



Empirical evidence of an approaching alternate state produced by intrinsic community dynamics, climatic variability and management actions

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ABSTRACT: A major challenge to ecologists is identifying factors that make a system susceptible to regime shifts or state transitions. Theory and modelling have suggested a number of indicators to warn of approaching tipping points, but empirical tests of their validity are few. We tested 2 indicators, change to a key species and increased temporal variability, in a harbour, a system type rarely studied for regime shifts and alternate states. Long-term monitoring over 20 yr on a number of intertidal sandflats allowed us to document change and determine potential contributing factors. We detected decreasing abundance in the key species and increased temporal variability (flickering) of community composition before a trophic and functional change to an alternate community type. Detection of these indicators occurred despite cyclic patterns in community and population dynamics and a relatively fast and permanent change of one external condition (nutrients). We provide evidence that this shift was the product of a relatively small change in management of sewage disposal, combined with climate dynamics and mediated through changes in a key species, a tubeworm that provides biogenic habitat structure, stabilises sediment and affects dispersal and recruitment. These factors all interacted to escalate the effect of the relatively small changes in nutrients across a tipping point.

KEY WORDS: Tipping point · Thresholds · Key species · Regime shift · Macrofauna

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INTRODUCTION

In the last 2 decades there has been increased documentation of regime shifts in ecological systems. These phenomena occur when a system passes a threshold and fundamentally changes in structure and function (Hughes et al. 2005, de Young et al. 2008). Now, however, the challenge has shifted from documenting shifts to identifying factors that make a system susceptible to rapid changes in a world of multiple stressors and non-linear dynamics. A strict mathematical evaluation of the size of the basins of attraction needed to mathematically define alternative states in ecological systems might be difficult for natural systems where observational and process noise are present (Sugihara 1994). Nevertheless, 2 promising indicators of impending regime shifts or state change are large changes in the abundance of key species (Thrush et al. 2009) and

increased temporal variability (flickering; Oborny et al. 2005, van Nes & Scheffer 2005, Carpenter & Brock 2006, Scheffer et al. 2009) in key factors that drive ecosystem dynamics. However, empirical tests of such indicators are rare.

Regime shifts in marine systems are commonly documented for coastal and shelf-depth systems (Edwards & Richardson 2004, Ware & Thomson 2005, Casini et al. 2009) rather than estuarine and harbour systems. This is surprising given the degree of anthropogenic activity that has impacted estuarine and harbour ecosystems over human history (Thrush et al. 2004, McCormick-Ray 2005, Altieri & Witman 2006, Lotze et al. 2006). Although these are easy marine ecosystems to sample, part of the problem is the practicality of collecting broad-scale ecological data with a historical focus on point-source impacts, rather than cumulative and broad-scale change. While the major agents of

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change in estuaries worldwide (fishing, nutrient and sediment loading and habitat change) are generally considered to occur along spatial gradients, the potential for cumulative effects and multiple stressor interactions is high, with such interactions likely to result in sudden rather than gradual change (Thrush et al. 2008a,b, Thrush & Dayton 2010).

Key species sensitive to a stressor may affect resilience and precipitate large changes (Thrush et al. 2009). Species that dominate local function are known from many systems, with individual species driving ecosystem responses. Such species may not characterise all elements of functional performance, but their importance can be easily quantified. In soft-sediment habitats, common in estuarine systems, changes in species that influence sediment stability or nutrient processing are thought to result in major shifts in ecosystem performance and the ability of the system to resist stress (Lohrer et al. 2004, Norkko et al. 2006, van Nes & Scheffer 2007). For example, the loss of suspension-feeding bivalves has been suggested to profoundly change trophic relationships and ecosystem function (Nichols et al. 1986, Airolidi et al. 2008). Species that create structure in what would otherwise be a homogenous plain of mud and sand are important in modifying boundary flows and sediment transport and creating habitats for other organisms (Thrush 1991, Zajac et al. 2003, Levin & Dayton 2009). In particular, polychaete tube mats have been shown to be important to benthic community composition and sediment stability (Fager 1964, Mills 1969, Levin 1982, Noji & Noji 1991, Thrush et al. 1996, Friedrichs et al. 2000). However, functionally important species, even when dominant, are not necessarily resistant to stress (Allison 2004, Schiel et al. 2006), and interactions between anthropogenic and natural change are increasingly being reported (e.g. van de Koppel et al. 2001, Cranfield et al. 2003, Frank et al. 2005, Coco et al. 2006, Heithaus et al. 2008, Casini et al. 2009, Volkenborn et al. 2009).

