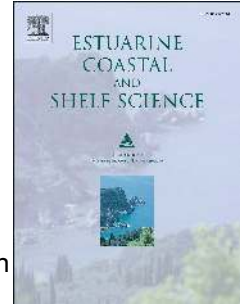


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Detecting ecological thresholds and tipping points in the natural capital assets of a protected coastal ecosystem

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1 Detecting Ecological Thresholds and Tipping Points in the Natural 2 Capital Assets of a Protected Coastal Ecosystem.

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7 Key words: Thresholds, Tipping points, Marine Protected Areas, Multiple stressors, Natural capital,
8 Poole Harbour.

9 Abstract

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

31 1 Introduction

32
33 Concern about abrupt and potentially irreversible ecosystem transitions is growing rapidly, as they
34 may have significant implications for human wellbeing and are forecast to increase with intensifying
35 climatic change and environmental degradation (Scheffer *et al.*, 2001; Rockström *et al.*, 2009). Such
36 transitions may result from an abrupt change in underlying drivers (e.g. land cover change, nutrient
37 inputs), from an interaction between drivers, or from an abrupt change in the state of the ecosystem
38 with a small or smooth change in drivers (Andersen *et al.*, 2009). Another possibility is a threshold
39 driven by a positive feedback loop, which is often referred to as a tipping point (Scheffer *et al.*, 2009;
40 2012). While identifying such thresholds and tipping points can be challenging to identify in practice,
41 evidence is increasingly indicating that nonlinear threshold responses could be widespread.
42 Incorporating information about such responses into management plans can facilitate improved
43 management outcomes (Huggett, 2005; Foley *et al.*, 2015). Issues of particular importance to
44 environmental policy and practice include development of techniques to identify where and when
45 thresholds are likely to be encountered (Bestelmeyer *et al.*, 2011; Newton, 2016) and identification

46 of the underlying mechanisms so that appropriate management responses can be identified (e.g. in
47 the relationships between shorebird mortality and shellfish stock resources; Goss-Custard *et al.*,
48 2004).

49
50 While the importance of ecological thresholds, tipping-points and associated phenomena is
51 increasingly being recognised (e.g. deYoung *et al.*, 2008; Hughes *et al.*, 2013; Levin & Möllmann,
52 2015), few previous studies have examined their occurrence in transitional systems such as estuaries
53 and harbours (although see Hewitt *et al.*, 2010). This is surprising as such systems typically deliver a
54 number of valuable goods and services (Barbier *et al.*, 2011) but at the same time are subject to
55 more human-induced pressures than most other marine systems (McLusky & Elliott, 2004). In
56 particular, harbours (which may be classified as estuaries or lagoons; Humphreys, 2005) often
57 provide examples of conflicts between high ecological value and intensive human use. The current
58 research was designed to help address this knowledge gap. The purpose of this research was to use
59 a combination of time series data and statistical techniques to examine the occurrence of thresholds
60 and tipping points in Poole Harbour, UK, a Special Protection Area (SPA) of high ecological and socio-
61 economic value. Owing to the breadth of definitions surrounding the concept of tipping points, we
62 start by outlining the definitions adopted here and the underlying theory.

63 **2 Defining tipping points in the natural capital components of ecological systems**

64
65 Tipping points have been defined in a number of different ways. For example, in their consideration
66 of the Earth's climate system, Lenton *et al.* (2008) defined a tipping point as the critical point at
67 which the future state of the system is qualitatively altered by a small perturbation. Similarly
68 Scheffer *et al.* (2012) referred to a tipping point as a situation where a local perturbation can cause a
69 domino effect resulting in a system transition. Tipping points in complex systems have been widely
70 interpreted as equivalent to critical transitions, phase transitions or fold bifurcations (Lenton *et al.*,
71 2008, Scheffer *et al.*, 2009; Ashwin *et al.*, 2012). Such concepts derive from theories of dynamical
72 systems, including bifurcation and catastrophe theories. Application of these theories has
73 highlighted a number of ways in which tipping points can occur, for example by a change in the
74 external conditions of a system, or a change in the state of the system itself (Ashwin *et al.*, 2012, van
75 Nes *et al.*, 2016).

76
77 While application of dynamical systems theory to the climate system is now well established (Lenton
78 *et al.*, 2008), its application to understand the dynamics of terrestrial and marine ecosystems has
79 been the focus of some debate. Policy makers and land managers increasingly want to understand
80 how different forms of environmental change might affect the condition of natural capital (NC), and
81 the flow of multiple ecosystem services (ES) to human society (Mace *et al.*, 2015). As dynamical
82 systems models are typically defined in relation to a single independent variable, simultaneous
83 consideration of multiple and potentially interacting drivers of ecological change represents a
84 significant analytical challenge. As noted by Donahue *et al.* (2016), the multidimensionality of
85 ecological responses requires explicit consideration of multidimensional disturbances or causes of
86 change. The challenges of applying dynamical systems theory to real-world ecosystems are
87 illustrated by the concept of ecological resilience. Much of the recent literature on this concept is
88 based on the assumption that ecosystems have multiple stable equilibria, with tipping points
89 occurring between them (Donahue *et al.*, 2016). Definitions of ecological resilience focus on the
90 capacity of a system to maintain its essential structure and function when confronted with external
91 perturbations (Quinlan *et al.*, 2016). Yet the empirical evidence for the existence of such multiple
92 stable states is very limited (Petraitis, 2013); most ecosystems are far from the equilibria assumed by
93 theory (Donahue *et al.*, 2016), and other assumptions on which the underlying theory is based are
94 often not met in field situations (Newton, 2016). Consequently, ecological resilience has proved very
95 difficult to measure in practice (Quinlan *et al.*, 2016, Biggs *et al.*, 2012, Cantarello *et al.*, 2017).

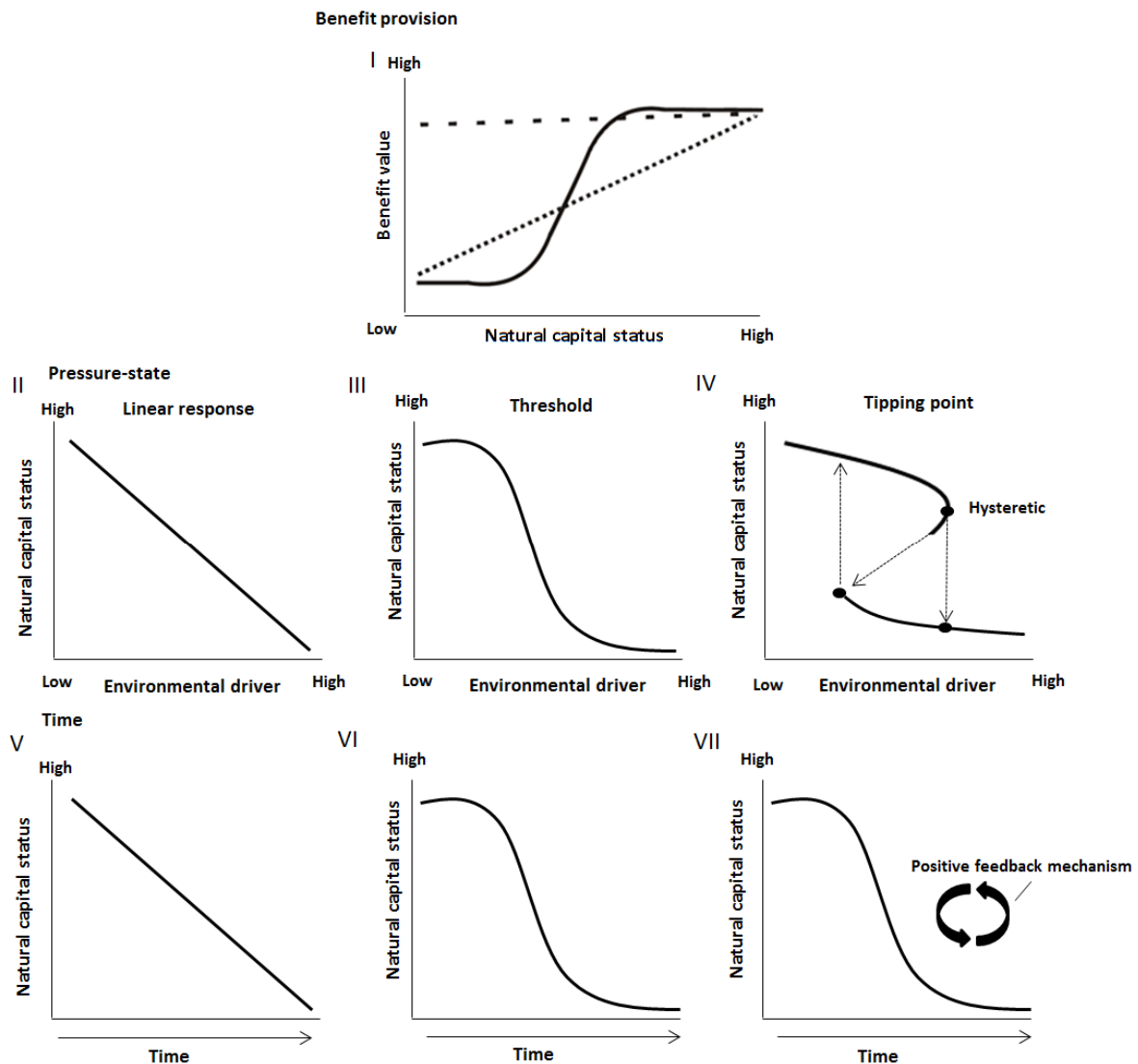
96 Together with the semantic confusion surrounding resilience, these problems have resulted in the
97 concept being misapplied in both policy and practice (Newton, 2016).

98
99 We therefore follow van Nes *et al.* (2016) in applying the term ‘tipping point’ to any situation where
100 accelerating change caused by a positive feedback drives the system to a new state. We make no
101 assumptions about whether the ecosystem in question is characterised by the existence of multiple
102 stable states (Petraitis, 2013), and we do not make an explicit link between tipping points and
103 dynamical systems theory. As highlighted by van Nes *et al.* (2016), this broader definition of a tipping
104 point is consistent with the work of Gladwell (2000), who did so much to popularize the concept. The
105 existence of an intrinsic positive feedback process that drives accelerating change differentiates
106 concept tipping point from a broader category of abrupt ecosystem change, which we refer to as an
107 ecological threshold. Any situation where there is an abrupt change in ecosystem structure or
108 function can be considered as an ecological threshold (Groffman *et al.*, 2006). Ecological thresholds
109 may also usefully be differentiated from decision or management thresholds, or regulatory limits
110 (Johnson, 2013), which are based on values of system state variables that should prompt specific
111 management actions (Martin *et al.*, 2009). Following van Nes *et al.* (2016), we therefore restrict the
112 term ‘tipping point’ to a subcategory of ecological threshold where the abrupt change is driven by a
113 positive feedback mechanism.

