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Detecting ecological thresholds and tipping points in the natural capital assets of a protected coastal ecosystem

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ABSTRACT

Concern about abrupt and potentially irreversible ecosystem thresholds and tipping points is increasing, as they may have significant implications for natural capital and human wellbeing. Although well established in theory, there are few empirical studies that provide evidence for these phenomena in coastal and estuarine ecosystems, despite their high value for provision of ecosystem services. To determine the likelihood of such events, we tested two statistical methods; sequential T-test analysis (STARS) and generalised additive models (GAMs) in a harbour ecosystem. These methods were applied to time series data spanning up to 25 years coupled with analysis of the relationships between drivers and natural capital asset flows. Results of the STARS analysis identified nonlinear thresholds in three of the natural capital assets of Poole harbour; mudflat area, Manila clam stocks and wader/wildfowl numbers, as well as an increase in several drivers affecting the harbour. The most prominent threshold was recorded in the Manila clam fisheries of the harbour, with stocks in two locations of the harbour declining by 73–78% between 2006 and 2008. We suggest that the historic decline in the Manila clam stocks of the harbour were partly attributable to illegal fishing pressure although other factors such as disease and lease bed holders switching to other species were also likely to have contributed. More recently (2015-onwards) wild clam stocks of the harbour have increased thanks to improved management measures by local authorities. Generalised additive models also identified the contribution of macroalgal mats, sediment shoaling and river flows to historic changes in mudflat area, saltmarsh area and wader/wildfowl numbers. We conclude that information on thresholds and tipping points obtained using these approaches can potentially be of value in a management context, by focusing attention on the interactions and positive feedbacks between drivers that may cause abrupt change in coastal ecosystems.

1. Introduction

Concern about abrupt and potentially irreversible ecosystem transitions is growing rapidly, as they may have significant implications for human wellbeing and are forecast to increase with intensifying climatic change and environmental degradation (Scheffer et al., 2001; Rockström et al., 2009). Such transitions may result from an abrupt change in underlying drivers (e.g. land cover change, nutrient inputs), from an interaction between drivers, or from an abrupt change in the state of the ecosystem with a small or smooth change in drivers (Andersen et al., 2009). Another possibility is a threshold driven by a positive feedback loop, which is often referred to as a tipping point (Scheffer et al., 2009, 2012). While identifying such thresholds and tipping points can be challenging to identify in practice, evidence is increasingly indicating that nonlinear threshold responses could be widespread. Incorporating information about such responses into management plans can facilitate improved management outcomes (Huggett, 2005; Foley et al., 2015). Issues of particular importance to environmental policy and practice include development of techniques to identify where and when thresholds are likely to be encountered (Bestelmeyer et al., 2011; Newton, 2016) and identification of the underlying mechanisms so that appropriate management responses can be identified (e.g. in the relationships between shorebird mortality and shellfish stock resources; Goss-Custard et al., 2004).

While the importance of ecological thresholds, tipping-points and associated phenomena is increasingly being recognised (e.g. deYoung et al., 2008; Hughes et al., 2013; Levin and Möllmann, 2015), few previous studies have examined their occurrence in transitional systems such as estuaries and harbours (although see Hewitt and Thrush, 2010). This is surprising as such systems typically deliver a number of valuable goods and services (Barbier et al., 2011) but at the same time are subject to more human-induced pressures than most other marine

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systems (McLusky and Elliott, 2007). In particular, harbours (which may be classified as estuaries or lagoons; Humphreys, 2005) often provide examples of conflicts between high ecological value and intensive human use. The current research was designed to help address this knowledge gap. The purpose of this research was to use a combination of time series data and statistical techniques to examine the occurrence of thresholds and tipping points in Poole Harbour, UK, a Special Protection Area (SPA) of high ecological and socio-economic value. Owing to the breadth of definitions surrounding the concept of tipping points, we start by outlining the definitions adopted here and the underlying theory.

2. Defining tipping points in the natural capital components of ecological systems

Tipping points have been defined in a number of different ways. For example, in their consideration of the Earth's climate system, Lenton et al. (2008) defined a tipping point as the critical point at which the future state of the system is qualitatively altered by a small perturbation. Similarly Scheffer et al. (2012) referred to a tipping point as a situation where a local perturbation can cause a domino effect resulting in a system transition. Tipping points in complex systems have been widely interpreted as equivalent to critical transitions, phase transitions or fold bifurcations (Lenton et al., 2008; Scheffer et al., 2009; Ashwin et al., 2012). Such concepts derive from theories of dynamical systems, including bifurcation and catastrophe theories. Application of these theories has highlighted a number of ways in which tipping points can occur, for example by a change in the external conditions of a system, or a change in the state of the system itself (Ashwin et al., 2012; van Nes et al., 2016).

While application of dynamical systems theory to the climate system is now well established (Lenton et al., 2008), its application to understand the dynamics of terrestrial and marine ecosystems has been the focus of some debate. Policy makers and land managers increasingly want to understand how different forms of environmental change might affect the condition of natural capital (NC), and the flow of multiple ecosystem services (ES) to human society (Mace et al., 2015). As dynamical systems models are typically defined in relation to a single independent variable, simultaneous consideration of multiple and potentially interacting drivers of ecological change represents a significant analytical challenge. As noted by Donohue et al. (2016), the multidimensionality of ecological responses requires explicit consideration of multidimensional disturbances or causes of change. The challenges of applying dynamical systems theory to real-world ecosystems are illustrated by the concept of ecological resilience. Much of the recent literature on this concept is based on the assumption that ecosystems have multiple stable equilibria, with tipping points occurring between them (Donohue et al., 2016). Definitions of ecological resilience focus on the capacity of a system to maintain its essential structure and function when confronted with external perturbations (Quinlan et al., 2016). Yet the empirical evidence for the existence of such multiple stable states is very limited (Petraitis, 2013); most ecosystems are far from the equilibria assumed by theory (Donohue et al., 2016), and other assumptions on which the underlying theory is based are often not met in field situations (Newton, 2016). Consequently, ecological resilience has proved very difficult to measure in practice (Quinlan et al., 2016; Biggs et al., 2012; Cantarello et al., 2017). Together with the semantic confusion surrounding resilience, these problems have resulted in the concept being misapplied in both policy and practice (Newton, 2016).

We therefore follow van Nes et al. (2016) in applying the term ‘tipping point’ to any situation where accelerating change caused by a positive feedback drives the system to a new state. We make no assumptions about whether the ecosystem in question is characterised by the existence of multiple stable states (Petraitis, 2013), and we do not make an explicit link between tipping points and dynamical systems theory. As highlighted by van Nes et al. (2016), this broader definition of a tipping point is consistent with the work of Gladwell (2000), who did so much to popularize the concept. The existence of an intrinsic positive feedback process that drives accelerating change differentiates concept tipping point from a broader category of abrupt ecosystem change, which we refer to as an ecological threshold. Any situation where there is an abrupt change in ecosystem structure or function can be considered as an ecological threshold (Groffman et al., 2006). Ecological thresholds may also usefully be differentiated from decision or management thresholds, or regulatory limits (Johnson, 2013), which are based on values of system state variables that should prompt specific management actions (Martin et al., 2009). Following van Nes et al. (2016), we therefore restrict the term ‘tipping point’ to a subcategory of ecological threshold where the abrupt change is driven by a positive feedback mechanism.