Detecting change in any natural ecosystem must be done against a background of variability, and to date, the usefulness of increased temporal variability as an indicator of an approaching threshold has been demonstrated only by numerical simulation (Carpenter 2003, Carpenter & Brock 2006). Empirical time series are generally considered too noisy for this concept to be of use (Collie et al. 2004, de Young et al. 2008, but see Zaldivar et al. 2008). Estuaries, in particular, have for a long time been considered highly dynamic due to temporal variation in environmental conditions. Nevertheless, stable, resilient communities at multiple sites over time scales that exceed the life span of many common macrofaunal species were detected in a harbour ecosystem (Manukau Harbour, 37° 57' S,

174° 42' E) on the west coast of New Zealand, despite climate-driven interannual variability in wind-wave disturbances (Turner et al. 1995). Since then, continual bimonthly monitoring over 20 yr (1987–2007) at 2 sites (AA and CB, Fig. 1) demonstrate ongoing stability, despite temporal dynamics in a number of the species being related to the El Niño Southern Oscillation (ENSO) (Hewitt & Thrush 2009b).

However, at a third site (CH, Fig. 1), monitored bimonthly between 1987–1996 and 1999–2007, a marked shift in community composition occurred after cessation of oxidation pond discharge in April 2001. The shortest distance from the monitored site to the discharge point was 7 km which, given the complexity of harbour hydrodynamics and the timing of discharge from the oxidation ponds, represents a minimal distance. The oxidation pond discharge had been a low level source of enrichment for over 20 yr. Prior to the cessation in oxidation pond discharge, this large sandflat (3 km²) was dominated by the tube-mat forming polychaete *Boccardia syrtis* which disappeared post-cessation. Tube-mat forming macrofauna, when densities are high, can play significant roles in soft-sediment habitats. Specifically, *B. syrtis* performs important functions in stabilising sediment and influencing the dispersal of post-settlement individuals (Cummings et al. 1996, Thrush et al. 1996), and a previous survey in Manukau Harbour suggested a response to the slight enrichment provided by the sewage discharge (Ellis et al. 2000). Cessation also decreased water column nutrients and chlorophyll *a* (chl *a*) (Wilcock & Martin 2003). Thus, we anticipated that the lowered organic content would result in a decreased tube-mat and concomitant changes in community structure and function to an alternate state. The major question asked of the data was whether we

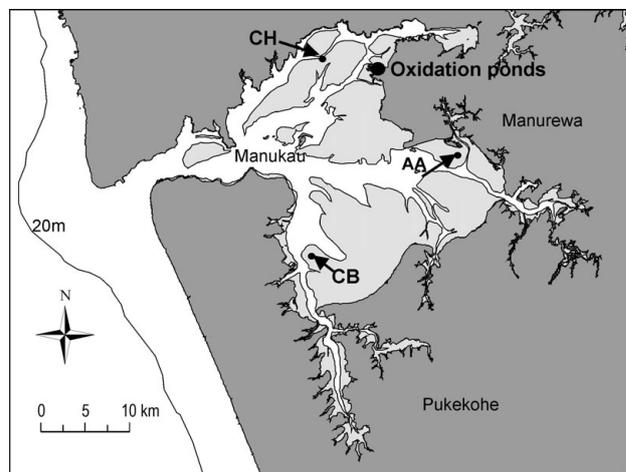


Fig. 1. Location of sites (CH, AA and CB) and sewage discharge (oxidation ponds) in the intertidal part of Manukau Harbour (shaded light grey), New Zealand

would observe increased temporal variability in community composition before this trophic and functional change occurred.

MATERIALS AND METHODS

Sampling was conducted at three 9000 m² sites within Manukau Harbour (349 km²), with sites >10 km apart (Fig. 1). The sites were all situated on large, relatively homogeneous, intertidal sandflats at the mid-tide level, whose physical appearances were reasonably similar across the sites. Manukau Harbour has 2 main hydrodynamic areas: the southern half, within which AA and CB are located, and the northern half, where CH is located. Two of the sites (AA and CB) were sampled every 2 mo between October 1987 and February 2003. The other site (CH) was sampled every 2 mo between October 1987 and October 1996 and then again between April 1999 and February 2007.

Twelve replicate cores were taken from each site on each sampling occasion in the following way. The site was divided into 12 equal area sectors and 1 core sample (13 cm diameter, 15 cm depth) was taken from a random location within each sector. To limit the influence of the small-scale spatial autocorrelation (Thrush et al. 1989) and preclude any localised modification of populations by previous sampling events, core samples were not positioned within a 5 m radius of each other or any samples collected in the preceding 6 mo.

After collection, the macrobenthos were separated from the sediments by sieving (500 µm mesh) and preserved with 70% isopropyl alcohol in seawater. Macrofauna were then identified to the lowest practical level (generally species), and counted. Taxon abundances from all replicates taken at a single time and site were averaged.