114
115 Here we examine the occurrence of thresholds and tipping points in relation to provision of multiple
116 ecosystem services in a coastal ecosystem. To achieve this, we employ a conceptual framework
117 based on the reviews conducted by Mace *et al.* (2015) and the Natural Capital Committee (NCC,
118 2014). Here, NC is defined as assets, stocks or the elements of nature that directly and indirectly
119 produce value or benefits to people (NCC, 2014), such as ecological communities or habitat types.
120 Following Mace *et al.* (2015), the status of these natural assets can be measured using metrics of the
121 area, and condition of these communities. In the context of environmental degradation and its
122 potential impact on human society, the form of the relationship between the condition of a natural
123 asset and provision of benefits is of particular importance. Environmental degradation may lead to a
124 decline in natural asset status, which will reduce the benefits provided to people. The form of this
125 decline represents a key knowledge gap (Folke *et al.*, 2011; NCC, 2014), but could potentially include
126 threshold responses or tipping points (Figure 1 (I)). In addition, we hypothesize that the relationship
127 between anthropogenic drivers (or pressures) and NC status may also demonstrate a threshold
128 response or a tipping point (Figure 1 (II,III,IV)).

129
130 The relationships between anthropogenic drivers (or pressures) and NC status may also vary over
131 time, demonstrating either linear or nonlinear trends (Figure 1 (V-VII)). If an environmental driver
132 intensified over time, then it could produce a threshold response in NC status, or a tipping point if a
133 positive feedback mechanism were influential. Tipping events (IV & VII) are often considered
134 difficult to reverse because of a phenomenon known as hysteresis (Meyer, 2016). This implies that
135 the system cannot recover by retracing the path followed during degradation. Instead, the
136 environmental driver that caused the transition has to be reduced further than the threshold value
137 that caused the initial transition. Ultimately, if environmental degradation leads to an abrupt decline
138 in natural asset status, this will reduce the benefits provided to people, either temporarily or
139 permanently.

140



141
 142 **Figure 1:** (I) Alternative forms of forms of natural capital asset–benefit relationships, as hypothesized
 143 by Mace *et al.* (2015). The solid black line illustrates how the value of benefits might change in
 144 response to variation in the status or condition of natural assets, which could be caused by
 145 environmental degradation. The dashed line shows a threshold response (or tipping point). Panels
 146 (II–IV) show the relationship between NC status to changing conditions or environmental drivers
 147 which might be: II. Linear response. III. Nonlinear, non-hysteretic response of ecosystem state as a
 148 function of a pressure (threshold) or IV. Tipping point (hysteretic), representing a nonlinear change
 149 driven by an intrinsic positive feedback mechanism and with respect to changing conditions or
 150 environmental drivers. Finally, panels (V–VII) show how a responding system may change through
 151 time when they respond to an escalating driver according to the linear or abrupt equilibrial
 152 behaviour shown in (II–IV).

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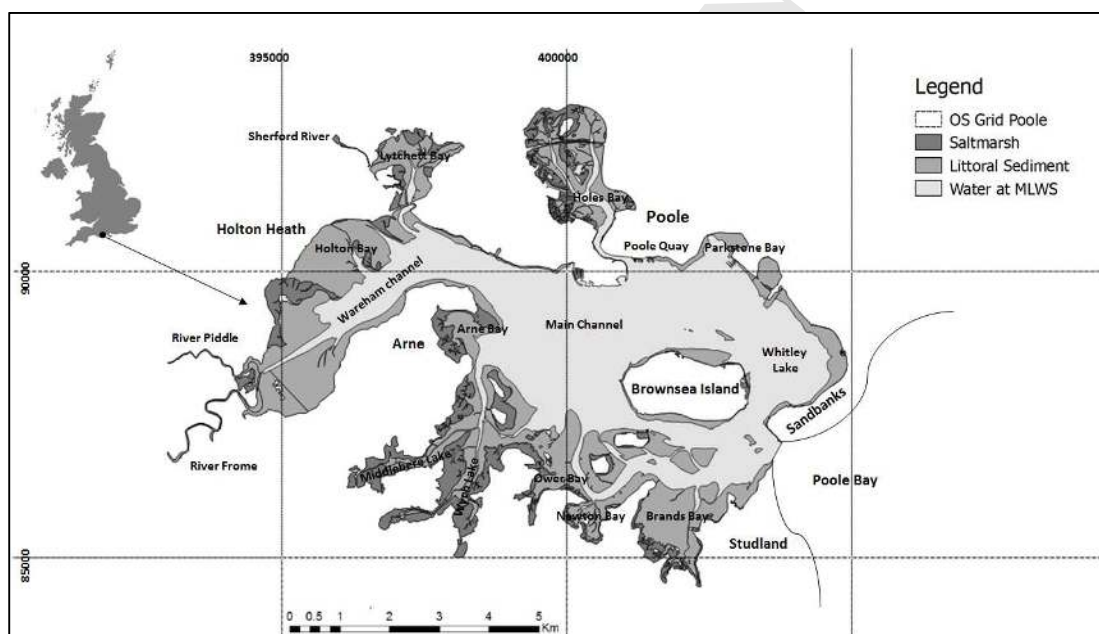
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158 3 Methods

159 3.1 Details of study area: Poole Harbour

160 Poole Harbour is a large natural harbour of nearly 4,000 ha (Underhill-Day, 2006) located on the
 161 coast of Dorset in southern England (Lat. 50° 42' 44" Long. 2° 03' 30" W) in the United Kingdom
 162 (Figure 2). Although classified as an estuary (as several rivers flow into it), Poole Harbour has many
 163 of the qualities of a large lagoon, owing to the narrow entrance and limited tidal range (Humphreys,
 164 2005). A diverse set of habitats from saltmarsh and reedbed (*Phragmites australis*) to valley mire
 165 and lowland heathland provide a host of different ecosystem services such as recreation, coastal
 166 protection and increased water quality to a catchment of over 142,100 people (Office for National
 167 Statistics, 2010). Ecologically, the intertidal mudflats, sandflats and marshes support large numbers
 168 of wintering wildfowl and waders that are of national and international significance. The harbour
 169 and its adjacent landscape also hold a number of other national statutory designations that serve to
 170 protect the natural environment, including being classified as a Site of Special Scientific Interest
 171 (SSSI), a Special Protection Area (SPA) designated under the EU Birds Directive and a Ramsar site.
 172 Under the EC Shellfish Waters Directive, Poole Harbour (with the exception of Holes Bay) is also
 173 designated as a shellfish water and is the location of fishing and aquaculture activities, which in 2005
 174 were worth in excess of £2 million per year to the local economy (Jensen *et al.*, 2004). However,
 175 despite its high economic and conservation value, the occurrence of ecological thresholds and
 176 tipping points in the NC assets of Poole Harbour has not been examined previously.
 177



178
 179 **Figure 2** Map of Poole Harbour ©Crown Copyright and database right (2010) Ordnance Survey
 180 Licence Number 1000022021. Open water, Saltmarsh & Sediment data from East Dorset Habitat
 181 map© Environment Agency, 2010.

182 183 3.2 Data collection

184 Data for four different categories of NC components were gathered for the period 1980-2015 (Table
 185 1). Three NC stocks of interest (mudflat area, saltmarsh area and wader/wildfowl numbers) were
 186 chosen owing to their immediate importance for conservation within the SPA, while the potential
 187 stocks of the Manila clam in the harbour (*Ruditapes philippinarum*) were also investigated based on
 188 their significant commercial importance and the potential benefit flows provided by the landings of
 189 clams into Poole Harbour. To test potential pressure-state relationships, data for possible drivers in

190 the harbour were sourced from the literature, environmental data-bases and monitored instrument
 191 records (Table 2). For example we used tidal river flow and water quality data from the River Frome
 192 at East Stoke gauging station (ID: 44207) to represent a county level watershed driver. In the
 193 absence of long-term fishing effort data (e.g. fishing effort, frequency trawled) fleet capacity (i.e.
 194 number of licenced clam boats) was used as a proxy for fishing pressure (Piet *et al.*, 2006). As
 195 fishermen in Poole Harbour utilise a unique “pump-scoop” dredge to harvest the Manila clam (95%
 196 of catch is typically clam landings; Clarke *et al.*, 2017) fleet capacity is likely an effective pressure
 197 indicator that describes the impact induced by fishing activities on the system.

198 **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 Spectrographic Imaging and direct survey.	1980-2015	Environment Agency field data. (Bryan <i>et al.</i> , 2013).
Manila clam stocks (<i>Ruditapes philippinarum</i>)	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 two minutes. During these two minutes 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 Spectrographic 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.

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

Drivers	Indicator	Time series	Data source
Fishing pressure (Manila clam <i>Ruditapes philippinarum</i>)	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 $\geq 75\%$ cover and $> 2 \text{ kgm}^{-2}$ biomass (ha) in Poole Harbour as a whole. Areas derived from aerial photography, Compact Airborne Spectrographic Imaging and direct survey.	1980-2015	Environment Agency field data (Bryan <i>et al.</i> , 2013)
Nutrient loading (Nitrates)	Dissolved nitrate concentration ($\text{mg NO}_3\text{-N l}^{-1}$)	1980-2015	River Frome at East Stoke - Centre for Ecology & Hydrology, & FBA (Freshwater Biological Association); Bowes <i>et al.</i> (2011).
Nutrient loading (Phosphates)	Soluble reactive phosphorus concentration ($\mu\text{g l}^{-1}$)	1980-2015	River Frome at East Stoke - Centre for Ecology & Hydrology, & FBA (Freshwater Biological Association); Bowes <i>et al.</i> (2011)
Riparian water flows.	Mean annual river flow (m^3s^{-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 ($^{\circ}\text{C}$)	1980-2015	Cefas Coastal Temperature Network Station 23; Channel Coastal Observatory from 2011.

213

214 **3.3 Data analysis**

215 Based on criteria outlined by Collie *et al.* (2004), Bestelmeyer *et al.* (2011), Carpenter (2011) and
 216 Samhuri *et al.* (2017) we followed a step-wise process for detecting and characterising thresholds
 217 and their driver-response interactions. The workflow can be summarised in three parts: (1) explore
 218 the potential for nonlinear relationships in the time series data, (2) determine appropriate pressure-
 219 state relationships, and (3) identify any pressure-state thresholds and the location (inflection point)
 220 and strength of the thresholds. Before any analysis was conducted, we normalised each set of
 221 ecological and environmental time series data by subtracting the mean and scaling by the standard
 222 deviation. Where necessary, we averaged intra-annual measures to create a single annual time
 223 series for each variable, noting that this may increase the possibility of detecting significant
 224 thresholds and tipping points (Samhuri *et al.*, 2017).

225

226 The first step was to locate and statistically test one or more breakpoints in time series data with the
 227 purpose of identifying the potential existence of nonlinear thresholds occurring over time.
 228 Significant breakpoints in each time-series data set (Table 1 and 2) were identified by performing a
 229 sequential analysis of mean values using the sequential T-test analysis (STARS) method (Rodionov,
 230 2004). The STARS algorithm was set to detect significant ($p \leq 0.01$) shifts in the mean value and the
 231 magnitude of fluctuations in the time series data by using a modified two-sided Student's t-test.
 232 Three different cut-off lengths ($l = 5$, $l = 10$ and $l = 15$) were used to test the sensitivity of results
 233 obtained from STARS analyses. Tipping points are often associated with short periods of variability
 234 and so an initial cut-off length of 5 was chosen.