Here we examine the occurrence of thresholds and tipping points in relation to provision of multiple ecosystem services in a coastal ecosystem. To achieve this, we employ a conceptual framework based on the reviews conducted by Mace et al. (2015) and the Natural Capital Committee (NCC, 2014). Here, NC is defined as assets, stocks or the elements of nature that directly and indirectly produce value or benefits to people (NCC, 2014), such as ecological communities or habitat types. Following Mace et al. (2015), the status of these natural assets can be measured using metrics of the area, and condition of these communities. In the context of environmental degradation and its potential impact on human society, the form of the relationship between the condition of a natural asset and provision of benefits is of particular importance. Environmental degradation may lead to a decline in natural asset status, which will reduce the benefits provided to people. The form of this decline represents a key knowledge gap (Folke et al., 2011; NCC, 2014), but could potentially include threshold responses or tipping points (Fig. 1 (I)). In addition, we hypothesize that the relationship between anthropogenic drivers (or pressures) and NC status may also demonstrate a threshold response or a tipping point (Fig. 1 (II,III,IV)).

The relationships between anthropogenic drivers (or pressures) and NC status may also vary over time, demonstrating either linear or nonlinear trends (Fig. 1 (V-VII)). If an environmental driver intensified over time, then it could produce a threshold response in NC status, or a tipping point if a positive feedback mechanism were influential. Tipping events (IV & VII) are often considered difficult to reverse because of a phenomenon known as hysteresis (Meyer, 2016). This implies that the system cannot recover by retracing the path followed during degradation. Instead, the environmental driver that caused the transition has to be reduced further than the threshold value that caused the initial transition. Ultimately, if environmental degradation leads to an abrupt decline in natural asset status, this will reduce the benefits provided to people, either temporarily or permanently.

3. Methods

3.1. Details of study area: Poole Harbour

Poole Harbour is a large natural harbour of nearly 4000 ha (Underhill-Day, 2006) located on the coast of Dorset in southern England (Lat. 50° 42′ 44″ Long. 2° 03’ 30” W) in the United Kingdom (Fig. 2). Although classified as an estuary (as several rivers flow into it), Poole Harbour has many of the qualities of a large lagoon, owing to the narrow entrance and limited tidal range (Humphreys, 2005). A diverse set of habitats from saltmarsh and reedbed (*Phragmites australis*) to valley mire and lowland heathland provide a host of different ecosystem services such as recreation, coastal protection and increased water quality to a catchment of over 142,100 people (Office for National Statistics, 2010). Ecologically, the intertidal mudflats, sandflats and marshes support large numbers of wintering wildfowl and waders that are of national and international significance. The harbour and its adjacent landscape also hold a number of other national statutory designations that serve to protect the natural environment,

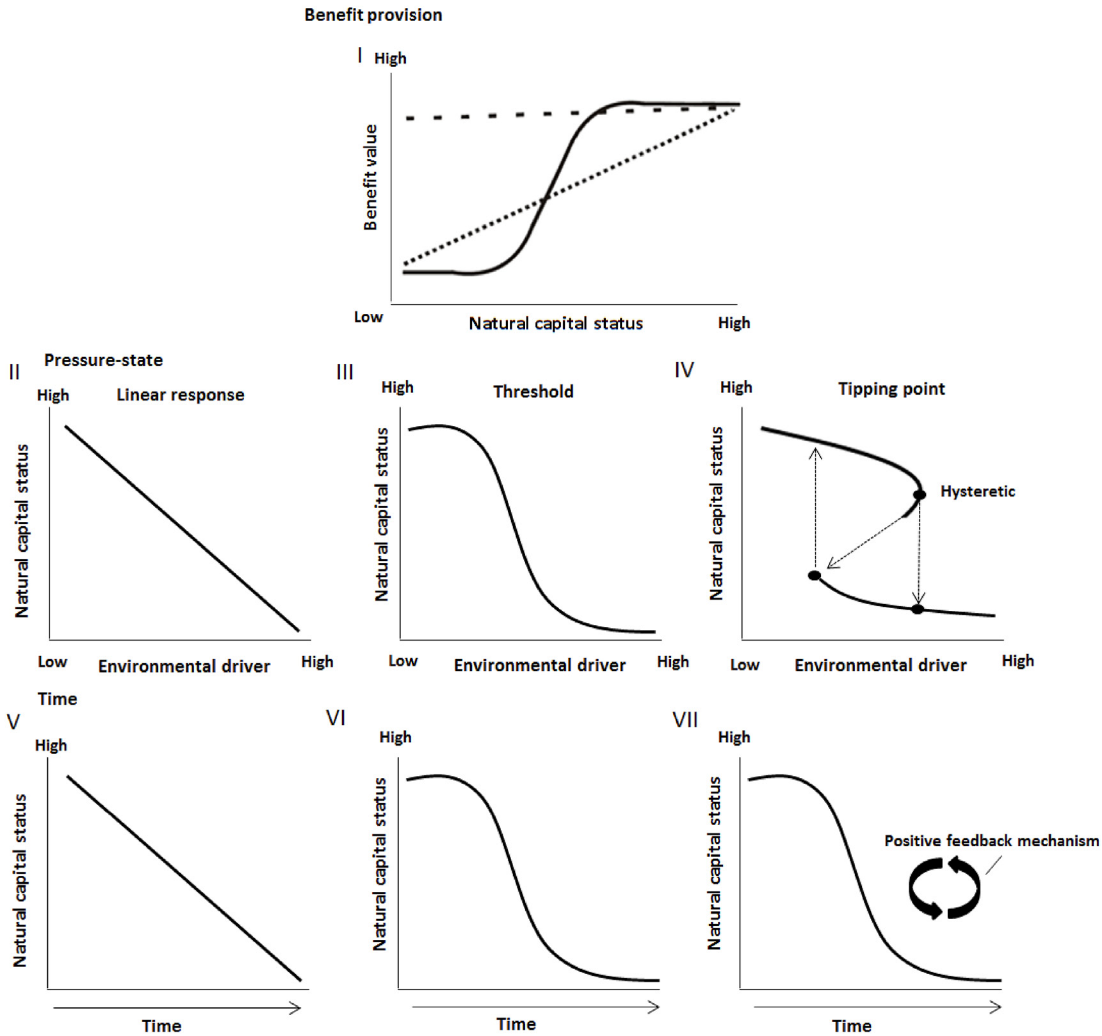

Fig. 1. (I) Alternative forms of forms of natural capital asset–benefit relationships, as hypothesized by Mace et al. (2015). The solid black line illustrates how the value of benefits might change in response to variation in the status or condition of natural assets, which could be caused by environmental degradation. The dashed line shows a threshold response (or tipping point). Panels (II-IV) show the relationship between NC status to changing conditions or environmental drivers which might be: II. Linear response. III. Nonlinear, non-hysteretic response of ecosystem state as a function of a pressure (threshold) or IV. Tipping point (hysteretic), representing a nonlinear change driven by an intrinsic positive feedback mechanism and with respect to changing conditions or environmental drivers. Finally, panels (V-VII) show how a responding system may change through time when they respond to an escalating driver according to the linear or abrupt equilibrial behaviour shown in (II–IV).

including being classified as a Site of Special Scientific Interest (SSSI), a Special Protection Area (SPA) designated under the EU Birds Directive and a Ramsar site. Under the EC Shellfish Waters Directive, Poole Harbour (with the exception of Holes Bay) is also designated as a shellfish water and is the location of fishing and aquaculture activities, which in 2005 were worth in excess of £2 million per year to the local economy (Jensen et al., 2004). However, despite its high economic and conservation value, the occurrence of ecological thresholds and tipping points in the NC assets of Poole Harbour has not been examined previously.

