Manuscript Details

Manuscript number	ECSS_2017_747_R1
Title	Detecting Ecological Thresholds and Tipping Points in the Natural Capital Assets of a Protected Coastal Ecosystem
Article type	Research Paper

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 generalized 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/benefit flows of the harbour; mudflat area, Manila clam landings 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, which declined by -95% over a period of 4 years. Generalized additive models identified the contribution of macroalgal mats, sediment shoaling and river flows to historic changes in mudflat area, saltmarsh area and wader/wildfowl numbers. The relatively recent cessation in the Manila clam fishery of the harbour was partly attributable to increased fishing pressure although other factors such as disease are also likely to have contributed. 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.

Keywords	Thresholds;Tipping points;Marine Protected Areas;Multiple stressors;Natural capital;Poole Harbour.
Taxonomy	Biological Sciences Mathematical Methods, Complex Systems

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Submission Files Included in this PDF

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To the Editor   Date 21/05/2018

Reference: ECSS_2017_747

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

Journal: Estuarine, Coastal and Shelf Science

Dear Editor

We would like to thank you for the opportunity to resubmit a revised copy of this manuscript. We would also like to take this opportunity to express our thanks to the three reviewers for their feedback and helpful comments for correction or modification. We believe they have resulted in an improved revised manuscript, which you will find uploaded alongside this document. We tried to be responsive to your concerns. As such, we have endeavoured to extend the paper's contributions by enhancing each section, including making them more succinct while removing or re-writing sections that did not add to the overall message of the paper.

In summary we have made substantial changes to the analysis and structure of the manuscript including:

- We have shortened the introduction by over 15%.
- Attempted to clarify the difference between thresholds and tipping points with examples.
- Sharpened the language throughout the whole document.
- Added more detail to our methods section.
- Re-analysed all of our results, based on a smaller number of natural capital proxies and drivers.
- Added the potential contribution of multiple stressors to each NC variable, which gives justification for further assessment of such relationships. We also note that investigating interactions between variables could be the next logical research step.
- Re-written the entire results, discussion and conclusion sections.
- Moved any discursive text to the discussion.
- Discussed in detail the potential feedback mechanisms that may be responsible for any declines in natural capital assets and how they relate to our conceptual framework in our introduction.
- We also discuss potential threshold limits found and their relevance for management.
- Added additional information as appendices.

We have also attempted to answer all of the other comments and concerns raised by the reviewers on a point by point basis, which are appended alongside our responses to this letter. We very much hope the revised manuscript is accepted for publication in the Journal of Estuarine, Coastal and Shelf Science.

Sincerely,

Dr Stephen Watson on behalf of the authors.

Author response to the general comments

We would like to thank the three reviewers for taking the time to review our manuscript in such detail and as a consequence the paper has been significantly improved as a result. We appreciate you taking the time to offer us your comments and insights related to the paper. We found your feedback very constructive. We tried to be responsive to your concerns. As such, we have endeavoured to extend the paper's contributions by enhancing each section, including making them more succinct while removing or we-writing sections that did not add to the overall message of the paper.

- As such we have shortened the introduction by over 15%.
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- Added additional information as appendices.

We have also attempted to answer all of the other comments and concerns raised by the reviewers on a point by point basis (see below) and have grouped comments where similar. However, due to extensive nature of the revised edition many of the comments were no longer applicable to the revised version. We have tried to highlight this were necessary.

Comments from the editors and reviewers:

-Editor: The Guest Editor and Reviewers consider this offering to be of interest to the Special Issue so I would encourage you to respond to all these comments and resubmit a revised version.

-Guest Editor: In light of the reviews, the authors might want to consider a less ambitions paper that focusses down on a smaller number of more secure asset/proxy/driver relationships

General comments

Sharpening the language around the discussion and conclusions so as to avoid unfounded speculation.

The overall conclusions seem timid, conventional and unexceptional; which rather reduces the value of the paper. Frankly, a method of analysis should offer benefit in direct proportion to its complexity; it is no benefit to produce a complicated analysis only for it to support simplistic interventions that could have been identified by a much more simple treatment: too many algal mats - lower eutrophication, too few manila clam - stop killing them. Just as an example – imagine if the paper had concluded that any fishing pressure above 50% of MSY of clams would increase the likelihood of major saltmarsh collapse within 5 years by 200%. That would be a useful thing to know, not obvious – that would justify a long time to try to understand the statistical methods which do not falsify the conclusion, or falsify an alternative.