235 To determine appropriate pressure-state relationships, model selection tests were then carried out
 236 using stepwise generalised additive models (GAMs) performed using R 3.4.5 statistical software (R
 237 Development Core Team, 2016). Similar techniques have successfully been used to detect threshold
 238 responses in ecological data (Large *et al.*, 2013) as they are non-parametric and capable of modelling
 239 nonlinear responses. They are robust and more flexible than linear methods when using unequally

240 spaced data (Large *et al.*, 2013), while offering a robust approach for detecting threshold responses
241 (Toms & Villard, 2015). As change in one element of NC stocks can either directly or indirectly affect
242 the dependence of other NC stocks or their associated benefit flows (Beaumont *et al.*, 2008), we also
243 tested interrelationships between these variables. For example, biomass of invertebrates in mudflat
244 often provides an important food source for waders and wildfowl, thus any change in a mudflats
245 total area may affect such populations.

246 For statistically significant pressure-state relationships ($p \leq 0.01$), we fitted separate generalised
247 additive models (GAMs) in R to test for nonlinearities. A smoothing function was applied to each
248 explanatory variable. If smoothing functions are not properly fitted in the model, complex over-
249 fitting is likely to result. To minimise this risk, we used integrated model cross-validation algorithms
250 to ensure that the modes selected were as robust as possible (Rodionov & Overland, 2005). An
251 eigenvalue optimisation process was carried out to prevent overfitting using the “mgcv” package in
252 R (Wood, 2011). Generalised cross validation (GCV) was used to estimate a smoothing parameter for
253 each term. Smoothing terms with penalised regression splines with an added penalty for each term
254 were used so that the number of knots (the x-value at which the two pieces of the model connect)
255 for each term could be reduced to zero. Through this eigenvalue optimization process, smoothing
256 terms with linear functions in response to pressure variables could effectively be removed from the
257 model if it did not improve the fit (Wood, 2004). As the goal of this research was to identify possible
258 nonlinear threshold values that can inform decision criteria, we rejected GAM models that were
259 more adequately explained using a linear model (Wood & Augustin, 2002). Model selection tests
260 using Akaike's Information Criterion (AIC) were performed on GAMs with different knot
261 combinations to find the knot allocation that resulted in the best fit to the data. The relative
262 importance or explained variance (R^2) of each pressure-state variable in the regression model was
263 calculated and checked using the LMG metric with the relaimpo package in R (Groemping, 2007).
264 From this analysis, we calculated 95% confidence intervals *via* bootstrapping of the residuals in order
265 to allow for autocorrelation (Vinod & López-de-Lacalle, 2009). This procedure generated a range of
266 pressure-state values where a GAMs smoothing function changes trajectory and indicates where
267 threshold might occur. Quantitative estimates of a threshold were defined as the point of inflection
268 where the second derivative changes sign (e.g. Samhouri *et al.*, 2010, Large *et al.*, 2013; 2015).

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270 **4 Results**

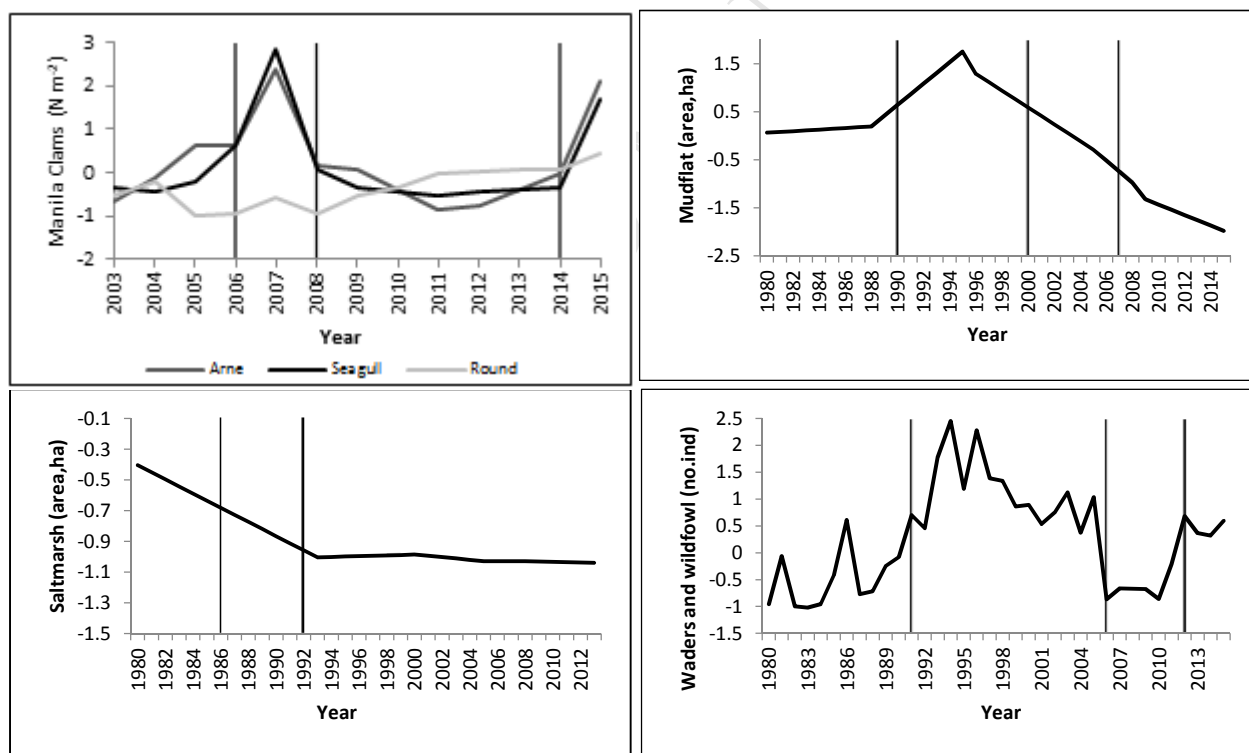
271 **4.1: Time-series trends, thresholds and ecosystem responses**

272 Breakpoint (STARS) analysis of the time series data available for Poole Harbour provided empirical
273 evidence of recent environmental degradation in three of the four NC assets: mudflat area,
274 saltmarsh area and Manila clam stocks (Figure 3). A brief description of the results for each NC asset
275 follows, along with the results from the assembled driver data (Table 3), (see also Appendix 1).

276 Following their introduction to the harbour in the late 1980's Manila clam stocks increased
277 considerably in the Arne and Seagull Island areas between 2003 and 2007, but experienced strong
278 abrupt shifts between 2007 and 2008 with reduced clam densities persisting at below pre 2006
279 mean values until 2014. Results of the STARS algorithm (Table 3) suggest that the magnitude of the
280 changes detected in 2008 were the greatest of any variable tested (~ 3.18 - 3.26 respectively). There
281 were however, strong indications of recovery in recorded stocks at these sites in 2015, with
282 significant breakpoints ranging in magnitude from (~ 2.93 - 3.02 respectively). Stocks of Manila clam
283 recorded at Round Island have conversely increased steadily across the time period, with little signs
284 of abrupt changes. Towards the intertidal areas of the harbour, the mudflats and saltmarshes both
285 showed significant signs of erosion across their respective time periods. The decline in mudflat area

286 over the twenty-five year interval was the more pronounced of the two assets, declining by up to
 287 two standard deviations away from the mean value in 1980. Over this time interval, saltmarsh area
 288 declined for the first decade then remained relatively stable. This was associated with an increase in
 289 mudflat area from 1988 until the mid-1990s, values declining thereafter. Populations of waders and
 290 wildfowl increased after 1980 reaching a peak in the mid-1990s, thereafter declining such that by
 291 2005-2010 values were close to those encountered in the early 1980s. Since then, numbers have
 292 increased somewhat. It should be noted that these trends only give a “snapshot” of the overall
 293 status of the resident bird populations and do not reveal trends for individual species.

294 The highest STARS value for the driver data was obtained for phosphate values in the harbour (1.95)
 295 which have declined considerably since the 1980's. The second strongest shift in the drivers (1.46 &
 296 1.86) was marked by an increase in macroalgal mats across the harbour between 1996 and 2010,
 297 followed by a marginal decline from 2011-2015 (Appendix 1). Changes in nitrate concentrations and
 298 the water temperature both showed increasing trends over the multidecadal period, leading
 299 towards a catchment with a high eutrophic status. River flow trends for the catchment also indicate
 300 a year on year increase in flow rate. A single low STARS value (0.12) was detected for sediment
 301 shoaling in our proxy site of the Wareham channel, with sediment initially increasing the depth of
 302 the channel between 1980 and 1995, before crossing a threshold and thereafter decreasing channel
 303 depth. A plausible shift in fishing pressure in 2004 and 2008 can also be seen, coinciding with a
 304 decline in Manila clam stocks (Figure 3).



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

311 **Table 3:** Summary of the STARS index values of the environmental drivers and natural assets
 312 (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

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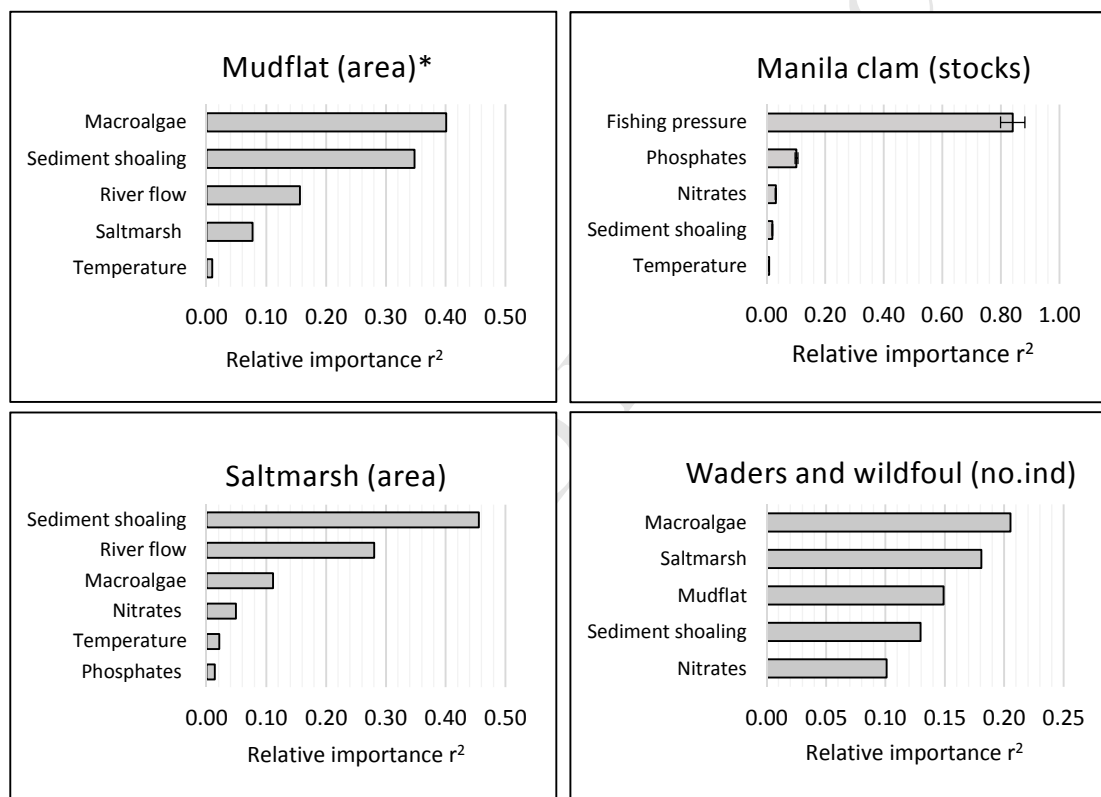
314 4.2 The relative contribution of multiple pressures to natural capital stocks

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

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

Natural capital stocks	Drivers								
	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

320 We found that macroalgal mats (area), sediment shoaling and river flow were the most important
 321 predictors for explaining the variability in area of both mudflats and saltmarsh. This finding is
 322 confirmed based on the r^2 evidence ratio (Figure 4) with the three covariates explaining 91% and
 323 85% of the total variance of each model respectively. Macroalgal mats and saltmarsh were the most
 324 important predictors of wader and wildfowl stocks with a relative importance of 0.21% and 0.18%
 325 and were significant at $p \leq 0.01$. Although mudflat area and sediment shoaling were not significant
 326 for determining wader and wildfowl stocks, they had a high relative importance in explaining the
 327 variability of the final models (0.13-0.15%). Fishing pressure was the only significant ($p \leq 0.01$)
 328 predictor of Manila clam stocks in Arne Bay and Seagull Island with a relative importance of ~84%
 329 respectively. As no environmental variables were significant in influencing the Round Island Manila
 330 clam populations, we removed this time series from the next step of full GAM analysis. Other
 331 variables were less important for all indices, ranging from 0.01 to a relative importance of 0.13 (see
 332 Figure 4).