3.2. Data collection

Data for four different categories of NC components were gathered for the period 1980–2015 (Table 1). Three NC stocks of interest (mudflat area, saltmarsh area and wader/wildfowl numbers) were chosen owing to their immediate importance for conservation within the SPA, while the potential stocks of the Manila clam in the harbour (*Ruditapes philippinarum*) were also investigated based on their significant commercial importance and the potential benefit flows provided by the landings of clams into Poole Harbour. To test potential pressure-state relationships, data for possible drivers in the harbour were sourced from the literature, environmental data-bases and monitored instrument records (Table 2). For example we used tidal river flow and water quality data from the River Frome at East Stoke gauging station (ID: 44,207) to represent a county level watershed driver. In the absence of long-term fishing effort data (e.g. fishing effort, frequency trawled) fleet capacity (i.e. number of licenced clam boats) was used as a proxy for fishing pressure (Piet et al., 2006). As fishermen in Poole Harbour utilise a unique "pump-scoop" dredge to harvest the Manila clam (95% of catch is typically clam landings; Clarke et al., 2017) fleet capacity is likely an effective pressure indicator that describes the impact induced by fishing activities on the system.

3.3. Data analysis

Based on criteria outlined by Collie et al. (2004), Bestelmeyer et al. (2011), Carpenter et al. (2011) and Samhouri et al. (2017) we followed a step-wise process for detecting and characterising thresholds and their driver-response interactions. The workflow can be summarised in three

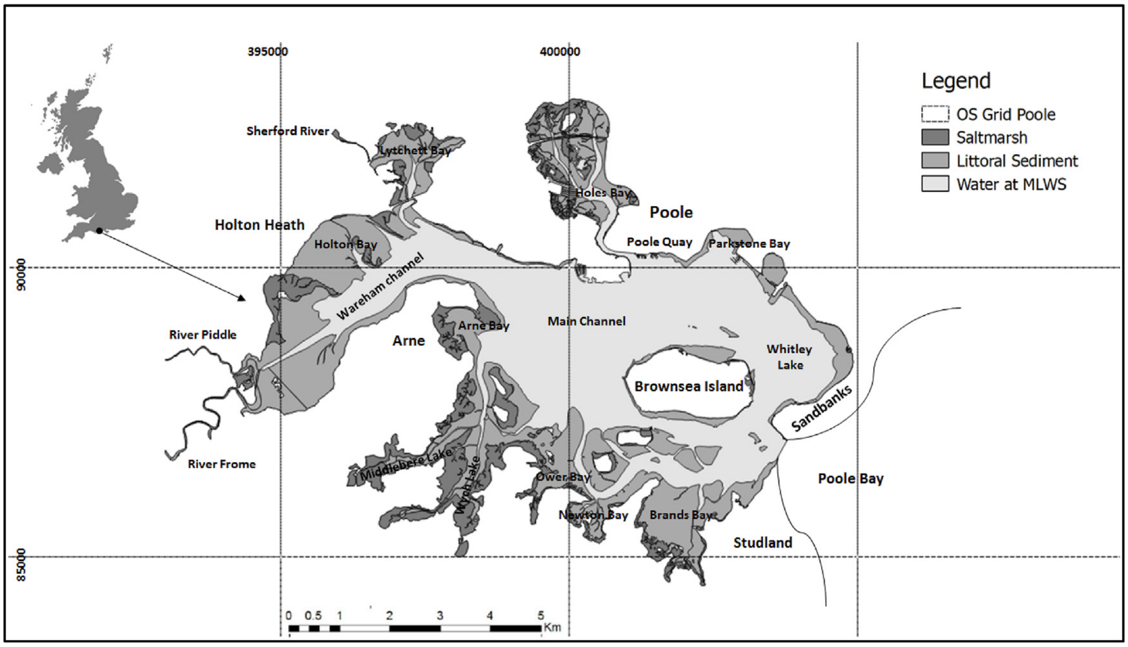

Fig. 2. Map of Poole Harbour ©Crown Copyright and database right (2010) Ordnance Survey Licence Number 1000022021. Open water, Saltmarsh & Sediment data from East Dorset Habitat map© Environment Agency, 2010.

parts: (1) explore the potential for nonlinear relationships in the time series data, (2) determine appropriate pressure-state relationships, and (3) identify any pressure-state thresholds and the location (inflection point) and strength of the thresholds. Before any analysis was conducted, we normalised each set of ecological and environmental time series data by subtracting the mean and scaling by the standard deviation. Where necessary, we averaged intra-annual measures to create a single annual time series for each variable, noting that this may increase the possibility of detecting significant thresholds and tipping points (Samhouri et al., 2017).

The first step was to locate and statistically test one or more breakpoints in time series data with the purpose of identifying the potential existence of nonlinear thresholds occurring over time. Significant breakpoints in each time-series data set (Tables 1 and 2) were identified by performing a sequential analysis of mean values using the sequential T-test analysis (STARS) method (Rodionov, 2004). The STARS algorithm was set to detect significant ($p \leq 0.01$) shifts in the mean value and the magnitude of fluctuations in the time series data by using a modified two-sided Student's t-test. Three different cut-off lengths ($l = 5$, $l = 10$ and $l = 15$) were used to test the sensitivity of results obtained from STARS analyses. Tipping points are often associated with short periods of variability and so an initial cut-off length of 5 was chosen.

To determine appropriate pressure-state relationships, model selection tests were then carried out using stepwise generalised additive models (GAMs) performed using R 3.4.5 statistical software (R Development Core Team, 2016). Similar techniques have successfully been used to detect threshold responses in ecological data (Large et al., 2013) as they are non-parametric and capable of modelling nonlinear responses. They are robust and more flexible than linear methods when using unequally spaced data (Large et al., 2013), while offering a robust approach for detecting threshold responses (Toms and Villard, 2015). As change in one element of NC stocks can either directly or indirectly affect the dependence of other NC stocks or their associated benefit flows (Beaumont et al., 2008), we also tested interrelationships between these variables. For example, biomass of invertebrates in mudflat often provides an important food source for waders and wildfowl, thus any change in a mudflats total area may affect such populations.

For statistically significant pressure-state relationships ($p \leq 0.01$), we fitted separate generalised additive models (GAMs) in R to test for nonlinearities. A smoothing function was applied to each explanatory variable. If smoothing functions are not properly fitted in the model, complex over-fitting is likely to result. To minimise this risk, we used integrated model cross-validation algorithms to ensure that the modes selected were as robust as possible (Rodionov and Overland, 2005). An eigenvalue optimisation process was carried out to prevent overfitting using the "mgcv" package in R (Wood, 2011). Generalised cross validation (GCV) was used to estimate a smoothing parameter for each term. Smoothing terms with penalised regression splines with an added penalty for each term were used so that the number of knots (the x-value at which the two pieces of the model connect) for each term could be reduced to zero. Through this eigenvalue optimisation process, smoothing terms with linear functions in response to pressure variables could effectively be removed from the model if it did not improve the fit (Wood, 2004). As the goal of this research was to identify possible nonlinear threshold values that can inform decision criteria, we rejected GAM models that were more adequately explained using a linear model (Wood and Augustin, 2002). Model selection tests using Akaike's Information Criterion (AIC) were performed on GAMs with different knot combinations to find the knot allocation that resulted in the best fit to the data. The relative importance or explained variance (R^2) of each pressure-state variable in the regression model was calculated and checked using the LMG metric with the relaimpo package in R (Grömping, 2006). From this analysis, we calculated 95% confidence intervals *via* bootstrapping of the residuals in order to allow for autocorrelation (Vinod & López-de-Lacalle, 2009). This procedure generated a range of pressure-state values where a GAMs smoothing function changes trajectory and indicates wherea threshold might occur. Quantitative estimates of a threshold were defined as the point of inflection where the second derivative changes sign (e.g. Samhouri et al., 2010, Large et al., 2013, 2015).

4. Results

4.1. Time-series trends, thresholds and ecosystem responses

Breakpoint (STARS) analysis of the time series data available for Poole Harbour provided empirical evidence of recent environmental

Table 1
Proxies used for assessing natural capital assets (stocks) in Poole Harbour.