Non-metric multidimensional scaling on Bray-Curtis similarities based on untransformed data was used to graphically represent changes in communities at the 3 sites over time. Differences in community composition between different periods were assessed using analysis of similarities (ANOSIM) using PrimerE (Clarke & Gorley 2006) for each site separately. Temporal variability in community compositions was assessed for each year using average Bray-Curtis dissimilarities (similarity percentage [SIMPER]; PrimerE; Clarke & Gorley 2006) and the index of multivariate dispersion (PrimerE; Warwick & Clarke 1993) based on square root-transformed data.

From 1999 to 2007, the following variables were available (as monthly point measurements) that were likely to respond to the change in wastewater treatment: water column ammoniacal-nitrogen, nitrate-nitrogen, soluble and total phosphorus and dissolved

oxygen concentrations; and sediment chl *a* concentrations. Two measures of ENSO were also available: the Southern Oscillation index (SOI; Troup SOI, see www.bom.gov.au/climate/glossary/soi.shtml; McBride & Nicholls 1983); and Z1, an index of atmospheric pressure variation across New Zealand that encapsulates the strength of the westerly winds (Salinger & Mullan 1999). These ENSO measures were converted to 2 yr moving averages as they proved most useful in predicting temporal variations in species abundances (Hewitt & Thrush 2009b). Cross correlation analysis was used to determine the lag period between these variables and the abundance of common taxa. These variables were included as explanatory variables, along with the abundance of *Boccardia syrtis*, in multiple regressions predicting the abundance of common taxa and in a redundancy analysis. Forward selection was used to determine the important environmental variables for the canonical correspondence analysis. Variables were eliminated from regression models using backwards selection with an exit value of $p > 0.15$ (Crawley 1993). Initially, multiple regressions included an autoregressive term; however, this was never significant. Model variables were also permuted and end models checked for best fit using adjusted r^2 and Akaike's Information Criterion values. Co-linearity diagnostics and variance inflation factors were examined (Belsley et al. 1980), homogeneity of variance was evaluated by plotting residual versus predicted values and normality was assessed via normal probability plots. Log-transformations and Poisson error structures were used as required. The relative importance of variables in the final models to the predicted species abundance was assessed using their standardised slope estimates.

RESULTS

Community dynamics

Stable communities were observed at the 2 continuously monitored sites within the harbour (AA and CB), with no significant differences observed between the time periods 1987–2000 and 2003–2007 ($p > 0.05$). The ordination space occupied by the full time series was only slightly greater than that apparent in the first 5.5 yr of monitoring (Fig. 2). However, the ordination space occupied by the site near the oxidation ponds (CH) changed markedly, with community compositions of the time periods 1987–2000 and 2003–2007 being significantly different from each other ($p < 0.05$) (Fig. 2). Immediately after the cessation (2001–2002), the community composition swung between the initial and new states and was not significantly different from

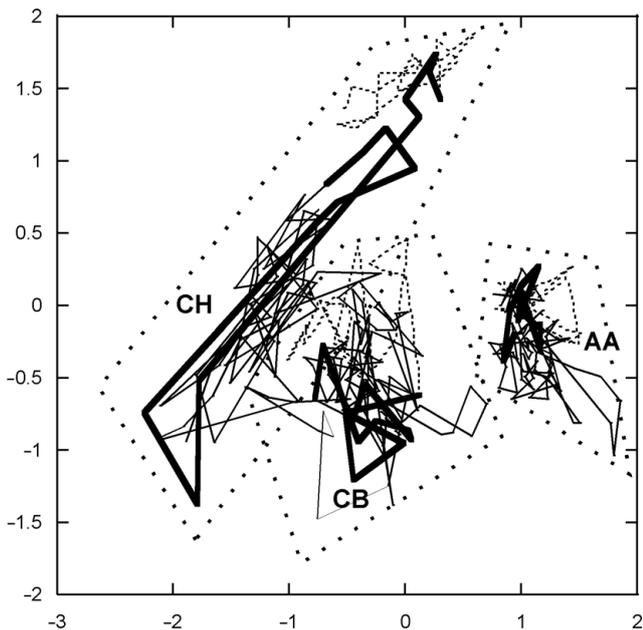


Fig. 2. Ordination space covered by community data for all sites. Sampling times between 1987 and 2000 are connected by thin lines, 2001 and 2003 are connected by thick lines and 2003 and 2007 are connected by dotted lines. The area covered by each space is delineated by a thick dotted line

either time period ($p > 0.05$). Importantly, this transition phase encompassed more of the ordination space, emphasising high community variability, than either the initial or new phase.