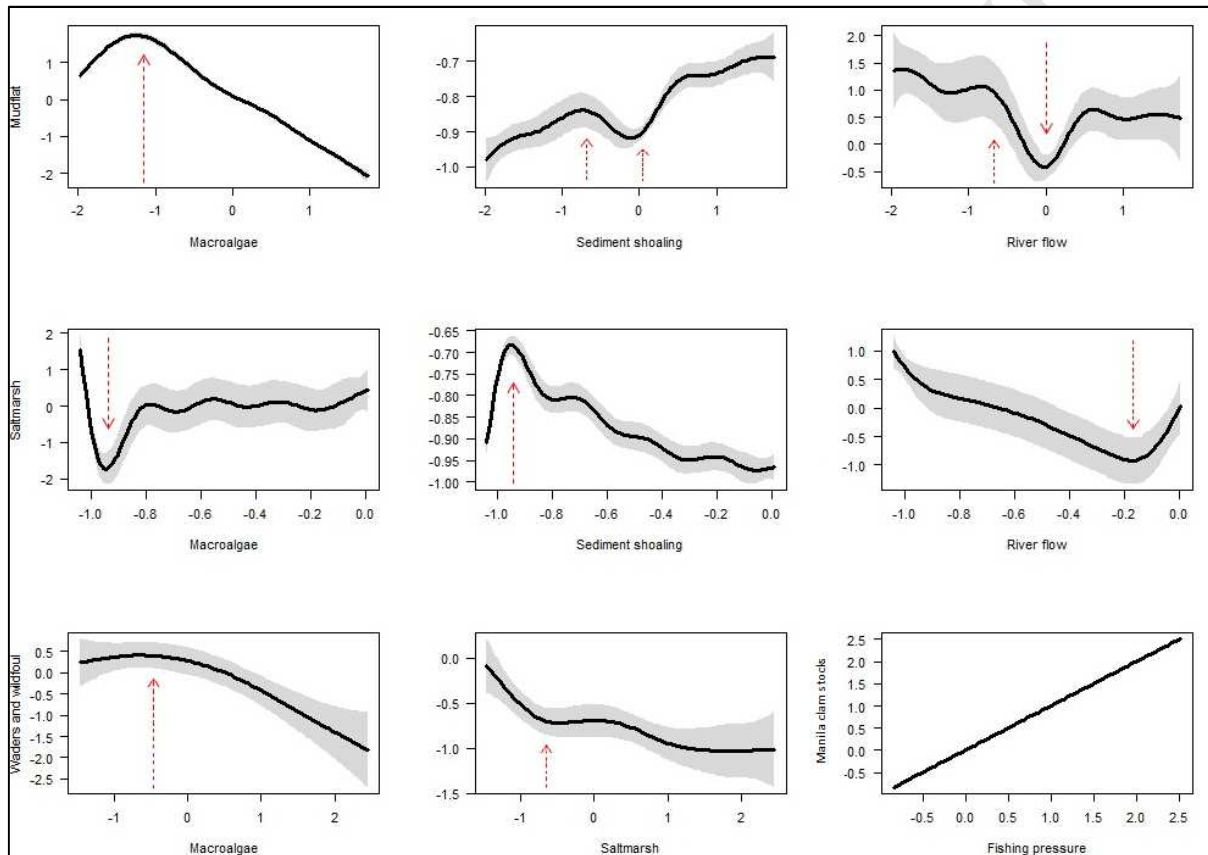


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347 **Figure 4:** Relative importance of different pressures for each of the natural capital stock models. The
 348 proportion of variance explained by the final model(s) was: mudflat area (99.16%), Manila clam
 349 stocks for Arne and Seagull Island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

351 The full GAM analyses allowed identification of relationships between NC status and significant
 352 pressures. Macroalgal mats showed evidence for negative nonlinear relationships (Figure 5) with
 353 three NC proxies namely mudflat area, saltmarsh area and numbers of wading birds. Sediment
 354 shoaling generally increased with mudflat area and a significant positive trend was observed at a
 355 value of ~ -0.9 (SD). Saltmarsh vs sediment shoaling also showed an increasing trend before crossing
 356 a threshold at ~ -0.9 (SD) and then decreasing to below its initial value. Mudflat area also showed a
 357 negative nonlinear relationship with river flow, with a clear threshold observed $\sim 0.2-0$ (SD). The
 358 relationship between saltmarsh area and river flow was best described as a hockey stick, such that

359 saltmarsh area was negatively associated with river flow at values < -0.2 (SD), but then inverted to a
 360 positive trend when river flow was not significantly different from zero. As macroalgal mat area
 361 increased wader and wildfowl numbers decreased, particularly at higher values of the former, with a
 362 threshold response evident at $\sim 0.08-0.05$ (SD) for both pressure-states. Similarly there was a
 363 generally negative relationship between wader and wildfowl numbers and saltmarsh area, with a
 364 threshold again detected at around -0.5 (SD). There was no evidence for nonlinear responses or
 365 thresholds in Manila clam stocks in response to fishing pressure in either Arne Bay or Seagull Island,
 366 suggesting a purely linear relationship between the variables. Overall, of the three proxies for NC
 367 stocks with nonlinear responses, all three showed evidence for thresholds in relation to more than
 368 one pressure.



369 **Figure 5** GAMs of the four normalised natural capital stocks response to pressures ($p \leq 0.01$), where
 370 the horizontal black line represents significant positive or negative trends, representing a significant
 371 deviation from zero (i.e. the mean). The grey polygon represents 95% confidence intervals and red
 372 dotted arrow indicates the best estimate of the location of a threshold (i.e., where the second
 373 derivative is most different from zero within the threshold range). *Mudflat area excludes saltmarsh
 374 and macroalgal mats.

375 5 Discussion

376 In this study, we employed STARS and generalised additive models (GAMs) to identify trends and
 377 thresholds in pressure-time series relationships. Using this analysis we identified distinct points
 378 where four NC assets of the harbour (Manila clam stocks, mudflat area, saltmarsh area and
 379 waders/wildfowl numbers) have been substantially changed in the past, and the potential drivers of
 380 that may have caused such variabilities. Although the STARS technique has been previously been
 381 used to identify thresholds in ecological time series data (Moellmann *et al.*, 2009; Conversi *et al.*,
 382 2010), the present study is the first to employ this method to empirically identify thresholds within a

383 NC framework and one of only a few studies to use such analysis in a transitional estuarine system
384 (e.g, Chevillot *et al.*, 2016).

385 **5.1 Trends, thresholds, and fundamental features from STARS analysis**

386 In applying STARS to available drivers for the Poole Harbour ecosystem, the following picture
387 emerges. The 1980-2015 period was categorised by three steadily increasing endogenous pressures
388 (i.e. emanating from the surrounding catchment and within the system; Elliott, 2011) including
389 nitrate concentrations, macroalgal mats and river flows. With respect to these drivers, nitrate
390 loading, a common driver of algal growth and water quality (McGlathery *et al.*, 2007; Lyons *et al.*,
391 2014), has shifted the estuarine watershed beyond the long-term safe loading limits determined by
392 the Water Framework Directive for the catchment, leading towards an “unfavourable-bad”
393 eutrophic status (Howarth & Marino, 2006; Conley *et al.*, 2009). The current Nitrogen Reduction
394 Strategy (Kite *et al.*, 2012) for the catchment identifies the main source of nitrogen to be diffuse
395 agricultural inputs (73%) with nitrogen entering the harbour forecast to rise further over the next
396 few decades. This is owing to a lag effect of nitrogen leaving the riparian soil zone of surrounding
397 agricultural land and entering the harbour. The consequences of crossing this threshold are likely to
398 be the continued expansion of macroalgal mats fuelled by rising concentrations of nitrate and other
399 inorganic nitrogen compounds in harbour waters. These effects could be compounded by the
400 observed rise in river flow levels since the 1980’s, which may act to convey more nitrogen into the
401 harbour owing to the poor flushing characteristics of the Harbour (Dyrynda, 2005). In contrast,
402 phosphate concentrations entering the harbour have decreased substantially since the 1980’s. This
403 is likely due to substantial land use changes and improvements to phosphorous stripping sewage
404 treatment processes in the catchments of the two main rivers (Frome and Piddle) discharging into
405 Poole Harbour. Evidence of a shift in sediment shoaling in the Wareham channel and fishing
406 pressure on Manila clam populations occurred about the time as the dramatic declines in Manila
407 clam landings (2004-2007). Results from the STARS analysis suggest that the magnitude of the
408 changes in sediment in the Wareham channel were relatively minor, concurring with reports that
409 since 1980 many channels have deepened in most parts of the harbour (May, 2005). In this study we
410 only considered one exogenous pressure (i.e. those emanating from outside the system; Elliott
411 2011), in the form of water temperature, which showed evidence of a shift to warmer waters
412 around 1989. Over recent decades, an increase in temperature and associated changes in
413 precipitation and sea level rise have been observed in Europe as well as other parts of the world
414 (Pachauri *et al.*, 2014) and it expected such trends will continue in the future.

415

416 Among the NC proxies of the harbour, several significant thresholds were identified in the time
417 series data. Relating these changes back to our conceptual framework outlined in Figure 1, STARS
418 results here show saltmarsh area of the harbour to have declined linearly (Type V) between 1980-
419 1988 before stabilising since 1994 at ~400 ha. Longer term trends (1890-2013) in the saltmarsh
420 species *Spartina anglica* by Gardiner (2015) describe the rapid colonisation of the perennial grass
421 over the mudflats between 1890 and 1924 before passing a threshold, and since then there has
422 been much loss of *Spartina* across the harbour. Despite evidence here that this degradation may
423 have now ceased, there is local evidence (e.g. in Holes Bay) that show *Spartina* is still receding in
424 some locations (Gardiner *et al.*, 2007).