Natural capital assets (stock)	Potential ecosystem services	Indicator	Time series	Data source
Intertidal mudflat (area)	Carbon storage, (Regulating) Marine invertebrate habitat (Supporting/Habitat)	Area of mudflat and other littoral sediment (excluding saltmarsh and macroalgal mats) in Poole Harbour as a whole (ha). Areas derived from aerial photography, Compact Airborne Spectographic Imaging and direct survey.	1980–2015	Environment Agency field data. (Bryan et al., 2013).
Manila clam stocks (*Ruditapes philippinarum*)	Food (Provisioning) Nutrient cycling (Regulating).	Annual stock surveys for Manila clam were obtained for three sites in the harbour: Arne Bay, Seagull Island and Round Island. Samples were collected at each site using a trailed pump scoop dredge which was towed along the seabed in circular motions for 2 min. During these 2 min the number of rotations made by the vessel was recorded. The dredge was then lifted aboard the vessel and the contents were emptied into a sample bucket. Three replicate samples were taken at each site and the mean density ($N.m^{-2}$) of each catch recorded.	2003–2015	Southern Inshore Fisheries and Conservation Authority (IFCA) field data. The methodology is described in: SIFCA (2017).
Saltmarsh (area)	Nutrient cycling and coastal protection (Regulating), Marine invertebrate habitat (Supporting/Habitat)	Trends in saltmarsh area (ha) in Poole Harbour derived from aerial photography, Compact Airborne Spectographic Imaging.	1980–2013	Raybould (2005); Gardiner (2015).
Wildfowl and waders	Birdwatching (Cultural)	The harbour wide average density of all species of wildfowl and waders known per year (N).	1980–2015	Wetland Bird Survey (WeBS) data.

degradation in three of the four NC assets: mudflat area, saltmarsh area and Manila clam stocks (Fig. 3). A brief description of the results for each NC asset follows, along with the results from the assembled driver data (Table 3), (see also Appendix 1).

Following their introduction to the harbour in the late 1980's Manila calm stocks increased considerably in the Arne and Seagull Island areas between 2003 and 2007, but experienced strong abrupt shifts between 2007 and 2008 with reduced clam densities persisting at below pre 2006 mean values until 2014. Results of the STARS algorithm (Table 3) suggest that the magnitude of the changes detected in 2008 were the greatest of any variable tested (~3.18–3.26 respectively). There were however, strong indications of recovery in recorded stocks at these sites in 2015, with significant breakpoints ranging in magnitude from (~2.93–3.02 respectively). Stocks of Manila clam recorded at Round Island have conversely increased steadily across the time period, with little signs of abrupt changes. Towards the intertidal areas of the harbour, the mudflats and saltmarshes both showed significant signs of erosion across their respective time periods. The decline in mudflat area over the twenty-five year interval was the more pronounced of the two assets, declining by up to two standard deviations away from the mean value in 1980. Over this time interval, saltmarsh area declined for the first decade then remained relatively stable. This was associated with an increase in mudflat area from 1988 until the mid-1990s, values declining thereafter. Populations of waders and wildfowl increased after 1980 reaching a peak in the mid-1990s, thereafter declining such that by 2005–2010 values were close to those encountered in the early 1980s. Since then, numbers have increased somewhat. It should be noted that these trends only give a "snapshot" of the overall status of the resident bird populations and do not reveal trends for individual species.

The highest STARS value for the driver data was obtained for phosphate values in the harbour (1.95) which have declined considerably since the 1980's. The second strongest shift in the drivers (1.46 & 1.86) was marked by an increase in macroalgal mats across the harbour between 1996 and 2010, followed by a marginal decline from 2011 to 2015 (Appendix 1). Changes in nitrate concentrations and the water temperature both showed increasing trends over the multi-decadal period, leading towards a catchment with a high eutrophic status. River flow trends for the catchment also indicate a year on year increase in flow rate. A single low STARS value (0.12) was detected for sediment shoaling in our proxy site of the Wareham channel, with sediment initially increasing the depth of the channel between 1980 and 1995, before crossing a threshold and thereafter decreasing channel depth. A plausible shift in fishing pressure in 2004 and 2008 can also be seen, coinciding with a decline in Manila clam stocks (Fig. 3).

4.2. The relative contribution of multiple pressures to natural capital stocks

Based on multi-model inference with GAMs we quantified the relative importance of environmental variables to influence each of the four selected NC stocks. Of the thirty-six possible GAM models, ten were significant (Table 4) with the smoothing function included ($p \leq 0.01$).

We found that macroalgal mats (area), sediment shoaling and river flow were the most important predictors for explaining the variability in area of both mudflats and saltmarsh. This finding is confirmed based on the r^2 evidence ratio (Fig. 4) with the three covariates explaining 91% and 85% of the total variance of each model respectively. Macroalgal mats and saltmarsh were the most important predictors of wader and wildfowl stocks with a relative importance of 0.21% and 0.18% and were significant at $p \leq 0.01$. Although mudflat area and sediment shoaling were not significant for determining wader and wildfowl stocks, they had a high relative importance in explaining the variability of the final models (0.13–0.15%). Fishing pressure was the only significant ($p \leq 0.01$) predictor of Manila clam stocks in Arne Bay and Seagull Island with a relative importance of ~84% respectively. As no environmental variables were significant in influencing the Round

Table 2
Indicators of environmental drivers selected for analysis in the Poole Harbour system.

Drivers	Indicator	Time series	Data source
Fishing pressure (Manila clam *Ruditapes philippinarum*)	Number of licenced Manila clam boats in Poole Harbour. Clams are removed from the seabed using a pump scoop dredge which is towed along the seabed by small (under 10 m) fishing vessels.	1994–2015	Information on fishing activity has been obtained with consultation from a range of sources and organisations including Southern IFCA, and Poole Harbour Commissioner reports (Simpson, 2004).
Macroalgal mats (area)	Areas of macroalgal mats (ha) on mudflat and other littoral sediment (excluding saltmarsh) with ≥75% cover and > 2 kgm^{-2} biomass (ha) in Poole Harbour as a whole. Areas derived from aerial photography, Compact Airborne Spectographic Imaging and direct survey.	1980–2015	Environment Agency field data (Bryan et al., 2013)
Nutrient loading (Nitrates)	Dissolved nitrate concentration (mg NO_3-N l^{-1})	1980–2015	River Frome at East Stoke - Centre for Ecology & Hydrology, & FBA (Freshwater Biological Association): Bowes et al. (2011).
Nutrient loading (Phosphates)	Soluble reactive phosphorus concentration (μg l^{-1})	1980–2015	River Frome at East Stoke - Centre for Ecology & Hydrology, & FBA (Freshwater Biological Association); Bowes et al. (2011)
Riparian water flows.	Mean annual river flow (m^{3}s^{-1}) within the Frome and Piddle rivers.	1980–2015	National River Flow Archive; The Centre for Ecology & Hydrology (CEH)
Sediment shoaling	Mean channel depth (m) Wareham Channel.	1980–2015	Poole Harbour Commissioners (PHC); Raybould (2005)
Water temperature	Monthly recorded sea surface temperatures were averaged across the Poole Harbour time series data (°C)	1980–2015	Cefas Coastal Temperature Network Station 23: Channel Coastal Observatory from 2011.