Reviewer 2

Summary: overall I think this paper could be a valuable contribution, but it needs significant further work in simplifying and sharpening the language, checking the stats work, and especially sharpening the language around the discussion and conclusions so as to avoid unfounded speculation.

Overall the writing should be improved and sharpened up to avoid the turgid strings of jargon often associated with the soft science of ecosystem benefit analysis. The overall conclusions seem timid, conventional and unexceptional; which rather reduces the value of the paper. Frankly, a method of analysis should offer benefit in direct proportion to its complexity; it is no benefit to produce a complicated analysis only for it to support simplistic interventions that could have been identified by a much more simple treatment: too many algal mats - lower eutrophication, too few manila clam - stop killing them. Just as an example – imagine if the paper had concluded that any fishing pressure above 50% of MSY of clams would increase the likelihood of major saltmarsh collapse within 5 years by 200%. That would be a useful thing to know, not obvious – that would justify a long time to try to understand the statistical methods which do not falsify the conclusion, or falsify an alternative.

Reviewer 3

However, I have various concerns regarding the manuscript. First, it is in places rather confusing and poorly explained – for example a distinction is made between ecological thresholds and tipping points (driven by positive feedback process/mechanism) – and the paper claims to have identified examples of both but nowhere is evidence presented to explain why some thresholds were classed as being one type or the other (types III or IV).

Second, the authors say that they excluded relationships with no underlying causal mechanism – yet no clear causal mechanisms are presented for many of those relationships which are considered in detail eg manila clam landings (tonnes) vs the area of subtidal sediment (for which the proxy analysed is the mean depth (in m) of the Wareham channel). Understanding the causal mechanisms is critical to any attempt to implement management measures (and to justify those).

Third, although the manuscript correctly highlights the need for policy makers and site managers to be aware of ecological thresholds and tipping points, no really clear take home messages in respect of management implications emerge from this work – for example in the case of restoring the benefit attained from increasing manila clam landings what needs to be done/can be done in regard to drivers other than fishing pressure eg river flows, subtidal sediment depth and water temperature? This lack of clarity is not helped by the lack of any clear causal mechanisms being spelled out in regard to these and many of the other relationships.

Fourth, the manuscript highlights that often it is likely that interacting drivers are likely to be a common feature, yet this study only considers relationships between ecosystem benefits /assets and drivers in a univariate way. Many of the relationships that emerge may then be confounded by the influence of other drivers that might be better examined in a more complex statistical way. Finally, the manuscript needs a proof read as contains various errors here and there. There are also parts of the text in the "results" section that are discursive and ought to be in the Discussion section.

Abstract/ Introduction

-Reviewer 1

Intro, lines 51 and 54, the general term harbour is not very useful, as a harbour does not describe a type of ecosystem, unless referring to a particular Harbour, which may be e.g., a semi enclosed tidal lagoon, especially as in the intro other terms such as tipping point are defined in detail.

> *We agree with this comment and have clarified that Harbours may be classified as either estuaries or lagoons. We also mentioned that Poole harbour is an estuary with lagoon features lines in out methods section.*

-Reviewer 2

L 10 I assume that 'points' is missing.

> *Yes, we have amended this.*

This highlights the overuse of the phrase tipping points in the abstract. It makes the writing dull. Perhaps stop pre-defining it on first use… "…ecological thresholds and…" or "…potentially irreversible ecosystem thresholds and…", "nonlinear thresholds and…", each time followed by "tipping points" as if the phrase can't really stand on its own – if it can't:

best not use it in the title. In the first few sentences of the intro it gets defined within quotes. Then we have a full definition again:

This is illustrative of the writing in general which needs to be improved, made less wordy, and made far more direct. The first line begins with a gerund (an 'ing' word) – (L 31) this is risky, as it can lead to complicated sentences, it could be simply removed in this case. Several other sentences which follow start with 'while' which again serves to make them complex and boring. Most of the time these words are unnecessary.