The increased temporal variability at CH apparent in the ordination plot, for the 2 yr immediately after the management action (Fig. 2), is endorsed by significant increases in within-year dissimilarity and multivariate dispersion ($p = 0.001$ and 0.012 , respectively) (Fig. 3). The new community state was less temporally variable than the initial community.

The community pre-2001 was dominated by the tube-mat forming *Boccardia syrtis*, which exhibited both seasonal and multi-year temporal variation (Fig. 4). A number of other polychaetes and juveniles of the bivalve *Macomona liliana* were also numerically dominant (Table 1). Interface feeders (species that switch feeding mode between suspension and deposit feeding), deposit feeders, predators/scavengers and suspension feeders were all represented in the 10 most dominant taxa, with average numbers of 61, 20, 12 and 7 individuals per core, respectively. Immediately after the management action, species composition and the functional traits of the community changed somewhat (Table 1), with average abundances of interface feeders, deposit feeders, predators/scavengers and suspension feeders in the top 10 dominant taxa being 53, 25, 8 and 12 individuals, respectively. A number of species,

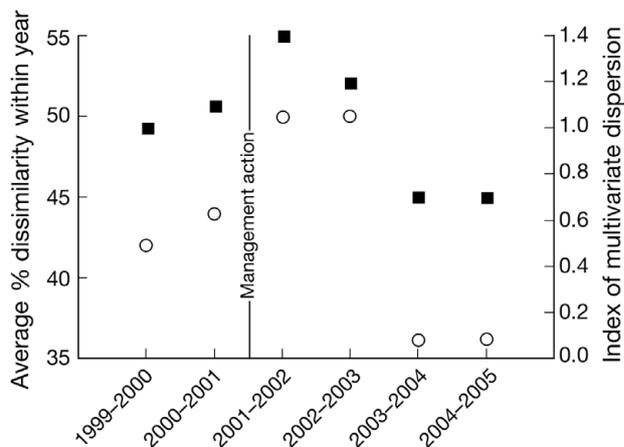


Fig. 3. Annual temporal variability in community structure, calculated as (O) average Bray-Curtis % dissimilarity and (■) index of multivariate dispersion from April to February, based on square root-transformed data at Site CH before and after the management action

mainly crustaceans, became highly temporally variable in abundance. Finally, a new community stabilised, dominated by a mix of deposit-feeding polychaetes and crustaceans, with some juveniles of the deposit-feeding bivalve *Soletellina siliqua* (Table 1). A major change in habitat occurred: from the tube-worm dominated state to one of destabilized sediment, with few protruding structures and surficial pits and holes, dominated by deposit feeders (average of 87 individuals in top 10 most dominant taxa). A trophic shift also occurred, with no interface or suspension feeders occurring in the top 10 taxa.

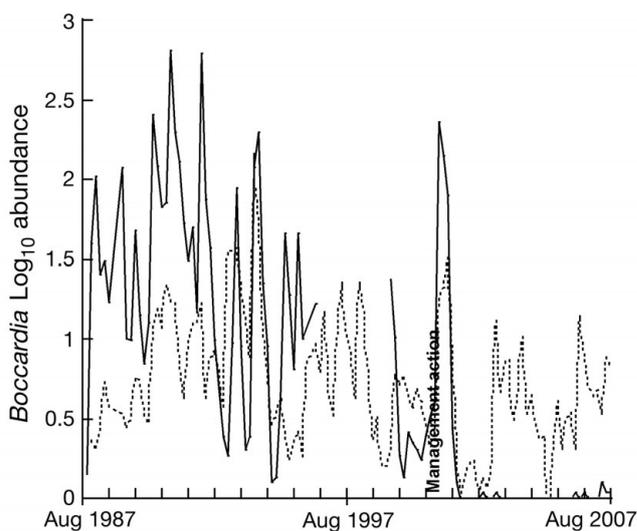


Fig. 4. *Boccardia syrtis*. Time series of abundances (\log_{10} -transformed) at the 2 sites at which it was abundant, (—) site CH and (.....) site CB

Table 1. Characteristics of the 10 most abundant taxa found during 3 different time periods: initial (1987–2000), between (2001–2002) and post (2003–2005) cessation of oxidation pond discharge. Abundance is given followed by the rank in parentheses. –: Zero abundances