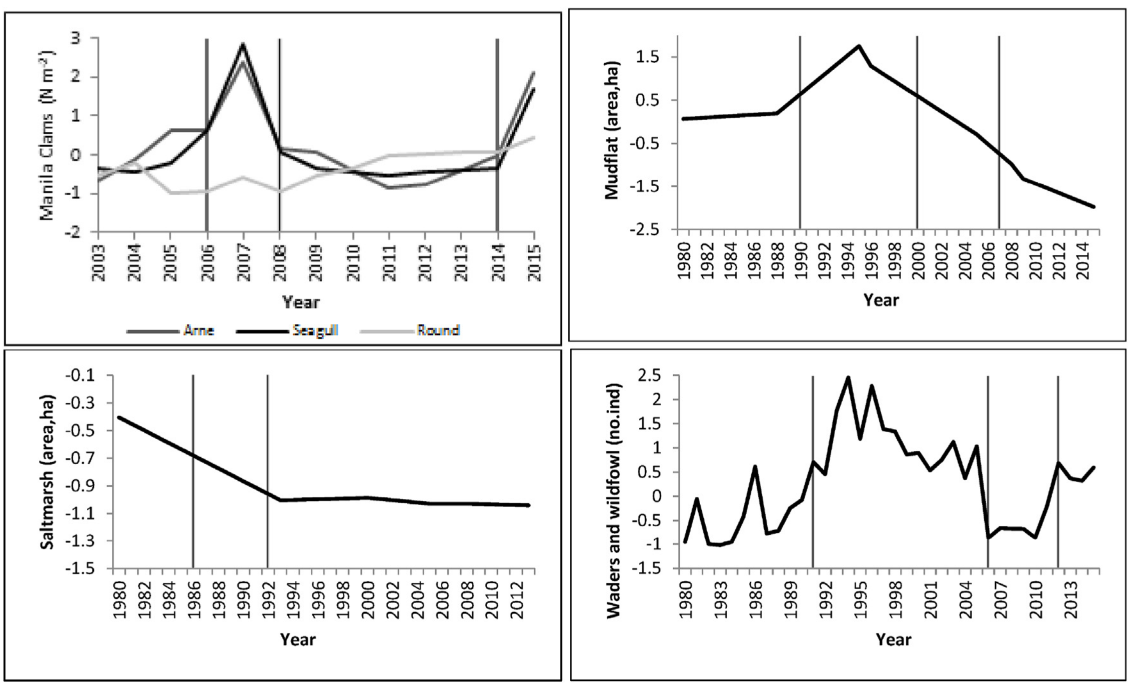

Fig. 3. STARS threshold detection of the four normalised natural capital assets in Poole Harbour, Manila clam stocks (N m^2), mudflat area (excluding saltmarsh and macroalgal mats) (ha), saltmarsh area (ha) and waders/wildfowl (no. individuals). The horizontal line(s) indicates the direction (positive or negative) of the trend representing a significant deviation from zero (i.e. the proxy mean over the time period). Vertical black lines represent statistically significant (p ≤ 0.01) breakpoints for individual trends from sequential Student's t-tests.

Island Manila clam populations, we removed this time series from the next step of full GAM analysis. Other variables were less important for all indices, ranging from 0.01 to a relative importance of 0.13 (see Fig. 4).

The full GAM analyses allowed identification of relationships between NC status and significant pressures. Macroalgal mats showed evidence for negative nonlinear relationships (Fig. 5) with three NC proxies namely mudflat area, saltmarsh area and numbers of wading birds. Sediment shoaling generally increased with mudflat area and a significant positive trend was observed at a value of ~ -0.9 (SD). Saltmarsh vs sediment shoaling also showed an increasing trend before crossing a threshold at ~ -0.9 (SD) and then decreasing to below its initial value. Mudflat area also showed a negative nonlinear relationship with river flow, with a clear threshold observed ~0.2–0 (SD). The relationship between saltmarsh area and river flow was best described as a hockey stick, such that saltmarsh area was negatively associated with river flow at values < −0.2 (SD), but then inverted to a positive trend when river flow was not significantly different from zero. As macroalgal mat area increased wader and wildfowl numbers decreased, particularly at higher values of the former, with a threshold response evident at ~0.08–0.05(SD) for both pressure-states. Similarly there was a generally negative relationship between wader and wildfowl numbers and saltmarsh area, with a threshold again detected at around −0.5 (SD). There was no evidence for nonlinear responses or thresholds in Manila clam stocks in response to fishing pressure in either Arne Bay or Seagull Island, suggesting a purely linear relationship between the variables. Overall, of the three proxies for NC stocks with nonlinear responses, all three showed evidence for thresholds in relation to more than one pressure.

Table 3
Summary of the STARS index values of the environmental drivers and natural assets (stocks).

Drivers/Natural capital stocks	Best estimate of threshold: Time series (STARS)	Magnitude of responses (STARS)
Fishing pressure	2004, 2007	1.78, 1.42
Macroalgal mats (area)	1989, 1996, 2010	0.85, 1.46, 1.86
Nitrates	1996, 2005, 2008	0.34, 0.32, 0.98
Phosphates	2011	1.95
River flow	N/A	N/A
Sediment shoaling	1996	0.12
Water temperature	1985, 1989	0.27, 0.56,
Manila clam stocks (Arne)	2006, 2008, 2014	2.26, 3.18, 2.93
Manila clam stocks (Seagull)	2006, 2008, 2014	2.25, 3.26, 3.02
Manila clam stocks (Round)	–	–
Mudflat excluding saltmarsh and macroalgal mats (area)	1990, 2000, 2007	0.26, 0.65, 0.62
Saltmarsh (area)	1986, 1992	0.54, 0.67
Waders and wildfowl	1991, 2006, 2012	1.59, 1.83, 1.76

5. Discussion

In this study, we employed STARS and generalised additive models (GAMs) to identify trends and thresholds in pressure-time series relationships. Using this analysis we identified distinct points where four NC assets of the harbour (Manila clam stocks, mudflat area, saltmarsh area and waders/wildfowl numbers) have been substantially changed in the past, and the potential drivers of that may have caused such variabilities. Although the STARS technique has been previously been used to identify thresholds in ecological time series data (Mollmann et al., 2009; Conversi et al., 2010), the present study is the first to employ this method to empirically identify thresholds within a NC framework and one of only a few studies to use such analysis in a transitional estuarine system (e.g, Chevillot et al., 2016).

5.1. Trends, thresholds, and fundamental features from STARS analysis

In applying STARS to available drivers for the Poole Harbour ecosystem, the following picture emerges. The 1980–2015 period was categorised by three steadily increasing endogenous pressures (i.e. emanating from the surrounding catchment and within the system; Elliott, 2011) including nitrate concentrations, macroalgal mats and river flows. With respect to these drivers, nitrate loading, a common driver of algal growth and water quality (McGlathery et al., 2007; Lyons et al., 2014), has shifted the estuarine watershed beyond the long-term safe loading limits determined by the Water Framework Directive for the catchment, leading towards an “unfavourable-bad” eutrophic status (Howarth and Marino, 2006; Conley et al., 2009). The current Nitrogen Reduction Strategy (Kite et al., 2012) for the catchment identifies the main source of nitrogen to be diffuse agricultural inputs (73%) with nitrogen entering the harbour forecast to rise further over the next few decades. This is owing to a lag effect of nitrogen leaving the riparian soil zone of surrounding agricultural land and entering the harbour. The consequences of crossing this threshold are likely to be the continued expansion of macroalgal mats fuelled by rising concentrations of nitrate and other inorganic nitrogen compounds in harbour waters. These effects could be compounded by the observed rise in river flow levels since the 1980's, which may act to convey more nitrogen into the harbour owing to the poor flushing characteristics of the Harbour (Dyrynda, 2005). In contrast, phosphate concentrations entering the harbour have decreased substantially since the 1980's. This is likely due to substantial land use changes and improvements to phosphorous-stripping sewage treatment processes in the catchments of the two main rivers (Frome and Piddle) discharging into Poole Harbour. Evidence of a shift in sediment shoaling in the Wareham channel and fishing pressure on Manila clam populations occurred about the same time as the dramatic declines in Manila clam landings (2004–2007). Results from the STARS analysis suggest that the magnitude of the changes in sediment in the Wareham channel were relatively minor, concurring with reports that since 1980 many channels have deepened in most parts of the harbour (May 2005). In this study we only considered one exogenous pressure (i.e. those emanating from outside the system; Elliott, 2011), in the form of water temperature, which showed evidence of a shift to warmer waters around 1989. Over recent decades, an increase in temperature and associated changes in precipitation and sea level rise have been observed in Europe as well as other parts of the world (Pachauri et al., 2014) and it expected such trends will continue in the future.