425 Trends of waders/wildfowl and mudflat area in the harbour both exhibited abrupt thresholds (Type
426 VI) at the estuarine scale with the most abrupt threshold response taking place in bird numbers
427 between 2007 and 2012. Irrespective of such abrupt shifts, as of 2012-2015, bird numbers of the
428 harbour were higher with those of the 1980’s but lower than the beginning of the 1990’s. One
429 possible reason for a general increase in bird numbers in the early 1990’s as suggested by Raybould

430 (2005) could be the larger invertebrate prey base opened up in the form of increasing area of
431 mudflats as saltmarsh receded. Evidence from STARS analysis also suggest that the decline in bird
432 numbers since the early 1990's could be related to the decline in total mudflat area around the same
433 time (1994), likely as a direct result of mudflats becoming increasingly covered by macroalgal mats.
434 The spread of macroalgae on mudflats has been implicated in the decline of wader/wildfowl
435 populations in many British estuaries (Tubbs & Tubbs, 1980; Anders *et al.*, 2009) including Poole
436 Harbour (Jones & Pinn, 2006), owing to its impact on invertebrates when macroalgal wet weight
437 biomass reaches 2 kg m^{-2} (Raffaelli *et al.*, 1991; 1999). Indeed, recent evidence presented by
438 Thornton (2016) based on field experiments conducted in Poole Harbour, suggests that bird species
439 preferred prey under lower macroalgal mat biomass ($\sim 800 \text{ g m}^{-2}$ wet weight), supporting a lowering
440 of the current legislative threshold of 2 kg m^{-2} to 1 kg m^{-2} . As the condition of mudflats, wading birds
441 and the extent of algal mats are sanctions under current legislation (JNCC 2004) for Poole Harbour, is
442 important to be able to reliably assess the impact from macroalgal mats on these NC assets.

443 In the Manila clam fishery of the harbour, free-living stocks in the harbour were shown to have
444 generally increased considerably since their introduction in the late 80's. However, an abrupt decline
445 in the densities of clams was observed at two sites of the harbour between 2006 and 2008, and
446 since the values have only recently (2015) shown signs of recovery. These changes were also the
447 greatest in magnitude of all the threshold responses observed in this study and fit the criteria
448 outlined in Figure 1 for a tipping point transition (i.e. type VII). However, at this point STARS analysis
449 could only provide qualitative evidence of the impact of drivers and potential feedback mechanisms
450 on the time series data. To quantitatively unravel the relative importance of different drivers as well
451 as potential feedback mechanisms (which are a prerequisite of a tipping point), we considered the
452 results from the GAMs, as explored further below. Moreover, in attempting to reconcile the
453 difference between clam stocks at various locations of the harbour we recognise that the three sites
454 investigated here are only a snapshot of the local populations. However, our results corroborate
455 with other larger studies (e.g. Herbert *et al.*, (2018)) that have looked at several sites across the
456 harbour (including our sites, albeit with different protocols), which suggest a fall in the number of
457 Manila clams at the harbour level between 2008-2009 (26 to 11 ind per m^2), but a relatively stability
458 in clam numbers from 2011-2015 at approximately 25-28 ind per m^2 , based on a resurvey of a
459 selected number of the original sites.

460 **5.2 The impact of multiple stressors on natural capital stocks**

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

471 The area of macroalgal mats was a significant predictor of mudflat area and saltmarsh area. For
472 example when algal mats increased above $\sim -1(\text{SD})$, we noted significant decreasing trends in the
473 area of both NC stocks. This is coherent with existing evidence that the smothering effect of
474 excessive macroalgal growth and the concentrations of nitrates causing them are damaging to the

475 habitats of this internationally important site (Herbert *et al.*, 2010). As such, these results support
476 recently proposed algal harvesting measures (Taylor, 2015) that have been suggested as a means to
477 reduce and recycle nitrogen, as well as to reduce the volume of green macro-algae, thus protecting
478 saltmarsh and mudflat habitats. While little information is available about the impacts that the
479 macroalgal mats have on the businesses of the harbour, there are a number of studies in other
480 estuaries (e.g. Troell *et al.*, 2005; Ferreira *et al.*, 2010) that indicate frequent macroalgal blooms can
481 cause significant biodiversity loss, aesthetic impacts and public health problems, effectively eroding
482 the benefit flows provided by NC stocks (as described in Figure 1, I).

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

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

513
514 Finally, we identified fishing pressure to be the only significant driver to have influenced the abrupt
515 time series trends in Manila clam stocks at two of the long term monitoring sites of the harbour. As
516 expected, the relationship between fishing pressure and clam stocks was entirely linear (II, Figure 1),
517 suggesting there was no definitive threshold where reducing fishing pressure could prevent the
518 collapse of clam stocks. As fishing effort is controlled by the density of clams (the minimum landing
519 size of Manila clams in Poole Harbour is 35 mm), this means that if the density of large sized clams
520 increases so does fishing effort, and when the density decreases so does fishing effort (Humphreys
521 *et al.*, 2007). This is analogous to a predator-prey system, whereby fishing effort increases after the
522 population density increases, before reducing again once the population of "legal" sized clams has

523 reduced. However, Unregulated and Unsustainable (IUU) fishing has been noted as a particular
524 problem for the fishery over the study period and before the introduction of the Permit Byelaw in
525 2015, there were significant illegal landings, the magnitude of which are unknown (Harris 2016).
526 While IUU fishing activities almost certainly would have affected the value of landings being
527 delivered into the harbour, the stock data used here (rather than landings) should highlight the
528 densities of clams available in the harbour indiscriminately of legal or illegal fishing. In response to
529 IUU fishing, enhanced enforcement by the local inshore fisheries and conservation authority (IFCA)
530 has led to a significant reduction in illegal fishing and there are signs from this survey and some
531 more recent stock assessments (SIFCA, 2017) that the new bylaws have had a positive impact on
532 stocks of clams in the harbour, with a recently awarded Marine Stewardship Council (MSC)
533 accreditation for Manila clams being designated as of 2018 (Williams & Davies 2018).

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

562 The increase in the wild stocks of a commercially attractive species such as Manila clam is also likely
563 to have substantial consequences on the wider ecology and economy of the harbour. For instance,
564 there is evidence that the introduction of the clams in the late 1980's has potentially had a positive
565 effect on the over-winter mortality of several wader/wildfowl species such as oystercatchers in the
566 Harbour (Caldow *et al.*, 2007). Thus, it could be suggested that if clam stocks were to continue to
567 increase this would have the potential to provide an indirect benefit to several European shorebird
568 populations *via* a spill-over effect increasing wild populations. There is also evidence that when

569 cultured at high densities Manila clams can provide other indirect benefits to humans such as
570 altering biogeochemical cycles, thereby reducing the effects of nutrient pollution and the
571 deployment of algal mats (Rose *et al.*, 2015), both of which are key issues for managers in Poole
572 Harbour. Furthermore, in terms of direct economic value, a recent report by Williams & Davies
573 (2018) suggests that although the overall landed weight of Manila clams and the value of landings
574 have decreased by 50% and 25% respectively since 2010, the direct Gross Value Added (GVA) added
575 to the local economy by the Manila clam is by a wide margin the highest of any species landed into
576 the harbour (£838,911per annum vs the next highest species: whelks £249,562, based on
577 2016/2017 data). This suggests there is a local economic interest in ensuring that clam stocks remain
578 high in the harbour. Nonetheless, such financial benefits must be balanced against the potential
579 problems of removing commercial quantities of Manila clams from Poole Harbour. For example,
580 there is evidence that the use of pump-scoop dredges can have significant impacts on the benthic
581 community by reducing fine sediment and some prey species available to wintering birds (Clarke *et al.*,
582 2017). Managing fisheries and aquaculture development in a way that does not lead to
583 deleterious ecosystem change is considered as a serious governance challenge not just in Poole
584 Harbour but in many marine protected areas around the world (Edgar *et al.*, 2014). One way to avoid
585 ecological tipping points as advocated by the FAO (The Food and Agriculture Organization of the
586 United Nations), could be through prudent application of the precautionary principle (Carvalho *et al.*,
587 2006).

588 **6 Conclusions**

589 Given the growing evidence that coastal and shallow marine ecosystems are increasingly
590 experiencing multiple disturbances, based on the numbers of studies reporting strong anthropogenic
591 impacts resulting from multiple drivers (Crain *et al.*, 2008; Halpern *et al.*, 2008; Hewitt *et al.*, 2015;
592 Gunderson *et al.*, 2016), both scientists and resource managers must confront the potential
593 challenges of nonlinear shifts in ecosystem structure and function (Crain *et al.*, 2009; Côté *et al.*,
594 2016). Yet, despite the ecological literature being replete with terms related to ecological thresholds,
595 tipping points and other concepts relating to multiple stable states (e.g. regime shifts), there is
596 currently very little empirical evidence that such transitions actually occur in estuaries and other
597 nearshore ecosystems (Nally *et al.*, 2014). Practical application of such concepts in a policy or
598 management context are impeded by several factors such as 1) terminological inconsistency; 2)
599 inadequacy of the temporal and spatial datasets for evaluating abrupt trends; 3) insufficient
600 demonstration of mechanistic links between human or natural factors that cause ecosystem change
601 (Capon *et al.*, 2015). In this study we have considered all three criteria and demonstrate that abrupt
602 nonlinear thresholds in NC assets may occur in transitional protected systems such as harbours. The
603 ecological thresholds that we have identified are driven by interactions among biophysical,
604 ecological, and socioeconomic mechanisms mainly at the catchment scale. As we often lack robust
605 ecological information in most systems to make *a priori* mechanistic predictions of where thresholds
606 will occur (Dodds *et al.*, 2010), we believe that the methods outlined in this paper could be used to
607 help local managers evaluate and articulate strategies to detect thresholds and tipping points in a
608 way that can be incorporated in resource management frameworks (*sensu* Selkoe *et al.*, 2015). This
609 would support global efforts by the United Nations Intergovernmental Oceanographic Commission
610 (IOC) and other international initiatives to improve the long term sustainability of resources within
611 large marine protected areas and their associated watersheds, with a particular focus on ecosystem
612 based approaches to deliver healthy marine ecosystems and sustained ES. Further research could
613 also usefully combine information on temporal trends with spatial data on status of NC and/or

614 multiple interacting drivers to create conceptual and dynamic modelling tools to support
615 management decision-making.

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625 **References**

626 Anders, N.R., Churchyard, T. and Hiddink, J.G., (2009). Predation of the shelduck *Tadorna tadorna* on
627 the mud snail *Hydrobia ulvae*. *Aquatic ecology*, 43(4), pp.1193.

628 Andersen, T., Carstensen, J., Hernandez-Garcia, E. and Duarte, C.M., (2009). Ecological thresholds
629 and regime shifts: approaches to identification. *Trends in Ecology and Evolution*, 24(1), pp.49-57.

630 Ashwin, P., Wieczorek, S., Vitolo, R. and Cox, P., (2012). Tipping points in open systems: bifurcation,
631 noise-induced and rate-dependent examples in the climate system. *Philosophical Transactions of the*
632 *Royal Society*, 370(1962), pp.1166-1184.