The poor writing distracts from the science content of the paper and so I will avoid any further criticism, save to say, the entire paper needs to be edited severely. Lines 130 to 143 are a particular case in point – turgid jargon trying to pin down generalisms, just a waste of space.

We have severely edited the paper, including the introduction section

Reviewer 3

Lines 103-108. Much is made of the distinction between ecological thresholds and a subcategory of these defined to be "tipping points" driven by a positive feedback mechanism. An example of the latter would be very helpful at this point in the text to clarify the distinction.

We have added an example to clarify this

Line 119 – is repetitious and can be deleted.

Deleted

Lines 120-125. The authors may find it of interest to know that the existence and management implications of non-linear thresholds in the relationships between shorebird mortality and shellfish stock resources in coastal ecosystems has been known about for the last couple of decades and used to inform shellfish stock management. Also, in the more marine environment many non-linear relationships between seabird productivity and forage fish stock biomass have been established recently and have the potential to influence fish stock management.

This is indeed insightful, we have integrated this comment and added a reference.

Figure 1. The legend refers to "the black lines". It is not clear which black lines are being referred to – they are all black. There is confusion in the plot axes labels between "natural asset status" and "natural capital status". Should these not be the same?

Changed to "dashed lines" and the figure has been changed to for all graphs to "natural capital status".

Methods

Data and meanings

L 149 etc., linear and non-linear have specific mathematical meanings which are different from the ordinary language meaning (especially in time series data). Perhaps use different words if your meaning is the conversational meaning. Steady change, abrupt change, smooth change, stright line change, etc..

L238 The mathematical meanings of linear and nonlinear have been used here. This needs to be clarified. Early references to linearity should be defined more carefully, where in mathematical language it means smoothness.

L258 to L263 I do not understand what was done here and why this was done and the impact of the doing of it. This may be down to my lack of knowledge or experience. Again by L265 I think the meaning of linearity in the mathematical sense has been confused with the concept of smoothness of transition. Can this be explained in simple terms - why was it done?

> *Tipping points have been actively studied in various applications as well as from a mathematical viewpoint. A key assumption in many arguments for the existence of variance and auto-correlation growth before a tipping point is to use a linearization argument, i.e., the leading-order term governing the deterministic (or drift) part of stochastic differential equation is linear. This assumption guarantees a local approximation in the normally hyperbolic regime before, but sufficiently bounded away from, a bifurcation which is often described in* nonlinear terms. We therefore use these terms to be consistent with the rest of the tipping point literature e.g. (Scheffer et al., 2001). *We have clarified L258-L263.*

L 196. Linear interpolation of missing data – this worries me. Why were the data missing? Does this linear interpolation imply a smoothness which is subsequently used in the analysis (as a contrast to the changes) etc. more about this later, it may be important.

Line 196-7. Given that this paper is all about identifying non-linearities it seems questionable to interpolate linearly between data points to fill in missing data. It is not clear for each dataset what the intervals of recording were and hence how much interpolation has gone on. I imagine that estimates of saltmarsh area from OS maps and aerial photography have been derived only infrequently so it would help to know the sampling intervals for each asset/benefit/driver. This should be listed in Table 1

L255 Are we still using time series that have missing values interpolated? Again these might bias the result, especially after further smoothing.

As the reviewer suggests, for numerous purposes, different time series are recorded and analysed to understand phenomena or/and behaviours of variables, to try to understand historic values, etc. Unfortunately, and for several reasons, there are gaps in data, irregular time steps of recordings, or removed data points that often need to be filled for data analysis, calibration of models, or for data with a regular time step. Generally in practice, incomplete series are the rule and interpolation is common in tipping point-time series analysis. In the revision we have shortened the duration of several of the time series analyses to partly counter this issue, meaning most data sets were largely complete. We also note that this approach may increase the possibility of detecting significant thresholds and tipping points but our main interest was in the preventative identification of potential thresholds rather than statistical significance.

ES

Line 160 the list of ecosystem services seems rather odd. Is freshwater an ecosystem service in Poole Harbour – it is saline? Also how about the provision of a sheltered harbour with deep water access to commercial freight vessels and ferries and shipbuilding firms (and all the associated local jobs that flow from those)– that must be amongst the most major ecosystem benefits arising from the harbour.