Among the NC proxies of the harbour, several significant thresholds were identified in the time series data. Relating these changes back to our conceptual framework outlined in Fig. 1, STARS results here show saltmarsh area of the harbour to have declined linearly (Type V) between 1980 and 1988 before stabilising since 1994 at ~400 ha. Longer term trends (1890–2013) in the saltmarsh species *Spartina anglica* by Gardiner (2015) describe the rapid colonisation of the perennial grass over the mudflats between 1890 and 1924 before passing a threshold, and since then there has been much loss of *Spartina* across the harbour. Despite evidence here that this degradation may have now ceased, there is local evidence (e.g. in Holes Bay) that show *Spartina* is still receding in some locations (Gardiner et al., 2007).

Trends of waders/wildfowl and mudflat area in the harbour both exhibited abrupt thresholds (Type VI) at the estuarine scale with the most abrupt threshold response taking place in bird numbers between 2007 and 2012. Irrespective of such abrupt shifts, as of 2012–2015, bird numbers of the harbour were higher than those of the 1980's but lower than the beginning of the 1990's. One possible reason for a general increase in bird numbers in the early 1990's as suggested by Raybould (2005) could be the larger invertebrate prey base opened up in the form of increasing area of mudflats as saltmarsh receded. Evidence from STARS analysis also suggest that the decline in bird numbers since the

Table 4
p-values for all GAM models analysed. Significant models (p ≤ 0.01) are shown in bold and with an (*).**Mudflat area excludes saltmarsh and macroalgal mats.

	Drivers								
Natural capital stocks	Fishing pressure	Mudflat (area)	Macroalgal mats (area)	Nitrates	Phosphates	Saltmarsh (area)	Sediment shoaling	River flow	Water temperature
Mudflat (area)**	N/A	N/A	**0.0032***	N/A	N/A	0.377	**0.0051***	**0.002***	0.265
Manila clam Arne (Stocks)	**0.003***	N/A	N/A	0.06	0.09	N/A	0.262	0.308	0.38
Manila clam Seagull Island (Stocks)	**0.002***	N/A	N/A	0.05	0.10	N/A	0.231	0.301	0.41
Manila clam Round Island (Stocks)	0.067	N/A	N/A	0.16	0.18	N/A	0.276	0.453	0.24
Saltmarsh (area)	N/A	0.377	**0.0017***	0.747	0.472	N/A	**0.0027***	**0.0021***	0.497
Waders and wildfowl	N/A	0.072	**0.0061***	0.678	0.965	**0.0051***	0.1390	N/A	N/A

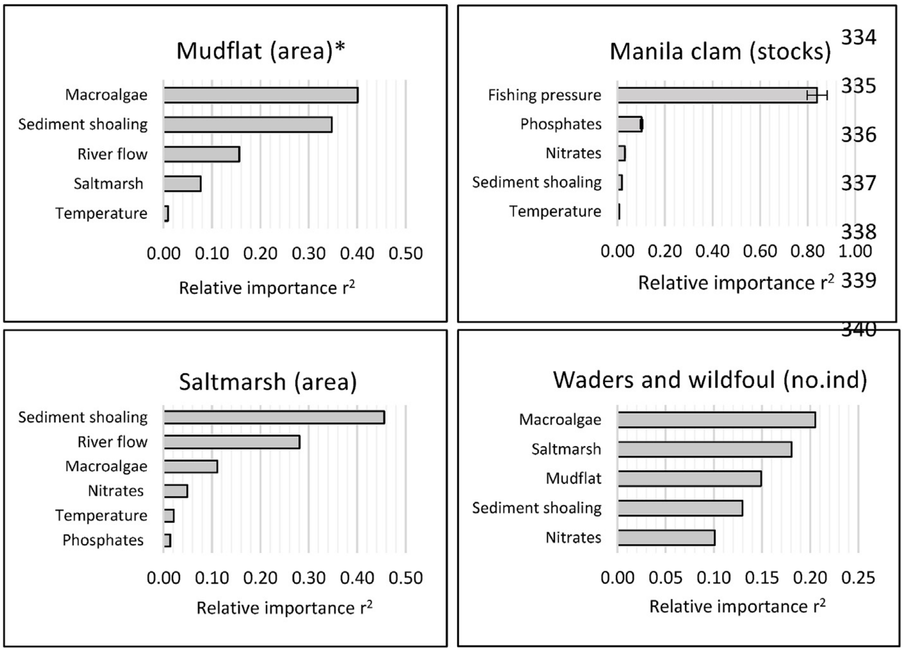

Fig. 4. Relative importance of different pressures for each of the natural capital stock models. The proportion of variance explained by the final model(s) was: mudflat area (99.16%), Manila clam stocks for Arne and Seagull Island (~97.6%), saltmarsh area (86.90%) and waders/wildfowl (76.54%). *Mudflat area excludes saltmarsh and macroalgal mats.

early 1990's could be related to the decline in total mudflat area around the same time (1994), likely as a direct result of mudflats becoming increasingly covered by macroalgal mats. The spread of macroalgae on mudflats has been implicated in the decline of wader/wildfowl populations in many British estuaries (Tubbs and Tubbs, 1980; Anders et al., 2009) including Poole Harbour (Jones and Pinn, 2006), owing to its impact on invertebrates when macroalgal wet weight biomass reaches 2 kg m^{-2} (Raffaelli et al., 1991, 1999). Indeed, recent evidence presented by Thornton (2016) based on field experiments conducted in Poole Harbour, suggests that bird species preferred prey under lower macroalgal mat biomass (~800 g m^{-2} wet weight), supporting a lowering of the current legislative threshold of 2 kg m^{-2} to 1 kg m^{-2}. As