Taxon	Habitat	Feeding mode	Period		
			Initial	Between	Post
<i>Boccardia syrtis</i>	Tube-dweller	Interface (mainly deposit)	1114 (1)	454 (1)	–
<i>Heteromastus filiformis</i>	Mobile, all sediment depths	Deposit	262 (2)	21 (7)	10 (8)
Nemertean	Mobile, all sediments	Predator/scavenger	106 (3)	36 (6)	40 (3)
<i>Sphaerosyllis semiverrucosa</i>	Mobile, all sediments depths	Predator/scavenger	96 (4)	–	–
<i>Euchone</i> sp.	Tube-dweller	Suspension	65 (5.5)	110 (2)	–
<i>Magelona dakini</i>	Mobile, sediment depths <2 cm	Deposit	65 (5.5)	95 (3)	316 (1)
Tanaidacea	Mobile	Suspension	48 (7)	–	–
<i>Macroclymenella stewartensis</i>	Tube-dweller	Deposit	45 (8)	19 (8)	34 (4)
<i>Macomona liliana</i>	Limited mobility	Interface (mainly deposit)	36 (9.5)	11 (10)	–
<i>Glycinde trifida</i>	Mobile, all sediment depths	Predator/scavenger	36 (9.5)	–	–
<i>Paracallioppe novaezelandiae</i>	Mobile, surface-dweller	Deposit	–	67 (4)	–
<i>Colurostylis lemerum</i>	Mobile, surface-dweller	Deposit	–	40 (5)	43 (2)
<i>Toridoharpinia hurleyi</i>	Mobile, surface-dweller	Scavenger	–	15 (9)	–
<i>Soletellina siliqua</i>	Limited mobility, surface deposit feeder	Deposit	–	–	20 (5)
Mysidacea	Limited mobility, surface-dweller	Deposit or predator/scavenger	–	–	19 (6)
<i>Waitangi brevirostris</i>	Mobile, all sediment depths	Deposit	–	–	16 (7)
<i>Syllis</i> spp.	Mobile, all sediment depths	Predator/scavenger	–	–	8 (9)

Interestingly, the previous dominant species did not necessarily become more temporally variable, partly because many of them already had pronounced seasonal and multi-year cycles (Hewitt & Thrush 2007). However, 27% of species that had been previously low in abundance (mean < 1 individual per core) now exhibited erratically higher abundances (i.e. increased mean and standard deviation). Many species, including some of the initial dominants, did not appear during the same seasons in which they were previously abundant. Species richness was markedly lower in the new community: annual average number of species varied from 35.2 to 42.3 in the initial years, 36.2 and 31.8 immediately prior to and after cessation, respectively, and 18.8 to 23.2 thereafter. The number of infrequently occurring taxa did not change, although most of these that were present during the initial period disappeared and were replaced by new species, 25% of which did not stabilise into the new community.

Table 2. Concentrations (mean \pm SE) of sediment chlorophyll *a* (chl *a*) and water column nitrate, ammonium and soluble phosphorus found during 3 periods: initial (1987–2000), between (2001–2002) and post (2003–2005) cessation of oxidation pond discharge. For sediment chl *a*, values are only available from 1999

Period	Sediment chl <i>a</i>	Water column		
		Nitrate	Ammonium	Phosphorus
Initial	17.5 \pm 3.1	0.20 \pm 0.07	0.37 \pm 0.07	0.11 \pm 0.007
Between	10.7 \pm 0.4	0.10 \pm 0.02	0.08 \pm 0.02	0.10 \pm 0.03
Post	7.7 \pm 0.5	0.09 \pm 0.01	0.08 \pm 0.01	0.06 \pm 0.005

Potential drivers of changes in population dynamics

Changes in water column nutrients and chl *a* content consistent with decreased sewage input were recorded in the vicinity of Site CH (Table 2; Wilcock & Martin 2003), and many of the changes in species abundances were to species expected to respond to such changes. For example, suspension feeders could be expected to decrease with decreases in water column chl *a*, and key polychaetes (e.g. *Boccardia syrtis* and *Heteromastus filiformis*) should also respond negatively to subtle decreases in organic loading (Ellis et al. 2000).

The redundancy analysis demonstrated that 66% of the variability in community composition could be explained by the 2 ENSO variables, sediment chl *a* content, water column nitrate concentrations and log₁₀-transformed densities of *Boccardia syrtis*. The canonical axes were significant at a p-level of 0.002.

Multiple regressions revealed that temporal variation in the abundance of only one species (*Colurostylis lemerum*) was not explainable by any of the predictor variables. Significant predictors for other species included variables reflecting changes in ENSO, the wastewater treatment or the abundance of *Boccardia syrtis* (Table 3). None of the species had ENSO variables alone selected as important predictors. Four of the species did not have *B. syrtis* abundance as an important predictor; for the others, the relative importance of *B. syrtis* relative to the other predictors varied from 20 to 100%.