633 Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R., (2011). The value of
634 estuarine and coastal ecosystem services. *Ecological monographs*, 81(2), pp.169-193.

635 Bateman, K. S., White, P., and Longshaw, M. (2012). Virus-like particles associated with mortalities of
636 the Manila clam *Ruditapes philippinarum* in England. *Diseases of aquatic organisms*, 99(2), pp.163-
637 167.

638 Beaumont, N.J., Austen, M.C., Mangi, S.C. and Townsend, M., (2008). Economic valuation for the
639 conservation of marine biodiversity. *Marine pollution bulletin*, 56(3), pp.386-396.

640 Bestelmeyer, B. T., Ellison, A. M., Fraser, W. R., Gorman, K. B., Holbrook, S. J., Laney, C. M., Sharma, S.
641 (2011). Analysis of abrupt transitions in ecological systems. *Ecosphere*, 2(12), pp.129.

642 Biggs, R., Schlüter, M., Biggs, D., Bohensky, E.L., BurnSilver, S., Cundill, G., Dakos, V., Daw, T.M.,
643 Evans, L.S., Kotschy, K. and Leitch, A.M., (2012). Toward principles for enhancing the resilience of
644 ecosystem services. *Annual review of environment and resources*, 37, pp.421-448.

645 Bowes, M.J., Smith, J.T., Neal, C., Leach, D.V., Scarlett, P.M., Wickham, H.D., Harman, S.A.,
646 Armstrong, L.K., Davy-Bowker, J., Haft, M. and Davies, C.E., (2011). Changes in water quality of the
647 River Frome (UK) from 1965 to 2009: Is phosphorus mitigation finally working?. *Science of the Total*
648 *Environment*, 409(18), pp.3418-3430.

649 Bowgen, K.M., Stillman, R.A., and Herbert, R.J.H, (2015). Predicting the effect of invertebrate regime
650 shifts on wading birds: Insights from Poole Harbour, UK. *Biological Conservation*, 186, pp.60-68.

- 651 Bryan, G., Kite, D., Money, R., Jonas, P. and Barden, R. (2013). Strategy for Managing Nitrogen in
652 the Poole Harbour catchment to 2035. Environment Agency; Natural England.
- 653 Caldwell, R.W., Stillman, R.A., dit Durell, S.E.L.V., West, A.D., McGroarty, S., Goss-Custard, J.D., Wood,
654 P.J. and Humphreys, J., (2007). Benefits to shorebirds from invasion of a non-native
655 shellfish. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1616), pp.1449-1455.
- 656 Cantarello, E., Newton, A.C., Martin, P.A., Evans, P.M., Gosal, A. and Lucash, M.S., (2017).
657 Quantifying resilience of multiple ecosystem services and biodiversity in a temperate forest
658 landscape. *Ecology and evolution*, 7(22), pp.9661-9675.
- 659 Capon, S.J., Lynch, A.J.J., Bond, N., Chessman, B.C., Davis, J., Davidson, N., Finlayson, M., Gell, P.A.,
660 Hohnberg, D., Humphrey, C. and Kingsford, R.T., (2015). Regime shifts, thresholds and multiple
661 stable states in freshwater ecosystems; a critical appraisal of the evidence. *Science of the Total
662 Environment*, 534, pp.122-130.
- 663 Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell,
664 J.F., Seekell, D.A. and Smith, L., (2011). Early warnings of regime shifts: a whole-ecosystem
665 experiment. *Science*, 332(6033), pp.1079-1082.
- 666 Carvalho, F.P., (2006). Agriculture, pesticides, food security and food safety. *Environmental science &
667 policy*, 9(7-8), pp.685-692.
- 668 Chevillot, X., Pierre, M., Rigaud, A., Drouineau, H., Chaalali, A., Sautour, B., and Lobry, J. (2016).
669 Abrupt shifts in the Gironde fish community: an indicator of ecological changes in an estuarine
670 ecosystem. *Marine Ecology Progress Series*, 549, pp.137-151.
- 671 Clarke, L.J., Esteves, L.S., Stillman, R.A. and Herbert, R.J.H, (2017). Impacts of a novel shellfishing gear
672 on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK. *Aquatic
673 Living Resources*, 31, pp.5.
- 674 Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C. and
675 Likens, G.E., (2009). Controlling eutrophication: nitrogen and phosphorus. *Science*, 323(5917),
676 pp.1014-1015.
- 677 Conversi, A., Umani, S. F., Peluso, T., Molinero, J. C., Santojanni, A., and Edwards, M. (2010). The
678 Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other
679 European basins. *Plos one*, 5(5), e10633.
- 680 Côté, I.M., Darling, E.S. and Brown, C.J., (2016). Interactions among ecosystem stressors and their
681 importance in conservation. *Proceedings of the Royal Society B*, 283(1824), pp.20152592.
- 682 Crain, C.M., Halpern, B.S., Beck, M.W. and Kappel, C.V., (2009). Understanding and managing human
683 threats to the coastal marine environment. *Annals of the New York Academy of Sciences*, 1162(1),
684 pp.39-62.
- 685 Crain, C.M., Kroeker, K. and Halpern, B.S., (2008). Interactive and cumulative effects of multiple
686 human stressors in marine systems. *Ecology letters*, 11(12), pp.1304-1315.
- 687 Crooks, S., and Pye, K. (2000). Sedimentological controls on the erosion and morphology of
688 saltmarshes: implications for flood defence and habitat recreation. *Geological Society*, London,
689 Special Publications, 175(1), pp.207-222.

- 690 deYoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R. I., Scheffer, M., and Werner, F. (2008).
691 Regime shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology and*
692 *Evolution*, 23(7), pp.402–409.
- 693 Dodds, W. K., Clements, W. H., Gido, K., Hilderbrand, R. H., and King, R. S. (2010). Thresholds,
694 breakpoints, and non-linearity in freshwaters as related to management. *Journal of the North*
695 *American Benthological Society*, 29(3), pp.988-997.
- 696 Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson,
697 A.L., Lurgi, M., McClean, D. and O'Connor, N.E., (2016). Navigating the complexity of ecological
698 stability. *Ecology letters*, 19(9), pp.1172-1185.
- 699 Durell, S.E.L.V., Stillman, R.A., Caldow, R.W., McGroarty, S., West, A.D. and Humphreys, J., (2006).
700 Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour,
701 UK. *Biological Conservation*, 131(3), pp.459-473.
- 702 Dyrzynda, P., (2005). 8. Sub-tidal ecology of Poole Harbour—An overview. In *Proceedings in marine*
703 *science* (7), pp.109-130.
- 704 Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S.,
705 Becerro, M.A., Bernard, A.T., Berkhout, J. and Buxton, C.D., (2014). Global conservation outcomes
706 depend on marine protected areas with five key features. *Nature*, 506(7487), p.216.
- 707 Elliott, M. (2011). Marine science and management means tackling exogenic unmanaged pressures
708 and endogenic managed pressures—a numbered guide. *Marine Pollution Bulletin*, 62, 651e655.
- 709 Ferreira, J.G., Andersen, J.H., Borja, A., Bricker, S.B., Camp, J., Cardoso da Silva, M., Garcés, E.,
710 Heiskanen, A.S., Humborg, C., Ignatiades, L. and Lancelot, C., (2010). Marine strategy framework
711 directive—task group 5 report eutrophication. *EUR*, 24338, pp.49.
- 712 Foley, M.M., Martone, R.G., Fox, M.D., Kappel, C.V., Mease, L.A., Erickson, A.L., Halpern, B.S., Selkoe,
713 K.A., Taylor, P. and Scarborough, C., (2015). Using ecological thresholds to inform resource
714 management: current options and future possibilities. *Frontiers in Marine Science*, 2, pp.95.
- 715 Folke, C., Jansson, Å., Rockström, J., Olsson, P., Carpenter, S.R., Chapin III, F.S., Crépin, A.S., Daily, G.,
716 Danell, K., Ebbesson, J. and Elmqvist, T., (2011). Reconnecting to the biosphere. *AMBIO: A Journal of*
717 *the Human Environment*, 40(7), pp.719-738.
- 718 Franklin, D.J., Humphreys, J., Harris, M., Jensen, A.C., Herbert, R.J.H. and Purdie, D.A. (2012). An
719 investigation into the annual cycle of phytoplankton abundance in Poole Harbour and its relationship
720 with Manila clam nutrition. Report for the Marine Management Organisation.
- 721 Gardiner, S. (2015). Physical drivers of saltmarsh change in enclosed microtidal estuaries (Doctoral
722 dissertation, University of Southampton).
- 723 Gardiner, S., S. Hanson, R. J. Nicholls, Z. Zhang, S. Jude, A. Jones, J. Richards, A. Williams, T. Spencer,
724 S. Cope (2007). *The Habitats Directive, Coastal Habitats and Climate Change - Case Studies from the*
725 *South Coast of the UK In Tyndall Centre Working Paper* pp.108.
- 726 Gladwell, M. (2000). *The Tipping Point*. Abacus, London.

- 727 Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G., Triplet, P., Dit Durell, S. L. V., and
728 McGrorty, S. (2004). When enough is not enough: shorebirds and shellfishing. *Proceedings of the*
729 *Royal Society of London B: Biological Sciences*, 271(1536), pp.233-237.
- 730 Goss-Custard, J.D. and Moser, M.E., (1988). Rates of change in the numbers of dunlin, *Calidris alpina*,
731 wintering in British estuaries in relation to the spread of *Spartina anglica*. *Journal of Applied Ecology*,
732 pp.95-109.
- 733 Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M.,
734 Palmer, M.A., Paerl, H.W., Peterson, G.D. and Poff, N.L., (2006). Ecological thresholds: the key to
735 successful environmental management or an important concept with no practical
736 application?. *Ecosystems*, 9(1), pp.1-13.
- 737 Grömping, U. (2006). Relative importance for linear regression in R: the package relaimpo. *Journal of*
738 *statistical software*, 17 (1), pp.1-27.
- 739 Gunderson, A.R., Armstrong, E.J. and Stillman, J.H., (2016). Multiple stressors in a changing world:
740 the need for an improved perspective on physiological responses to the dynamic marine
741 environment. *Annual Review of Marine Science*, 8, pp.357-378.
- 742 Halpern, B. S., McLeod, K. L., Rosenberg, A. A., and Crowder, L. B. (2008). Managing for cumulative
743 impacts in ecosystem-based management through ocean zoning. *Ocean and Coastal Management*,
744 51(3),pp.203–211.
- 745 Harris, M. R. (2016). A study of the naturalisation and dispersal of a non-native bivalve, the Manila
746 clam, *Ruditapes philippinarum* (Adams and Reeve 1850) in estuaries along the South coast of
747 England (Doctoral dissertation, University of Portsmouth).
- 748 Herbert, R.J., Grandfield F., Redford M., Rivers E., Hall A. and Harrison A. (2018) Littoral sediment
749 condition of Poole Harbour SSSI. BU Global Environmental Solutions (BUG) report (BUG2777) to
750 Natural England.pp 34.
- 751 Herbert, R.J., Ross, K., Huebner, R. and Stillman, R.A., (2010). Intertidal invertebrates and biotopes of
752 Poole Harbour SSSI and survey of Brownsea Island Lagoon.
- 753 Herbert, R.J., Willis, J., Jones, E., Ross, K., Hübner, R., Humphreys, J., Jensen, A. and Baugh, J., (2012).
754 Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam,
755 *Ruditapes philippinarum*, in the UK. *Journal of Biogeography*, 39(3), pp.585-599.
- 756 Hewitt, J. E., and Thrush, S. F. (2010). Empirical evidence of an approaching alternate state produced
757 by intrinsic community dynamics, climatic variability and management actions. *Marine Ecology*
758 *Progress Series*, 413, pp267–276.
- 759 Hewitt, J. E., Ellis, J.I. and Thrush, S.F., (2015). Multiple stressors, nonlinear effects and the
760 implications of climate change impacts on marine coastal ecosystems. *Global Change Biology*, 22(8),
761 pp.2665-2675.
- 762 Howarth, R.W. and Marino, R., (2006). Nitrogen as the limiting nutrient for eutrophication in coastal
763 marine ecosystems: evolving views over three decades. *Limnology and Oceanography*, 51(part2),
764 pp.364-376.

