C (low winter
282 temperatures), while at the sand site, high densities did not appear to be affected by SST at
283 all. Rainfall had an influence on lowest densities at both sites for *Macomona*, with lower
284 splitting values at the mud site (<77 m³/s) than the sand site (<223 m³/s). Highest densities of
285 *Austrovenus* were found with a strongly negative SOI in the previous month at the mud site
286 but at an even stronger negative SOI at the sand site.

287 *Hypothesis 4- functional trait responses and number of taxa versus individual species*

288 Functional trait groups did not produce less complex trees, interactions or non-monotonic
289 responses than individual species (Tables 3 and 4), although the variables selected as good
290 predictors did vary. Functional trait groups were more likely to have wave exposure as an
291 important factor than individual species (8 nodes across all traits *cf.* 0 at the mud site and 6
292 versus 1 at the sand site). There was also no consistent difference between functional traits
293 and individual species in the magnitude of the change between highest and lowest values
294 predicted by the trees. For the sand site, the % magnitude change was greater for individual
295 species than for functional traits (one sided t-test with equal variance, $p = 0.0375$), but there
296 was no significant difference for the mud site (one sided t-test with equal variance, $p =$
297 0.2032).

298

299 Number of taxa was the response variable best predicted at both sites (Table 1), with wave
300 exposure, temperature, ENSO and rainfall all important predictors of variation (Table 3). At
301 the sand site, wave exposure was the most important factor, with the highest number of taxa
302 found with more waves in years with a positive SOI (Table 5). Lowest numbers of taxa were
303 observed in years with a low numbers of waves. At the mud site, where waves were low, SST

304 was the most important factor. Highest numbers of taxa were observed with lower SST when
305 rainfall was high, lowest numbers were observed with higher SST and a strongly negative Z4.

306 DISCUSSION

307 Our results have important implications for how we should consider ecological responses to
308 climate change. We observed responses to climate change at all levels from individual
309 species to community level responses such as species richness and functional traits.
310 Interestingly, the number of taxa was the response variable best predicted at both sites,
311 suggesting that species richness has the potential to be strongly affected by climate change.
312 We observed indications that species that are near the edge of their tolerance to another
313 stressor may have a lower threshold. Thus, intact communities may be more resilient to
314 climatic disturbances, and may minimize the risk of population collapses and biodiversity
315 loss due to climate change (Hughes *et al.*, 2003). Although the magnitude of these effects we
316 observed were weak, they do imply that this is an important avenue for future research on
317 how communities respond to change.

318

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

325

326 Definite nonlinear responses to environmental variables were observed (hypothesis 1), with
327 all but one of our ecological response variables being better explained by regression tree
328 models than multiple linear regression. These nonlinearities usually involved thresholds, with
329 highest or lowest densities of biological response variables found nearer to the centre of the
330 observed environmental range, rather than occurring at either end. Importantly our results
331 suggest that responses are a result of interactions occurring between climate change-related
332 variables and highlight the potential for sudden changes. There is a body of marine literature
333 that suggest that interactive and non-independent effects may be important (Hoffman *et al.*,
334 2003; Reynaud *et al.*, 2003; Pörtner *et al.*, 2005).

335

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

347

348 Changes in the abundance of key species may result in far reaching effects, as frequently such
349 species perform more than a single function. For both sites, lower densities of *Macomona*
350 (up to 140% of average) were predicted to occur with increasing temperatures, in
351 combination with lower rainfalls and low SOI values. Similarly, low SOI values in
352 combination with lower rainfall were predicted to decrease densities of *Austrovenus* at the
353 sand site, but at the mud site increasing temperatures would result in increasing densities.
354 These changes would result in differences in the way nutrients are processed and exchanged
355 between the sediment and the water column and the degree of primary productivity. Adult
356 *Macomona* control macrofaunal community composition, pore water pressure gradients, the
357 presence of anoxic water at the sediment – water interface and nutrient fluxes (Thrush *et al.*,
358 2000; Thrush *et al.*, 2006; Volkenborn *et al.*, 2013; Thrush *et al.*, 2014). *Austrovenus*, while a
359 lesser driver of macrofaunal community composition, does control primary productivity,
360 nutrient fluxes and sedimentation rates (Thrush *et al.*, 2001; Thrush *et al.*, 2006; Sandwell *et*
361 *al.*, 2009; Hewitt & Cummings, 2013). A positive feedback loop has been demonstrated to
362 exist between mud content, sediment chlorophyll *a* and *Austrovenus* density in clear water
363 that is broken when light levels are decreased (Thrush *et al.*, 2014). Thus, changes in these
364 key dominants may control the potential for threshold responses and regime shifts in
365 ecosystem functioning in response to land-use change induced sediment inputs into the
366 coastal zone.