Table 3. R^2 and relative importance of variables predicting the abundance of species over time between 1999 and 2007 at Site CH for models using variables representing the El Niño Southern Oscillation (ENSO), changes to the wastewater treatment (sediment chlorophyll *a* [chl *a*]) and water column soluble phosphorus (SP), ammoniacal nitrogen [NH_4] and nitrate-nitrogen [NO_3]) and the \log_{10} abundance of *Boccardia syrtis* (Boc). The relative importance of each variable was calculated from its standardised parameter estimate.

–: Variable was not important. Full statistical results are in Appendix 1. All taxa common in one or more years were analysed

Taxon	R^2	ENSO	Chl <i>a</i>	SP	NO_3	NH_4	Boc
<i>Colurostylis lemurum</i>	<0.10	–	–	–	–	–	–
<i>Orbinia papillosa</i>	0.28	–	–	44.4	–	31.5	24.1
<i>Aglaophamus macroura</i>	0.37	30.5	69.5	–	–	–	–
<i>Nucula hartvigiana</i>	0.37	53.3	–	–	–	–	46.7
<i>Waitangi brevirostris</i>	0.40	30.9	–	30.9	–	38.2	–
<i>Sphaerosyllis semiverrucosa</i>	0.41	–	–	–	–	15.4	84.6
<i>Magelona dakini</i>	0.42	20.0	–	–	–	–	80.0
<i>Macroclymenella stewartensis</i>	0.46	30.9	–	–	–	41.5	27.6
<i>Austrovenus stutchburyi</i>	0.48	13.8	–	29.6	42.1	14.5	–
<i>Soletellina siliqua</i>	0.48	20.5	–	–	79.5	–	–
<i>Heteromastus filiformis</i>	0.52	29.7	–	–	–	–	71.3
<i>Owenia fusiformis</i>	0.59	22.8	–	–	–	56.5	20.7
<i>Macomona liliana</i>	0.69	–	73.7	–	–	–	26.3
<i>Euchone</i> sp.	0.85	15.7	–	–	–	–	84.3
<i>Glycinde trifida</i>	0.78	–	–	–	–	–	100.0

DISCUSSION

We observed a large change in an intertidal soft-sediment macrofaunal community preceded by 2 yr of high annual temporal variability in community composition. This increase in variability or flickering was detected despite natural seasonality in community and population dynamics. The changes appeared driven by subtle shifts in environmental drivers interacting with facilitation by the *Boccardia syrtis* tube mat, in a way consistent with complex system dynamics involving interactions across time scales and feedbacks (Pascual & Guichard 2005, Rietkerk & van de Koppel 2008). We suspect that this process was primarily driven from the bottom up. While there are large predators in this system, e.g. shorebirds and rays, densities of shore birds continued to be low and the rays actually feed on the tube-mat.

The temporal change in community structure and function was coincident and mechanistically concordant with a management action that resulted in small decreases in organic and primary nutrient loading and a prolonged ENSO event that affected temporal dynamics of a number of species throughout the harbour (Hewitt & Thrush 2009b). While there is yet no definition of the spatial and temporal extent of a change that represents an alternate state, we feel that the observed strong change in community composition and function that lasted for over 5 yr, albeit at one large sandflat, qualifies. Specifically, the change in community composition was accompanied by a change in biogenic habitat structure, with the removal of an extensive tube-mat that was likely to have consequent

changes to bioturbation rates, hydrodynamics and food sources for fish and birds. A trophic and feeding shift also occurred with numbers of predators/scavengers decreasing and deposit feeders increasing. Other monitored sites, located in a different hydrodynamic area of the harbour, did not exhibit similar changes

Increases in both spatial and temporal variance have been suggested as a potential predictor of approaching tipping points and regime shifts (Oborny et al. 2005, van Nes & Scheffer 2005, Brock & Carpenter 2006, Carpenter & Brock 2006, Scheffer et al. 2009). However, the numerical model simulations that have suggested these indicators are dependent on a high level of mechanistic knowledge. Few empirical studies have assessed the value of these indicators, although increased spatial variance in community composition variables during transition between alternative states has recently been observed in 2 systems (Litzow et al. 2008). Our results assess temporal variance and provide evidence of an increase in temporal variance for the 2 yr of the transition followed by a decrease to below the initial degree of variability. Interestingly, this increase in temporal variability of community composition was not a simple reflection of increases in the temporal variability of dominant species. Both increases and decreases in seasonal variability of dominants were observed, similar to the effect of stressors on the spatial variability of macrobenthic species abundances (Hewitt & Thrush 2009a).