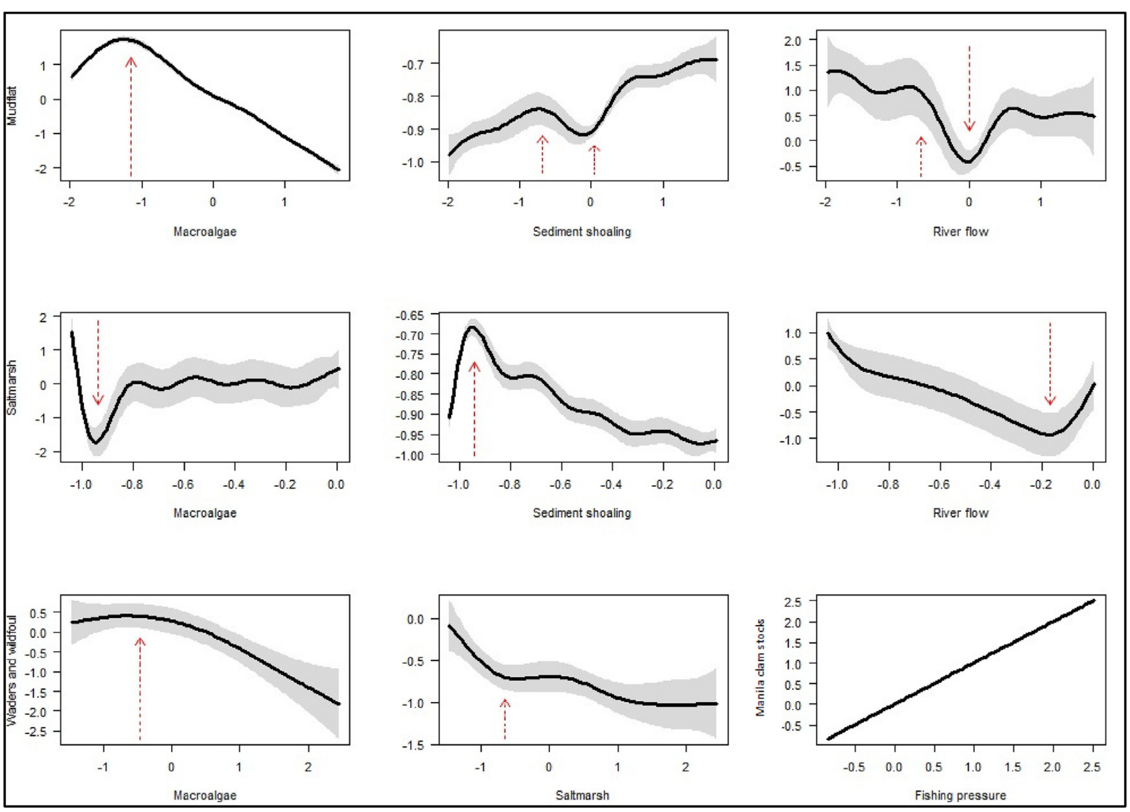

Fig. 5. GAMs of the four normalised natural capital stocks response to pressures (p ≤ 0.01), where the horizontal black line represents significant positive or negative trends, representing a significant deviation from zero (i.e. the mean). The grey polygon represents 95% confidence intervals and red dotted arrow indicates the best estimate of the location of a threshold (i.e., where the second derivative is most different from zero within the threshold range). *Mudflat area excludes saltmarsh and macroalgal mats. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the condition of mudflats, wading birds and the extent of algal mats are sanctions under current legislation (JNCC, 2004) for Poole Harbour, it is important to be able to reliably assess the impact from macroalgal mats on these NC assets.

In the Manila clam fishery of the harbour, free-living stocks in the harbour were shown to have generally increased considerably since their introduction in the late 1980's. However, an abrupt decline in the densities of clams was observed at two sites of the harbour between 2006 and 2008, and the values have only recently (2015) shown signs of recovery. These changes were also the greatest in magnitude of all the threshold responses observed in this study and fit the criteria outlined in Fig. 1 for a tipping point transition (i.e. type VII). However, at this point STARS analysis could only provide qualitative evidence of the impact of drivers and potential feedback mechanisms on the time series data. To quantitatively unravel the relative importance of different drivers as well as potential feedback mechanisms (which are a prerequisite of a tipping point), we considered the results from the GAMs, as explored further below. Moreover, in attempting to reconcile the difference between clam stocks at various locations of the harbour we recognise that the three sites investigated here are only a snapshot of the local populations. However, our results corroborate with other larger studies (e.g. Herbert et al. (2018)) that have looked at several sites across the harbour (including our sites, albeit with different protocols), which suggest a fall in the number of Manila clams at the harbour level between 2008 and 2009 (26–11 ind per m^2), but a relative stability in clam numbers from 2011 to 2015 at approximately 25–28 ind per m^2, based on a resurvey of a selected number of the original sites.

5.2. The impact of multiple stressors on natural capital stocks

By means of multi-model inference, we were able to determine statistically the relative contribution of fishing pressure, macroalgal mats, nitrates, phosphates, river flows, sediment shoaling and elevated water temperatures to the dynamics of four NC assets of Poole Harbour. This is important information for the management of the harbour, because any thresholds identified by asset-driver-state interactions indicate where particular management interventions might be needed to avoid abrupt changes occurring. However, the models that we generated in this research did not take into account the complex interactions that may occur between driver variables (e.g. Crain et al., 2008), and we may have missed important drivers from the analysis (e.g. sea level rise, disease, heavy metals and other pollutants). Hence, future studies could usefully account for interactions between a larger suite of drivers and NC relationships.

The area of macroalgal mats was a significant predictor of mudflat area and saltmarsh area. For example when algal mats increased above ~ -1(SD), we noted significant decreasing trends in the area of both NC stocks. This is coherent with existing evidence that the smothering effect of excessive macroalgal growth and the concentrations of nitrates causing them are damaging to the habitats of this internationally important site (Herbert et al., 2010). As such, notwithstanding potential negative ecological impacts, these results support recently proposed algal harvesting measures (Taylor, 2015) that have been suggested as a means to reduce and recycle nitrogen, as well as to reduce the volume of green macro-algae, thus protecting saltmarsh and mudflat habitats. While little information is available about the impacts that the macroalgal mats have on the businesses of the harbour, there are a number of studies in other estuaries (e.g. Troell et al., 2005; Ferreira et al., 2010) that indicate frequent macroalgal blooms can cause significant biodiversity loss, aesthetic impacts and public health problems, effectively eroding the benefit flows provided by NC stocks (as described in Fig. 1, I).

As suggested in the STARS analysis above, areas of macroalgal mats and saltmarsh were shown to have significant negative but mostly linear effects (II, Fig. 1) on wader and wildfowl numbers, with a threshold observed in both cases ~ -0.5 (SD). While mudflat area was not a significant predictor in our bird models, it did have a high relative importance in explaining the variation within models. Thus, as suggested by Bowgen et al. (2015) it is likely that waders/wildfowl in Poole Harbour are able to adapt to changes in their environment (e.g. increasing algal mats and reduced mudflat area) by switching to alternative habitats with different prey species and size classes, and may only undergo true tipping point transitions (i.e. VII, Fig. 1) under extreme scenarios (e.g. the total removal of invertebrates from a system). However, this generalisation was developed based on analysis of the wader/wildfowl populations as a whole, and it is likely that individual species may have responded very differently to the environmental changes documented here (e.g. Durell et al., 2006).

Two other environmental pressure variables, sediment shoaling and river flow, both responded to changes in mudflat and saltmarsh area in a deterministic manner. This is consistent with the fact that feedbacks between hydrodynamic forces and sediment accretion are key processes in shaping mudflats and saltmarshes (Kirwan and Murray, 2007; Wesenbeeck et al., 2008). Here we show that sediment shoaling rates had a generally positive effect on mudflat area but mainly a negative impact on saltmarsh area. *Spartina* has been well documented as affecting the sediment regime of the harbour (Raybould, 2005), acting to consolidate sediment by rhizome growth in periods of expansion and releasing sediment into the harbour as it dies back, in a density dependent negative feedback manner. While many different biogeochemical mechanisms and drivers can lead to saltmarsh change (Crooks and Pye, 2000), there is evidence that the loss of *Spartina* in the harbour is mainly attributable to physical mechanisms such as direct human destruction (urbanisation) and erosion caused by changes in hydrodynamics and/or morphology (Gardiner, 2015). The optimal river flow rates predicted by the smoothing functions (Fig. 5) suggest an abrupt threshold (III, Fig. 1) for mudflat area ~ -0.5 (SD) and a negative linear effect on saltmarsh, with a shift in both variables towards net accretion trend at the current mean values for these assets at the harbour level. Accumulating evidence already suggests that many of the ecosystem services provided by saltmarshes have been jeopardized by the dieback of *Spartina* including the ability of the marshes to (1) reduce water flows and retain sediment (Raybould, 2005), (2) remediate nutrients and store heavy metals (Hübner et al., 2010), (3) provide habitat for a variety of animals (Gardiner, 2015).