367

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534

535 SUPPORTING INFORMATION

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

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

539

540

541 FIGURES

542 Figure 1. Time series plots of environmental variables and number of taxa at both sites.

543 Number of taxa is given as average per 12 cores (13 cm diam x 15 cm deep).

544 Figure 2. Time series plots of abundance of biological response variables at the sand site.

545 Abundance is average abundance of 12 cores (13 cm diam x 15 cm deep).

546 Figure 3. Time series plots of abundance of biological response variables at the mud site.

547 Abundance is average abundance of 12 cores (13 cm diam x 15 cm deep).

548

549

550 Table 1. Percent explained by multiple linear regression vs regression tree models at each
 551 site. Blank cells are where final models explained < 10% of the variance. Also given is the
 552 magnitude of the difference between the highest value and lowest value group (as a % of the
 553 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
<i>Austrovenus</i>	13	23	172	123	30	173	79	
<i>Heteromastus</i>		30	94	69	14	23	105	63
<i>Macomona</i>	19	41	146	88		27	107	86
<i>Anthopleura</i>					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

554

555

556 Table 2. Variables driving the first two nodes in the regression trees summed over all
 557 response variables at each site. Supporting Information S2 shows the complete tree for each
 558 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

559

560

561 Table 3. Environmental variables important for the regression tree models at each site. The
 562 presence of two-way interactions are indicated by 'y', blank cells indicate no two way
 563 interactions. T= SST, W = wave exposure, R = rainfall, F = freshwater.