The ES of freshwater has been changed to water quality improvements

Line 192. This list of differing types of ecosystem services does not make for great reading – can the definitions of each be spelled out.

This line has been removed and reworked

Line 200. Why is subtidal sediment considered to be of regulatory importance?

We have removed subtidal sediment from the analysis

Lines 197-199. Here wader numbers are referred to as an "asset" yet elsewhere they are treated as a "benefit". I would tend to think of birds as an asset and the benefit that flows (to humans) from that asset is opportunities for birdwatching and /or the money that flows into the local economy from that birdwatching – eg all the Poole Harbour cruise boats etc.

We agree and have re-classified them as assets or stocks

Also, I am not sure that I would consider algal mats to be natural capital assets

We have moved algal mats to be considered as a driver (e.g on saltmarsh and mudflats)

L384 Table 4. I do not think bacteria is a driver on a par with fishing pressure or nutrient loading, bacteria are always present - much more likely to be driven variable in my opinion (thus this needs justification). Riparian river flows should be available. Why isn't dredging included as a driver - it must have a major impact and has changed overt the years?

Bacteria have been removed from the analysis. Sediment shoaling is included as a proxy relating to dredging.

Table 2 Is the number of licensed fishing boats a reliable proxy for fishing effort on manila clams? Many boats will not exploit this fishery in particular, or fish within the harbour. Unless the is data on dredging vessels in particular, which is not clear here.

L211 Number of licensed boats is a poor proxy for fishing pressure. The boats probably fished other stuff at other times, number of licenses could be determined by human factors, management, market etc., any number of drivers that themselves are chaotic. People hold licenses without using them. Landings are another thing, which are also related to unit effort, market, price, season etc. The whole complexity of fishing and fishing pressures underlies this simple numeric.

Regarding the above two comments, we agree that there are better indicators of fishing pressure but also note that fleet capacity can be used as a viable driver proxy in the absence of reliable fishing effort data (Piet et al., 2006). Such data was generally unavailable for Poole harbour as there might be for the bigger offshore fisheries. We have clarified that Clams are removed from the seabed using a pump scoop dredge which is towed along the seabed by small (under 10m) fishing vessels. Due to the targeted and unique way this species is fished - 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 still likely a good pressure indicator that describes the impact induced by fishing activities on the system. We have added these points to our methodology and discussion.

Line 187-188. I am not sure that the collapse in the manila clam fishery can be considered an "environmental" trend – rather the collapse in the population of manila clams itself might be the "environmental" trend. Also I am not sure that it follows from describing these trends that "ecological thresholds" per se "have been transgressed".

We have changed this to specify that manila clam populations have changed rather that the fishery has collapsed.

Table 1. Why is the mean depth of the Wareham channel (m) chosen as a proxy for the area of subtidal sediment in the harbour? The channel bottom may be made deeper by dredging but that does not change the area of subtidal sediment – just its depth. PHC conduct systematic harbour-wide bathymetric surveys. Presumably that will provide data on areas below certain shore levels?

We have removed subtidal sediment as a proxy

Table 1. references to the manila clam "benefit" should make clear that it is the landings that are being considered the benefit. It is not clear to me why nitrate and phosphate levels might be drivers of manila clam landings. Indeed it would be good if the plausible mechanisms linking all drivers to all assets/benefits were explained somewhere.

We have clarified throughout the manuscript that we are considering Manila clam landings and re-analysed the results and broadened our discussion section to discuss possible feedback mechanism's.

Table 1. The list of possible drivers for birds seems rather short – an obvious one would be the overall benthic prey resource. This was studied harbour wide in c 2010, and in 2002, and in the 1970s with multiple studies in the 1980s and 1990s together covering many areas.

> *Although interesting and possibly useful as a bird specific driver, we believe the available data for Poole Harbour was to patchy (temporally and methodologically), to be included with the analysis. We highlight this could be incorporated in the future.*

L212 Annual average SST. You're talking about tipping points and thresholds – why use an annual average? Why not a summertime range, summertime high, winter low, number of days over x, and temperature conditions that might push thresholds? Taking an annual mean seems to me to invite a non-threshold response.