Finally, we identified fishing pressure to be the only significant driver to have influenced the abrupt time series trends in Manila clam stocks at two of the long term monitoring sites of the harbour. As expected, the relationship between fishing pressure and clam stocks was entirely linear (II, Fig. 1), suggesting there was no definitive threshold where reducing fishing pressure could prevent the collapse of clam stocks. As fishing effort is controlled by the density of clams (the minimum landing size of Manila clams in Poole Harbour is 35 mm), this means that if the density of large sized clams increases so does fishing effort, and when the density decreases so does fishing effort (Humphreys et al., 2007). This is analogous to a predator-prey system, whereby fishing effort increases after the population density increases, before reducing again once the population of “legal” sized clams has reduced. However, Unregulated and Unsustainable (IUU) fishing has been noted as a particular problem for the fishery over the study period and before the introduction of the Permit Byelaw in 2015, there were significant illegal landings, the magnitude of which are unknown (Harris, 2016). While IUU fishing activities almost certainly would have affected the value of landings being delivered into the harbour, the stock data used here (rather than landings) should highlight the densities of clams available in the harbour indiscriminately of legal or illegal fishing. In response to IUU fishing, enhanced enforcement by the local inshore fisheries and conservation authority (IFCA) has led to a significant reduction in illegal fishing and there are signs from this survey and some more recent stock assessments (SIFCA, 2017) that the new bylaws have had a positive impact on stocks of clams in the harbour, with a recently awarded Marine Stewardship Council (MSC) accreditation for Manila clams being designated as of 2018 (Williams and Davies, 2018).

While fishing pressure is clearly a key driver in the population status of this species, it is also important to consider other mechanisms that could have could be responsible the abrupt shifts in the stocks seen in this study. For example, there is evidence that Manila clams cultured on the lease beds in the harbour were subject to recurring bouts of mass mortalities around 2006–2008 (Bateman et al., 2012), resulting in many lease holders switching to other aquaculture species such as oysters (Othniel Oysters Ltd, Personal Communication, June 2018). From the literature it is unclear what caused such events but viral infection combined with low winter temperatures and food availability are the most likely possibilities (Humphreys et al., 2007; Bateman et al., 2012; Franklin et al., 2012). Such occurrences provide an example of a potential positive feedback mechanism and possible evidence for a tipping point in the stocks of clams the harbour (i.e. type VII, Fig. 1). As viral infection reduces the fitness of the population (e.g. gamete release may be related to the metabolic depletion caused by the virus (Jasim Uddin et al., 2010)), the carrying capacity of the population is also lowered owing to a decreased resistance to disease, causing a powerful positive feedback that further decreases shellfish stocks. This in turn has socio-economic consequences, with local aquaculture businesses and regulators potentially switching to more lucrative species as the condition of the NC stock is reduced. Therefore, while the environmental conditions of Poole Harbour are currently favourable for Manila clam proliferation (as evidenced by the recent increase in the wild stocks of the harbour), different types of disturbance may have acted together to cause an abrupt decline in the Manila clam aquaculture fisheries of the harbour and therefore the stocks of clams that was observed. In accordance with theory (Scheffer et al., 2001), if a critical value of a press disturbance is exceeded, this may lead to a tipping point driven by a positive feedback mechanism, which could be triggered by a pulse disturbance. In this case study, fishing pressure (legal or illegal) and increasing water temperature can both be considered as press disturbances, the latter potentially increasing the risk of viral infections outbreaks, which represent a form of pulse disturbance. Such processes are not likely to be specific to Poole Harbour, with at least eleven estuaries in southern England currently accommodating naturalised populations of Manila clam (Humphreys et al., 2015) and mass mortality events of Manila clam now being reported in other locations around the world (Pretto et al., 2014; Nam et al., 2018).

The increase in the wild stocks of a commercially attractive species such as Manila clam is also likely to have substantial consequences on the wider ecology and economy of the harbour. For instance, there is evidence that the introduction of the clams in the late 1980's has potentially had a positive effect on the over-winter mortality of several wader/wildfowl species such as oystercatchers in the Harbour (Caldow et al., 2007). Thus, it could be suggested that if clam stocks were to continue to increase this would have the potential to provide an indirect benefit to several European shorebird populations *via* a spill-over effect increasing wild populations. There is also evidence that when cultured at high densities Manila clams can provide other indirect benefits to humans such as altering biogeochemical cycles, thereby reducing the effects of nutrient pollution and the deployment of algal mats (Rose et al., 2015), both of which are key issues for managers in Poole Harbour. Furthermore, in terms of direct economic value, a recent report by Williams and Davies (2018) suggests that although the overall landed weight of Manila clams and the value of landings have decreased by 50% and 25% respectively since 2010, the direct Gross Value Added (GVA) added to the local economy by the Manila clam is by a wide margin the highest of any species landed into the harbour (£838,911per annum vs the next highest species: whelks £249,562, based on 2016/2017 data). This suggests there is a local economic interest in ensuring that clam stocks remain high in the harbour. Nonetheless, such financial benefits must be balanced against the potential problems of removing commercial quantities of Manila clams from Poole Harbour. For example, there is evidence that the use of pump-scoop dredges can have significant impacts on the benthic community by reducing fine sediment and some prey species available to wintering birds (Clarke et al., 2017). Managing fisheries and aquaculture development in a way that does not lead to deleterious ecosystem change is considered as a serious governance challenge not just in Poole Harbour but in many marine protected areas around the world (Edgar et al., 2014). One way to avoid ecological tipping points as advocated by the FAO (The Food and Agriculture Organization of the United Nations), could be through prudent application of the precautionary principle (Carvalho, 2006).

6. Conclusions

Given the growing evidence that coastal and shallow marine ecosystems are increasingly experiencing multiple disturbances, based on the numbers of studies reporting strong anthropogenic impacts resulting from multiple drivers (Crain et al., 2008; Halpern et al., 2008; Hewitt et al., 2015; Gunderson et al., 2016), both scientists and resource managers must confront the potential challenges of nonlinear shifts in ecosystem structure and function (Crain et al., 2009; Côté et al., 2016). Yet, despite the ecological literature being replete with terms related to ecological thresholds, tipping points and other concepts relating to multiple stable states (e.g. regime shifts), these is currently very little empirical evidence that such transitions actually occur in estuaries and other nearshore ecosystems (Mac Nally et al., 2014). Practical application of such concepts in a policy or management context are impeded by several factors such as 1) terminological inconsistency; 2) inadequacy of the temporal and spatial datasets for evaluating abrupt trends; 3) insufficient demonstration of mechanistic links between human or natural factors that cause ecosystem change (Capon et al., 2015). In this study we have considered all three criteria and demonstrate that abrupt nonlinear thresholds in NC assets may occur in marine protected systems such as harbours. The ecological thresholds that we have identified are driven by interactions among biophysical, ecological, and socioeconomic mechanisms mainly at the catchment scale. As we often lack robust ecological information in most systems to make *a priori* mechanistic predictions of where thresholds will occur (Dodds et al., 2010), we believe that the methods outlined in this paper could be used to help local managers evaluate and articulate strategies to detect thresholds and tipping points in a way that can be incorporated in resource management frameworks (*sensu* Selkoe et al., 2015). This would support global efforts by the United Nations Intergovernmental Oceanographic Commission (IOC) and other international initiatives to improve the long term sustainability of resources within large marine protected areas and their associated watersheds, with a particular focus on ecosystem based approaches to deliver healthy marine ecosystems and sustained ES. Further research could also usefully combine information on temporal trends with spatial data on status of NC and/or multiple interacting drivers to create conceptual and dynamic modelling tools to support management decision-making.

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