- 765 Hübner, R., Herbert, R.J.H, and Astin, K.B., (2010). Cadmium release caused by the die-back of the
766 saltmarsh cord grass *Spartina anglica* in Poole Harbour (UK). *Estuarine, Coastal and Shelf*
767 *Science*, 87(4), pp.553-560.
- 768 Huggett, A.J., (2005). The concept and utility of 'ecological thresholds' in biodiversity
769 conservation. *Biological conservation*, 124(3), pp.301-310.
- 770 Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. and van Nes, E.H., (2013). Living
771 dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology &*
772 *Evolution*, 28(3), pp.149-155.
- 773 Humphreys, J. and May, V., (2005). Introduction: Poole Harbour in context. *Proceedings in Marine*
774 *Science*, 7, pp.1-7.
- 775 Humphreys, J., (2005). Salinity and tides in Poole Harbour: Estuary or lagoon?. *Proceedings in Marine*
776 *Science*, 7, pp.35-47.
- 777 Humphreys, J., Caldow, R.W., McGroarty, S., West, A.D. and Jensen, A.C., (2007). Population dynamics
778 of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters. *Marine*
779 *Biology*, 151(6), pp.2255.
- 780 Humphreys, J., Harris, M.R., Herbert, R.J.H, Farrell, P., Jensen, A. and Cragg, S.M., (2015).
781 Introduction, dispersal and naturalization of the Manila clam *Ruditapes philippinarum* in British
782 estuaries, 1980–2010. *Journal of the Marine Biological Association of the United Kingdom*, 95(6),
783 pp.1163-1172.
- 784 Jasim Uddin, M., Yang, H.S., Choi, K.S., Kim, H.J., Hong, J.S. and Cho, M., (2010). Seasonal changes in
785 *Perkinsus olseni* infection and gametogenesis in Manila clam, *Ruditapes philippinarum*, from
786 Seonjaedo Island in Incheon, off the west coast of Korea. *Journal of the world aquaculture*
787 *society*, 41(s1), pp.93-101.
- 788 Jensen, A. C., Humphreys, J., Caldow, R. W. G., Grisley, C., and Dyrinda, P. E. J. (2004). Naturalization
789 of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery
790 within Poole Harbour, Dorset. *Journal of the Marine Biological Association of the United*
791 *Kingdom*, 84(5), pp.1069-1073.
- 792 JNCC, (2004). Common Standards Monitoring Guidance for Littoral Sediment Habitats.
793 Peterborough: Joint Nature Conservation Committee.
- 794 Johnson, C.J., (2013). Identifying ecological thresholds for regulating human activity: Effective
795 conservation or wishful thinking?. *Biological Conservation*, 168, pp.57-65.
- 796 Jones, M. and Pinn, E., (2006). The impact of a macroalgal mat on benthic biodiversity in Poole
797 Harbour. *Marine pollution bulletin*, 53(1-4), pp.63-71.
- 798 Kirwan, M. L., and Murray, A. B. (2007). A coupled geomorphic and ecological model of tidal marsh
799 evolution. *Proceedings of the National Academy of Sciences*, 104(15), pp.6118-6122.
- 800 Kite, D.J., Bryan, G., Jonas, P. (2012). Strategy for Managing Nitrogen in Poole Harbour to 2035 (final
801 version 6 June 2013); Environment Agency Report.
- 802 Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. (2013). Defining trends and thresholds in responses
803 of ecological indicators to fishing and environmental pressures. *ICES Journal of Marine*
804 *Science*, 70(4), pp.755-767.

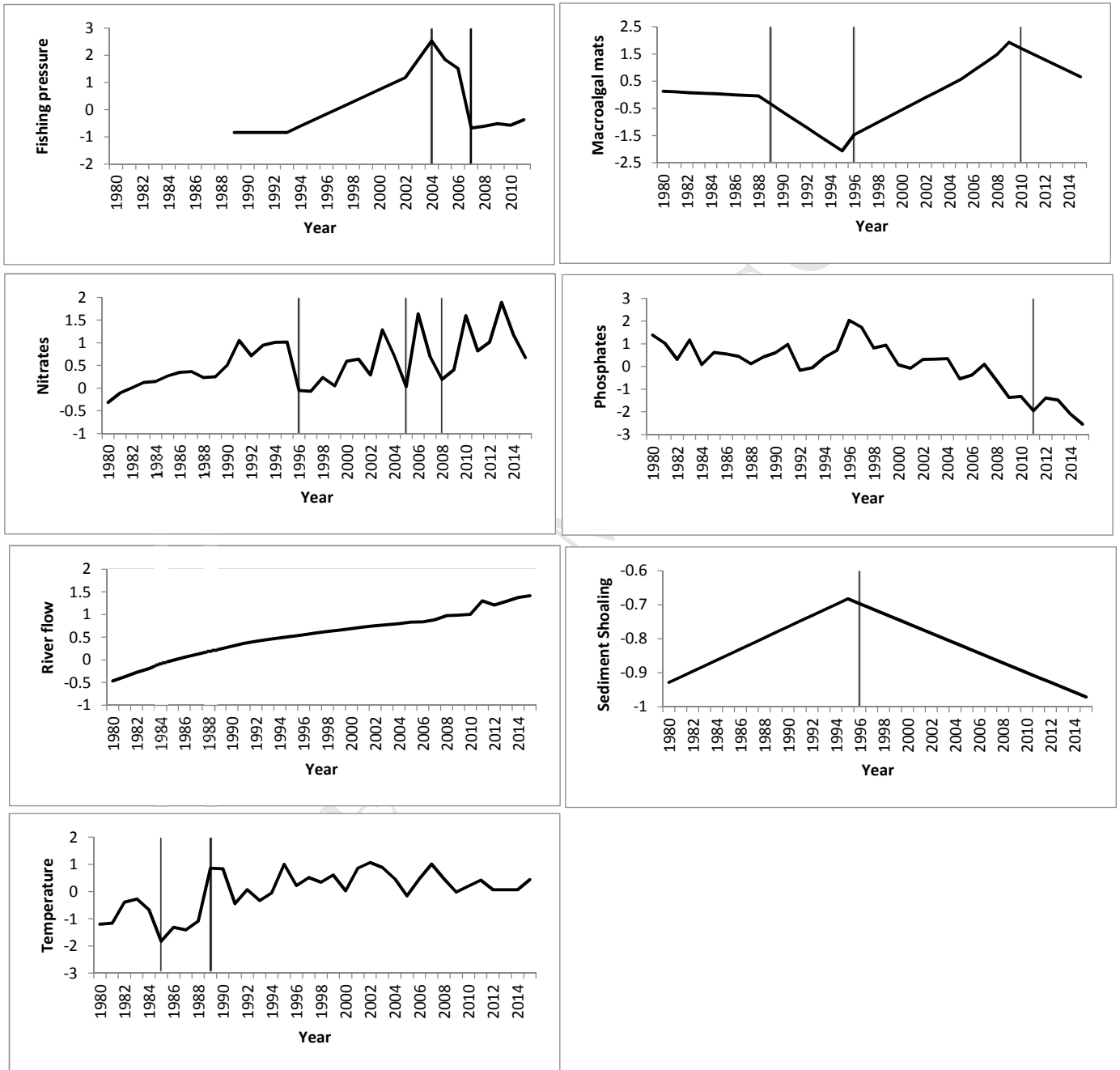
- 805 Large, S.I., Fay, G., Friedland, K.D. and Link, J.S., (2015). Critical points in ecosystem responses to
806 fishing and environmental pressures. *Marine Ecology Progress Series*, 521, pp.1-17.
- 807 Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., and Schellnhuber, H. J.
808 (2008). Tipping elements in the Earth's climate system. *Proceedings of the National Academy of*
809 *Sciences*, 105(6), pp.1786–1793.
- 810 Lenton, T.M., (2013). Environmental tipping points. *Annual Review of Environment and*
811 *Resources*, 38, pp.1-29.
- 812 Levin, P.S. and Möllmann, C., (2015). Marine ecosystem regime shifts: challenges and opportunities
813 for ecosystem-based management. *Philosophical Transactions of the Royal Society of London B:*
814 *Biological Sciences*, 370(1659), pp.20130275.
- 815 Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H.,
816 Queirós, A.M., Rilov, G., Somerfield, P.J. and Crowe, T.P., (2014). Macroalgal blooms alter community
817 structure and primary productivity in marine ecosystems. *Global change biology*, 20(9), pp.2712-
818 2724.
- 819 Mac Nally, R., Albano, C. and Fleishman, E., (2014). A scrutiny of the evidence for pressure-induced
820 state shifts in estuarine and nearshore ecosystems. *Austral Ecology*, 39(8), pp.898-906.
- 821 Mace, G. M., Hails, R. S., Cryle, P., Harlow, J., and Clarke, S. J. (2015). Towards a risk register for
822 natural capital. *Journal of Applied Ecology*, 52(3), pp.641–653.
- 823 Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C. and Kendall, W.L., (2009). Structured decision
824 making as a conceptual framework to identify thresholds for conservation and
825 management. *Ecological Applications*, 19(5), pp.1079-1090.
- 826 May, V., (2005). Geomorphology of Poole Harbour. In *Proceedings in Marine Science* (7), pp.25-34.
827 Elsevier.
- 828 McGlathery, K.J., Sundbäck, K. and Anderson, I.C., (2007). Eutrophication in shallow coastal bays and
829 lagoons: the role of plants in the coastal filter. *Marine Ecology Progress Series*, 348, pp.1-18.
- 830 McGrorty, S., and Goss-Custard, J. D. (1987). A review of the rehabilitation of areas cleared of
831 *Spartina*. *Institute of Terrestrial Ecology (Natural Environment Research Council), Dorset, UK*.
- 832 McLusky D.S, Elliott M., Transitional Waters: a new approach, semantics or just muddying the
833 waters? (2007) *Estuary Coast Shelf Science*, 71, pp.359-363.
- 834 Meyer, K. (2016). A mathematical review of resilience in ecology. *Natural Resource Modeling*, 29(3),
835 pp.339-352.
- 836 Mollmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M. and Axe, P. (2009).
837 Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a
838 discontinuous regime shift in the Central Baltic Sea. *Global Change Biology*, 15, pp.1377–1393
- 839 Nam, K.W., Jeung, H.D., Song, J.H., Park, K.H., Choi, K.S. and Park, K.I., (2018). High parasite burden
840 increases the surfacing and mortality of the Manila clam (*Ruditapes philippinarum*) in intertidal
841 sandy mudflats on the west coast of Korea during hot summer. *Parasites & vectors*, 11(1), p.42.
- 842 Natural Capital Committee. (2014). The state of natural capital: restoring our natural assets. Second
843 Report to the Economic Affairs Committee. Natural Capital Committee, HM Government UK.