Both the community change and the increased variance preceding it were detected despite natural variation in species abundances at a number of scales (from seasonal patterns to multi-year cycles). In Manukau

Harbour, 18 to 38% of common species exhibit seasonality, although most of these seasonal patterns were not consistent in timing or magnitude from year to year, and 15 to 26% of common taxa exhibited multi-year cycles in abundance from 3 to 9 yr in length (Hewitt & Thrush 2007). These temporal patterns were explainable to varying degrees by variables representing ENSO and smaller-scale location-specific environmental variables (up to 80 and 55% explained, respectively; Hewitt & Thrush 2009b). The natural variability in species abundances we observed over time did not always reflect highly variable communities, suggesting that species interactions are important in stabilising community dynamics (van Nes & Scheffer 2005). Species interactions, together with temporally small environmental shifts related to storm events, probably account for the unexplained variability in our regression analyses.

Regime shifts and tipping points are probably common in estuaries, as indicated by the number of studies reporting strong anthropogenic impacts, although in this case such a reaction was unexpected. While the management action itself was profound (removal of sewage ponds and increased sewage treatment), fast and permanent, the effect of the oxidation ponds had previously not been demonstrated to be large nor the spatial footprint to encompass our monitoring site 7 km away (3 to 5% increase in sediment organic content only within 1400 m; Ellis et al. 2000). Moreover, the resultant changes to water column nutrients were small relative to other reported eutrophication problems. We suggest 2 potential reasons for the large community composition, trophic and functional responses.

First, a tipping point can often result from a combination of gradual changes and a shock or interactions between intrinsic temporal dynamics and cumulative effects (Biggs et al. 2009). In our case it seems likely that the small change in water column nutrients interacted with ENSO-driven variation, producing a greater effect than would have been observed from either driver on their own. This highlights the importance of considering anthropogenic effects as occurring on the wave of natural changes, rather than expecting natural variability to obscure detection of anthropogenic effects or to assume that anthropogenic effects expected to be small or similar in size to natural variability will have little or no consequences. It also highlights the profound implications that changes to climate and climatic variability may be expected to have on the resilience of ecosystems to other anthropogenic impacts and management actions.

Second, the changes to water column nutrients did not have a simple direct effect; rather, effects for some species appeared mediated through changes to the tube-mat. Species that generate spatial structure are

expected to play a key role in regulating positive interactions between fast and slow processes and are thus likely to be key in defining complex dynamics and resilience (Dayton 2003, Rietkerk & Van de Koppel 2008, Thrush et al. 2009). *Boccardia syrtis* population dynamics are complex; beyond the correlation with ENSO cycles, the species exhibits 5 to 7 yr cycles that are not synchronous across the harbour, suggesting some strongly intrinsic control. Both through stabilising sediment and through the tube structure affecting recruitment, *B. syrtis* could have strong interactions with other species in the community. The system is therefore a cyclic one, where it could be postulated that the intrinsic seasonal and multi-year cycles in *B. syrtis* abundance result in the community oscillating to the border of the basin of attraction of an alternative attractor (Scheffer et al. 2009).

While the mechanistic details for this regime shift may well be system-specific, involving interactions of tube-mats, sediment stability and subtle changes in organic loading, it is unlikely that tube-dwellers are the only key species likely to have this effect. Removal of any species that provide structure in soft-sediment systems or species that provide high levels of bioturbation (van Nes & Scheffer 2007, Lohrer et al. 2008) or benthic–pelagic coupling (Airoldi et al. 2008) are likely to have far-reaching effects. When such species exhibit sensitivity to environmental or anthropogenic stressors, regime shifts may occur (Thrush et al. 2009). Suding et al. (2008) emphasised the importance of considering both functional and environmental response traits when predicting system responses to change. However, ecological surprises are common, and at least in some circumstances due to complex dynamics, emphasising the importance of developing and empirically testing indicators of approaching thresholds, tipping points or regime shifts (Doak et al. 2008, Thrush et al. 2009).

CONCLUSIONS

In our system, the effects of ENSO and the preference of *Boccardia syrtis* for slightly enriched sediment, together with the intrinsic population dynamics of *B. syrtis* and the intrinsic species interactions between it and the rest of the community, acted to escalate the effect of the relatively small changes in nutrients across a tipping point. We were lucky to have sufficiently good spatially and temporally resolved ecological and environmental data to detect and tease apart the mechanisms of change. The length of time series needed for detection of such changes is inevitably dependent on the resolution of the data and must exceed the length of dominant cyclic patterns (~9 yr for

our data; Hewitt & Thrush 2007). However, despite the noisy nature of real-world data, we could detect changes that foreshadowed a regime shift, which should be encouraging for both empirical researchers and management agencies.

Acknowledgements. This work was supported by FRST C01X0501. The Auckland Regional Council provided the long-term monitoring data from Manukau. Comments from a number of reviewers helped improve the manuscript.