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

564

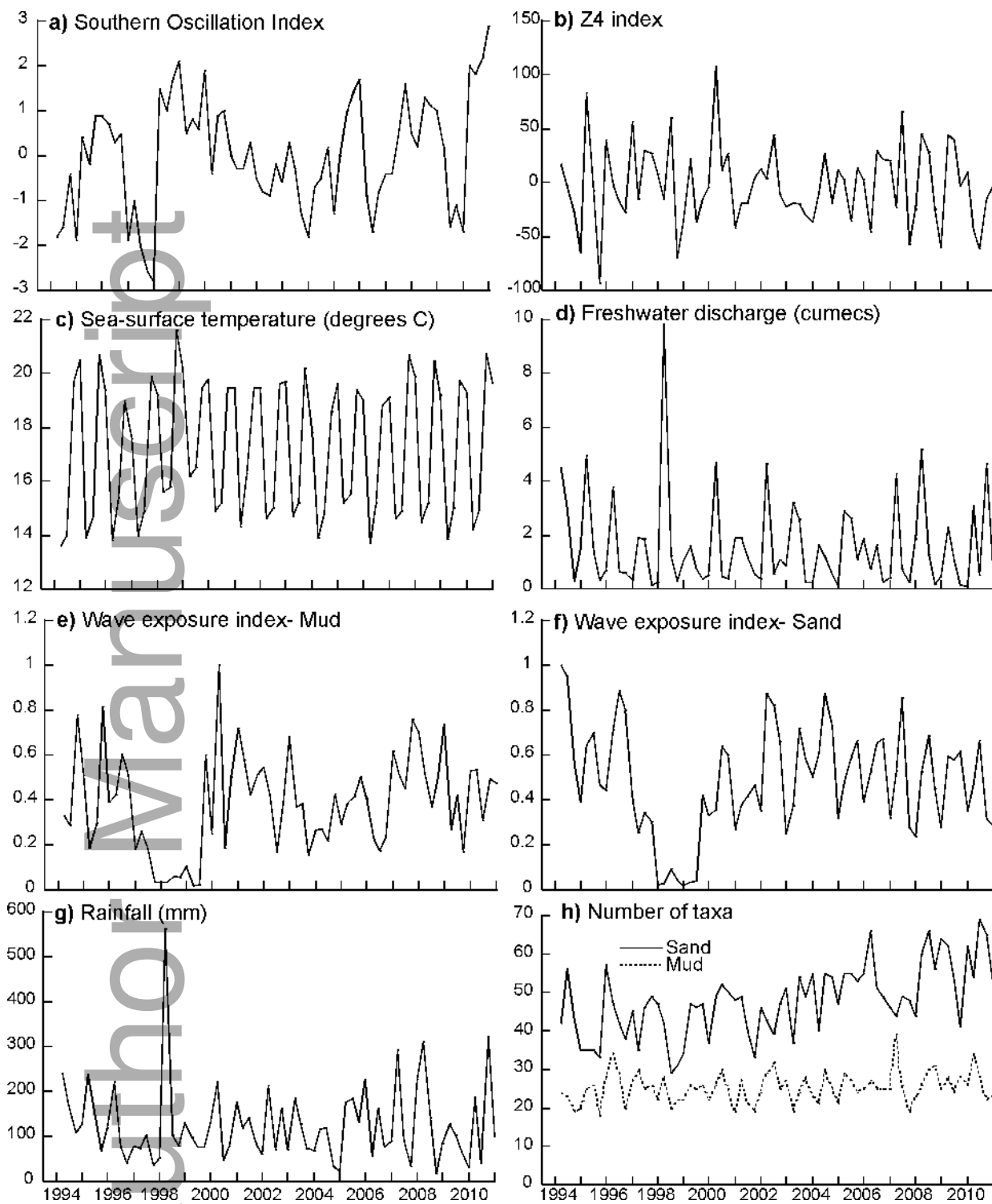
565 Table 4: Environmental variables with splits occurring more than once in the tree. Where the
 566 lowest or highest densities of the response variable show a unimodal response, the range of
 567 the environmental variable is given.

Mud Site		
Response variable	Environmental variable	Range
<i>Austrovenus</i>	SOI	Lowest 0.15 to -1.35
<i>Heteromastus</i>	SOI	Highest -0.25 to -1.45
<i>Macomona</i>	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		
Response variable	Environmental variable	Range
<i>Anthopleura</i>	Z4	Lowest 53 to 19
<i>Austrovenus</i>	SOI	Lowest -0.75 to -1.45
<i>Heteromastus</i>	SOI	Lowest 0.45 to -1.15
<i>Macomona</i>	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