- 844 Newton, A. C. (2016). Biodiversity Risks of Adopting Resilience as a Policy Goal. *Conservation Letters*,
845 9(5), pp.369–376.
- 846 Office of National Statistics (2010) Revised Annual Mid-year Population Estimates: 2001 to
847 2010: www.ons.gov.uk. [Accessed 22/10/2017]
- 848 Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L.,
849 Dahe, Q., Dasgupta, P. and Dubash, N.K., (2014). Climate change 2014: synthesis report. Contribution
850 of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on
851 Climate Change, *IPCC*, pp.151.
- 852 Petraitis, P. (2013). Multiple stable states in natural ecosystems. *OUP*, Oxford.
- 853 Piet, G. J., Quirijns, F. J., Robinson, L., and Greenstreet, S. P. R. (2006). Potential pressure indicators
854 for fishing, and their data requirements. *ICES Journal of Marine Science*, 64(1), pp.110-121.
- 855 Pretto, T., Zambon, M., Civettini, M., Caburlotto, G., Boffo, L., Rossetti, E. and Arcangeli, G., (2014).
856 Massive mortality in Manila clams (*Ruditapes philippinarum*) farmed in the Lagoon of Venice, caused
857 by *Perkinsus olseni*. *Bulletin of the European Association of Fish Pathologists*, 34(2), pp.43-53.
- 858 Quinlan, A.E., Berbés-Blázquez, M., Haider, L.J. and Peterson, G.D., (2016). Measuring and assessing
859 resilience: broadening understanding through multiple disciplinary perspectives. *Journal of Applied*
860 *Ecology*, 53(3), pp.677-687.
- 861 R Core Team. R: A language and environment for statistical computing. Version [3.3.5"]. Vienna: R
862 Foundation for Statistical Computing. Available from: URL <https://www.R-project.org/>.
- 863 Raffaelli, D., (1999). Nutrient enrichment and trophic organisation in an estuarine food web. *Acta*
864 *Oecologica*, 20(4), pp.449-461.
- 865 Raffaelli, D., Limia, J., Hull, S. and Pont, S., (1991). Interactions between the amphipod *Corophium*
866 *volutator* and macroalgal mats on estuarine mudflats. *Journal of the Marine Biological Association of*
867 *the United Kingdom*, 71(4), pp.899-908.
- 868 Raybould, A. (2005). History and ecology of *Spartina anglica* in Poole Harbour; In Humphreys, J. and
869 May, V. eds. *The Ecology of Poole Harbour*. Oxford: Elsevier, pp.71-90.
- 870 Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer,
871 M., Folke, C., Schellnhuber, H.J. and Nykvist, B., (2009). A safe operating space for
872 humanity. *Nature*, 461(7263), pp.472-475.
- 873 Rodionov, S., and Overland, J. E. (2005). Application of a sequential regime shift detection method to
874 the Bering Sea ecosystem. *ICES Journal of Marine Science*, 62(3), pp. 328-332.
- 875 Rodionov, S.N., (2004). A sequential algorithm for testing climate regime shifts. *Geophysical*
876 *Research Letters*, 31(9).
- 877 Rose, J.M., Bricker, S.B. and Ferreira, J.G., (2015). Comparative analysis of modeled nitrogen removal
878 by shellfish farms. *Marine pollution bulletin*, 91(1), pp.185-190.
- 879 Samhuri, J.F., Andrews, K.S., Fay, G., Harvey, C.J., Hazen, E.L., Hennessey, S.M., Holsman, K.,
880 Hunsicker, M.E., Large, S.I., Marshall, K.N. and Stier, A.C., (2017). Defining ecosystem thresholds for
881 human activities and environmental pressures in the California Current. *Ecosphere*, 8(6).

- 882 Samhuri, J.F., Levin, P.S. and Ainsworth, C.H., (2010). Identifying thresholds for ecosystem-based
883 management. *PLoS One*, 5(1), pp.e8907.
- 884 Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Van Nes,
885 E.H., Rietkerk, M. and Sugihara, G., (2009). Early-warning signals for critical
886 transitions. *Nature*, 461(7260), pp.53-59.
- 887 Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B., (2001). Catastrophic shifts in
888 ecosystems. *Nature*, 413(6856), pp.591-596.
- 889 Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., Van de Koppel, J.,
890 Van de Leemput, I.A., Levin, S.A., Van Nes, E.H. and Pascual, M., (2012). Anticipating critical
891 transitions. *Science*, 338(6105), pp.344-348.
- 892 Selkoe, K.A., Blenckner, T., Caldwell, M.R., Crowder, L.B., Erickson, A.L., Essington, T.E., Estes, J.A.,
893 Fujita, R.M., Halpern, B.S., Hunsicker, M.E. and Kappel, C.V., (2015). Principles for managing marine
894 ecosystems prone to tipping points. *Ecosystem Health and Sustainability*, 1(5), pp.1-18.
- 895 Selkoe, K.A., Blenckner, T., Caldwell, M.R., Crowder, L.B., Erickson, A.L., Essington, T.E., Estes, J.A.,
896 Fujita, R.M., Halpern, B.S., Hunsicker, M.E. and Kappel, C.V., (2015). Principles for managing marine
897 ecosystems prone to tipping points. *Ecosystem Health and Sustainability*, 1(5), pp.1-18.
- 898 SIFCA, (2017). Poole Harbour Bivalve Stock Survey 2017. Southern Inshore Fisheries and
899 Conservation Authority. Available: [http://www.southern-ifca.gov.uk/research-and-evidence-](http://www.southern-ifca.gov.uk/research-and-evidence-reports)
900 [reports](http://www.southern-ifca.gov.uk/research-and-evidence-reports)[Accessed 29/08/2018]
- 901 Simpson., M (2004). Poole Harbour Approach Channel Deepening and Beneficial Use of Dredged
902 Material EIA. Non-Technical Summary. Overview of the existing environment. Fishing activity.
903 Published report, Royal Haskoning, Exeter, Devon. pp.275-292.
904 https://www.phc.co.uk/downloads/channeldeepening/es10_fishing.pdf [Accessed 02/04/2018]
- 905 Taylor, D., (2015). Review of potential to remove harmful algae and reduce nitrogen load in Poole
906 Harbour. Commissioned by Dorset Local Nature Partnership. Available:
907 [www.wessexwater.co.uk/About-us/Environment/Catchment-partnerships/Poole-harbour/Algal-](http://www.wessexwater.co.uk/About-us/Environment/Catchment-partnerships/Poole-harbour/Algal-Harvesting-workshop)
908 [Harvesting-workshop](http://www.wessexwater.co.uk/About-us/Environment/Catchment-partnerships/Poole-harbour/Algal-Harvesting-workshop) [Accessed 02/04/2018]
- 909 Thornton, A. (2016). The impact of green macroalgal mats on benthic invertebrates and
910 overwintering wading birds (Doctoral dissertation, Bournemouth University).
- 911 Toms, J. and Villard, M.A., (2015). Threshold detection: matching statistical methodology to
912 ecological questions and conservation planning objectives. *Avian Conservation and Ecology*, 10(1).
- 913 Troell, M., Pihl, L., Rönnbäck, P., Wennhage, H., Söderqvist, T., and Kautsky, N. (2005). Regime shifts
914 and ecosystem services in Swedish coastal soft bottom habitats: when resilience is
915 undesirable. *Ecology and Society*, 10(1).
- 916 Tubbs, C. R. and Tubbs, J. M., (1980). Wader and Shelduck feeding distribution in Langstone Harbour,
917 Hampshire. *Bird Study*, 27 (4), 239-248
- 918 Tubbs, C.R., Tubbs, J.M. and Kirby, J.S., (1992). Dunlin *Calidris alpina alpina* in the Solent, southern
919 England. *Biological Conservation*, 60(1), pp.15-24.
- 920 Underhill-Day, J. C. (2006). A condition assessment of Poole Harbour European Marine Site.
921 Unpublished report, Footprint Ecology/Natural England. Dorset. England.

- 922 van Nes, E.H., Arani, B.M., Staal, A., van der Bolt, B., Flores, B.M., Bathiany, S. and Scheffer, M.,
923 (2016). What Do You Mean, 'Tipping Point'? *Trends in Ecology & Evolution*, 31(12), pp.902-904.
- 924 Vinod, H.D. and López-de-Lacalle, J., (2009). Maximum entropy bootstrap for time series: the
925 meboot R package. *Journal of Statistical Software*, 29(5), pp.1-19.
- 926 Wesenbeeck, B.K., van de Koppel, J., Herman, P.M., Bertness, M.D., van der Wal, D., Bakker, J.P. and
927 Bouma, T.J., (2008). Potential for sudden shifts in transient systems: distinguishing between local
928 and landscape-scale processes. *Ecosystems*, 11(7), pp.1133-1141.
- 929 Williams, C and Davies, W., (2018). A Tale of Three Fisheries The value of the small-scale commercial
930 fishing fleet , aquaculture and the recreational charter boat fleet , to the local economy of Poole.
931 NEF Consulting Limited. A Report to Southern IFCA. Available: [https://www.nefconsulting.com/a-](https://www.nefconsulting.com/a-tale-of-three-fisheries)
932 [tale-of-three-fisheries](https://www.nefconsulting.com/a-tale-of-three-fisheries) [Accessed 29/08/2018]
- 933 Wood, S.N. and Augustin, N.H., (2002). GAMs with integrated model selection using penalized
934 regression splines and applications to environmental modelling. *Ecological Modelling*, 157(2),
935 pp.157-177.
- 936 Wood, S.N., (2004). mgcv: GAMs with GCV smoothness estimation and GAMMs by REML/PQL. R
937 package version 1.1-8. *R Foundation for Statistical Computing*, Vienna, Austria.
- 938 Wood, S.N., (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of
939 semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical*
940 *Methodology)*, 73(1), pp.3-36.
- 941

Appendix 1: Normalised time series of environmental drivers, in Poole Harbour for the period 1980-2015. From top to bottom: fishing pressure (no. boats), macroalgal mats (area (ha)), nitrates ($\text{mg NO}_3 \text{ N l}^{-1}$), phosphates ($\mu\text{g l}^{-1}$), riparian water flows ($\text{m}^3 \text{ s}^{-1}$), sediment shoaling (m) and water temperature ($^\circ\text{C}$). Vertical black lines represent statistically significant ($p \leq 0.01$) breakpoints for individual trends from sequential Student's t-test.



Highlights: 3-5 bullet points, each max. 85 characters

- Addressing tipping points leads to improved management outcomes in MPAs.
- We identified nonlinear thresholds in several of the natural capital assets of Poole harbour.
- Abrupt nonlinear trends were the most common threshold identified from our time series analysis.
- Tipping points were detected most strongly in the Manila clam fisheries of the harbour
- Restoration targets need to consider multiple drivers not just recognisable drivers