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Appendix 1. Full statistics for the multiple regression analyses reported in Table 3. El Niño Southern Oscillation variables are the Southern Oscillation index (SOI) and Z1, changes to the wastewater treatment are sediment chlorophyll *a* (chl *a*) and water column soluble phosphorus (SP), ammoniacal nitrogen (NH₄) and nitrate-nitrogen (NO₃), and the log₁₀ abundance of *Boccardia syrtis* is represented as Boc. Lag: lags in months when a variable was lagged; MS: mean squares or deviances; test-value: χ^2 or *F*-value

Taxon	Source	Lag	df	MS	Test-value	p
<i>Orbinia papillosa</i>	Model		3	8.821	26.46	<0.0001
	Error		34	2.033		
	Intercept		1	0.338	0.22	0.6386
	NH ₄	12	1	0.047	14.04	0.0002
	SP	6	1	0.089	7.44	0.0064
	Boc		1	0.060	4.67	0.0307
<i>Aglaophamus macroura</i>	Model		2	0.497	9.32	0.0006
	Error		32	0.053		
	Chl <i>a</i>	4	1	0.024	-2.81	0.0084
	SOI		1	0.012	2.34	0.0254

Appendix 1 (continued)

Taxon	Source	Lag	df	MS	Test-value	p
<i>Nucula hartvigiana</i>	Model		2	21.993	11.25	0.0001
	Error		39	1.955		
	Intercept		1	0.566	-1.39	0.1723
	Z1	4	1	0.091	3.53	0.0011
	Boc		1	0.094	2.99	0.0048
<i>Waitangi brevisrostris</i>	Model		3	2.139	6.58	0.0016
	Error		29	0.325		
	Intercept		1	0.305	4.82	<0.0001
	NH ₄		1	0.108	-1.87	0.0719
	SP	2	1	0.067	-2.59	0.0149
<i>Sphaerosyllis semiverrucosa</i>	SOI		1	0.079	2.14	0.0407
	Model		2	0.067	13.62	<0.0001
	Error		39	0.005		
	Intercept		1	0.014	-0.65	0.5203
	NH ₄	4	1	0.005	3.97	0.0003
<i>Magelona dakini</i>	Boc		1	0.005	2.24	0.0308
	Model		2	1.078	15.11	<0.0001
	Error		41	0.071		
	Intercept		1	0.051	44.12	<0.0001
	SOI		1	0.014	1.62	0.1138
<i>Macroclymenella stewartensis</i>	Boc		1	0.018	-4.87	<0.0001
	Model		3	45.058	10.05	<0.0001
	Error		35	4.482		
	Intercept		1	0.906	0.21	0.8385
	NH ₄	10	1	0.220	-4.09	0.0002
<i>Austrovenus stutchburyi</i>	Z1	4	1	0.154	4.35	0.0001
	Boc		1	0.214	2.78	0.0087
	Model		4	0.250	7.84	0.0001
	Error		34	0.032		
	SP	4	1	0.020	2.38	0.0230
<i>Soletellina siliqua</i>	SOI		1	0.009	2.33	0.0257
	NO ₃	10	1	0.021	3.25	0.0026
	NH ₄	8	1	0.015	1.50	0.1430
	Model		2	28.782	57.56	<0.0001
	Error		38	1.611		
<i>Heteromastus filiformis</i>	Intercept		1	0.222	108.45	<0.0001
	NO ₃	6	1	0.223	15.96	<0.0001
	Z1	6	1	0.048	17.57	<0.0001
	Model		2	41.882	22.66	<0.0001
	Error		42	1.849		
<i>Owenia fusiformis</i>	Intercept		1	0.332	0.55	0.5838
	SOI		1	0.090	1.64	0.1084
	Boc		1	0.097	3.63	0.0008
	Model		3	31.080	16.09	<0.0001
	Error		33	1.932		
<i>Macomona liliana</i>	Intercept		1	0.696	-2.07	0.0460
	Boc		1	0.110	1.75	0.0898
	NH ₄	6	1	0.133	3.88	0.0005
	Z1	12	1	0.117	1.77	0.0865
	Model		2	105.404	210.81	<0.0001
<i>Euchone</i> sp.	Error		33	27.800		
	Intercept		1	0.187	0.02	0.8889
	Boc		1	0.038	6.78	0.0092
	Chl a	2	1	0.048	34.64	<0.0001
	Model		2	2.926	101.51	<0.0001
<i>Glycinde trifida</i>	Error		34	0.029		
	Intercept		1	0.085	-1.06	0.2968
	Z1	12	1	0.014	1.99	0.0549
	Boc		1	0.013	11.95	<0.0001
	Model		1	1195.017	152.04	<0.0001
<i>Glycinde trifida</i>	Error		42	7.860		
	Intercept		1	0.460	2.05	0.0466
	Boc		1	0.187	12.33	<0.0001