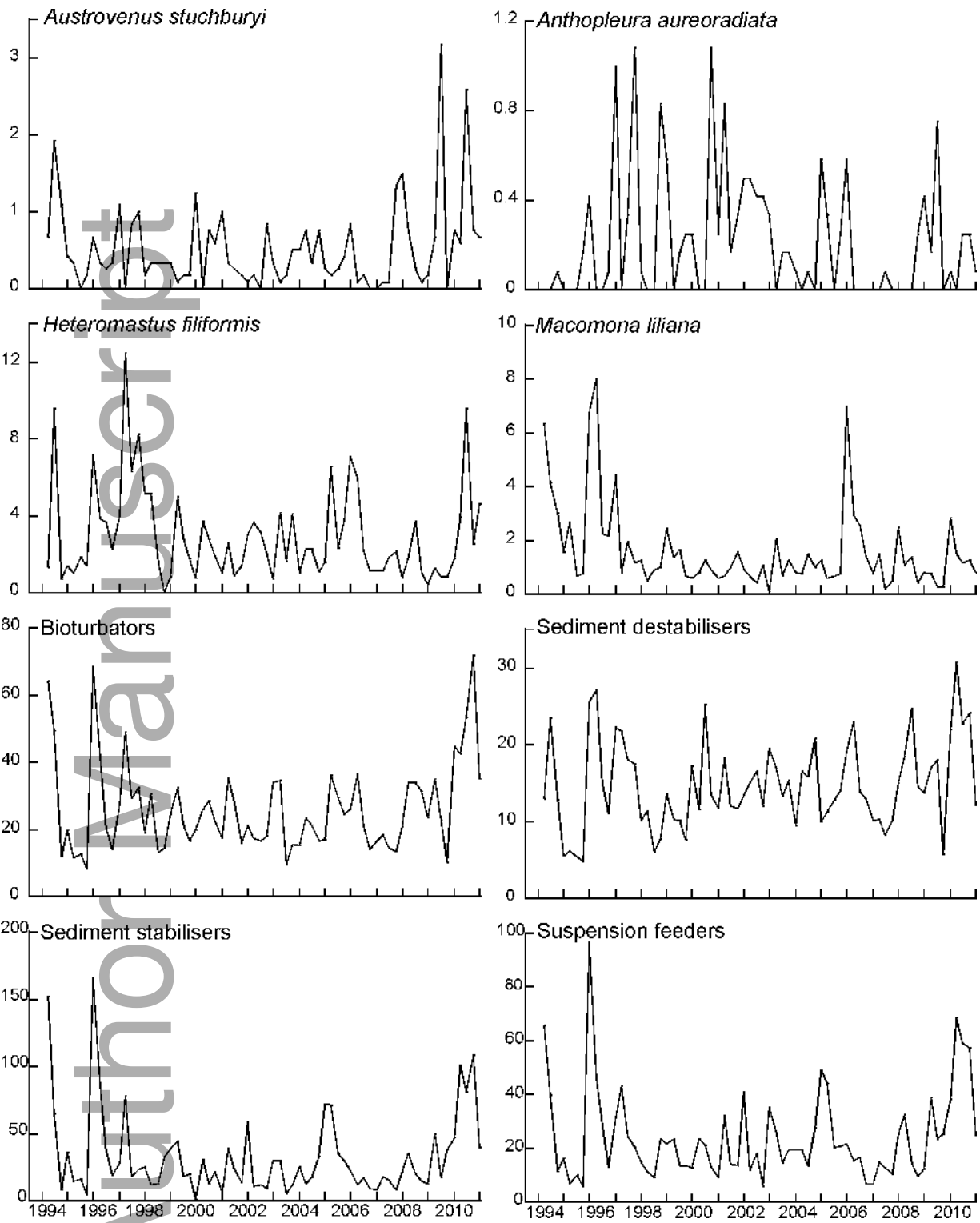
568
 569 Table 5: Summary of key environmental variables and split values identified at the mud and
 570 sand sites for which highest and lowest values of response variables occurred.

Response variable	Mud site		Sand site	
	Highest abundance	Lowest abundance	Highest abundance	Lowest abundance
<i>Anthopleura</i>			SST lag \geq 17.2 Waves $<$ 0.41	SST lag $<$ 17.2 Z4 lag 53 to -19
<i>Austrovenus</i>	SOI lag \leq -1.35	SOI lag $>$ 0.15	SOI $<$ -1.45	SOI -1.45 to -0.75

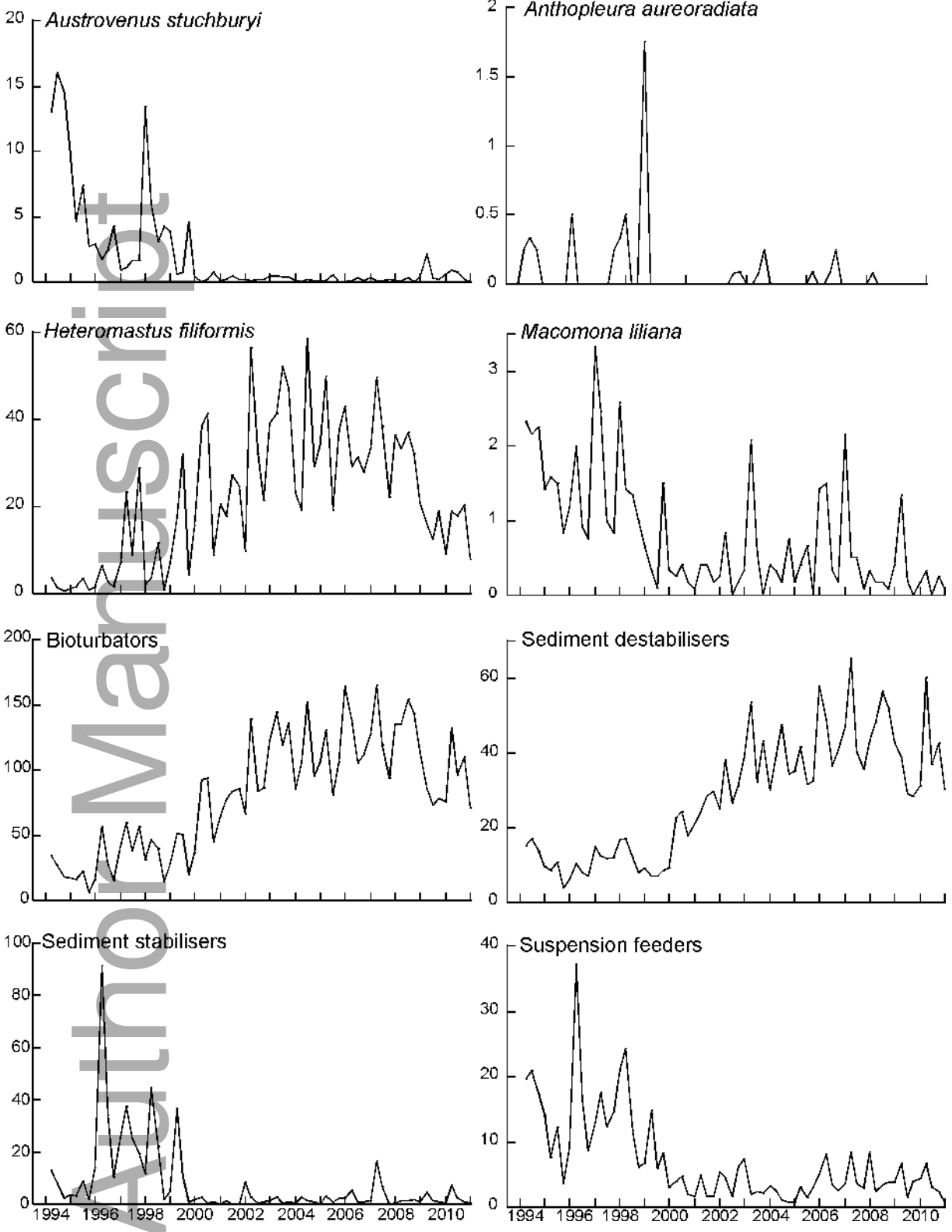
		Rain <222.6		SST<19.8
<i>Heteromastus</i>	SOI 1.45 to -0.25	SOI>-0.25	SOI lag<1.15	SOI lag≥1.15
		Rain < 131.6		Rain<176.6
		SST lag > 18.3		SST≥19.5
<i>Macomona</i>	SST<14.1	SST ≥14.1	Rain≥223	Rain <223
		SOI lag≥-1.15		SOI lag ≥ -1.15
		Rain≤76.5		SST lag<18.1
Stabilisers	SST<14.1	SST≥14.1	SST<14.3	SST≥14.3
		Waves 0.72 to 0.17		SOI <1.65
		SOI lag ≥1.65		Waves>0.49
Destabilisers	Waves≥0.17	Waves<0.17	SST≥14.5	SST≥14.5
	SOI ≥1.05		Waves 0.13 to 0.40	Waves<0.13
			SOI lag≥0.4	
Suspension- feeders	SST<14.1	SST≥14.1	SST<14.5	SST≥14.5
		Waves≥0.17		SOI 0.95 to 1.65
		SOI -0.7 to -1.65		
Bioturbators	Waves≥0.17	Waves<0.17	SST<14.5	SST≥14.5
	SOI≥-1.45			SOI lag<1.25
	FW≥0.69			FW<0.64
	SST lag≥15.9			Rain<61.6
No. of taxa	SST<15.7	SST≥15.7	Waves<0.14	Waves>0.14
	Rain≥185.7	Z4 lag<-26.5	SOI≥0.95	



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gcb_13176_f2.tif



gcb_13176_f3.tif