Also, is mean annual temp a useful measure of a driver? When max or min temperatures are critical for many organisms, especially for a non-native that may not yet be fully adapted? Similarly river flows if they (and associated rainfall/runoff) if salinity levels are critical for some. (point for discussion)

Table 2. Given the lagoonal nature of the harbour is water temperature data from Bournemouth a good proxy? Why is there no mention of sea-level rise as a key driver of change to eg area of intertidal mudflat and saltmarsh and subtidal sediment area?

Lines 319-320 – states no clear trends or thresholds were identified in the water temperature time series yet Fig 3 shows 2 statistically significant breakpoints.

in the plot against temperature there are no clam landing data points below 350? Why is there a nice linear relationship between clam landings and temperature (1989-2015) when temperature has scarcely varied over time?

It is stated that the relationship between clam landings and water temperature exhibited a smooth linear response but in table 3 this is clearly identified as a relationship with a significant threshold response with a smoothing term and 6 knots in the GAM.

Considering the six points we have changed the temperature data to instead use monthly *extended surface temperatures averaged across the Poole Harbour time series (°C) sensu (large et al., 2015).* Temperature vs clams is no longer significant.

STARS

L218 Is this after the gaps were filled in by linear interpolation? This gap filling is bound to impact the results of the STARS method. Clearly the process adds weight to the existing mean value of the timeseries. This is a potential problem with the statistical methods – STARS requires the time series to be of constant time interval. Perhaps it is possible to overcome gaps by choosing a different step length.

We have now tested three different cut-off lengths (l = 5, l = 10 and l = 15) to test the sensitivity of results obtained from STARS analyses.

Lines 218-224. Is setting $p<0.01$ sufficient to avoid wrongly identifying breakpoints in the light of the number of sequential analyses of mean values across all the time series? How many such tests were performed?

We have added additional details of the sensitivity tests conducted. Most papers e.g. Rodionov et al., 2005 test at <0.05 significance so we feel that <0.01 is justifiable.

Lines 315-316. Describes thresholds in phosphate level in 1997 and 2004. These are shown in Figure 3 (by the grey bars) but from looking at the plot there appears no obvious reason why thresholds were identified in those particular years. This is a general point – aLs many of the places on which grey lines appear in Figure 3 do not by visual inspection appear obvious places for them to be. Another example being riparian water flows. An explanation is needed as to why the grey line thresholds in Fig 3 appear not to be in obvious places in many cases.

These results have been re-analysed and an explanation for the breakpoints given in results section.

L370 Figure 4 appears to have been broken in my copy. There is no vertical scale – the figure is useless.

Figure 4. Is not terribly helpful and is referred to only once. Also, in my version the symbol for coliform bacteria is not visible in the key.

This has been replaced with a table in the final version.

L361 Figure 3. This needs major revision. All the timeseries need to have a common x-axis. This is critical to see the extent of the crossover. All the vertical scales need to be normalised. For instance the dramatic peak in the intertidal mudflat is obscured by a wide vertical scale. 1995 was clearly a major transition, also seems to be for the algal mats… what happened then? All the missing values which have been interpolated need to be highlighted.

Corrected and we have standardized each environmental time series by subtracting the mean and scaling by the standard deviation.

GAMS

Table 3. With 20 or more GAM models being explored is setting $P<0.05$ sufficiently precautionary? This table should be re-oriented to have the 8 drivers listed vertically and the 3 assets horizontally. Presumably the (B) shown in the waders * manila clam box is a typo for (L)?

This has been removed in the final version

Lines 164-165 The harbour is also a Ramsar wetland of international importance.

We have added this

Line 186. Saltmarsh has been in decline not just over the last few decades but for almost a century.

Yes, this was an oversite and we have amend this

Lines 235-236. It would help to provide absolute clarity as to how the GAMS were used to look for non-linearities in the time series BETWEEN the breakpoints already identified by the STARS method. Is that correct? Or were the GAMS applied across each entire time series including the breakpoints identified already by STARS? If so, why use two methods?

Lines 253-254. Are stating the obvious. If a GAM model has a p>0.05 it is not significant – it is not really then a choice to eliminate them. What happened to GAM models of intertidal mud and subtidal sediment (not listed in Table 3)– did all GAM models for these assets have p>0.05?

We have re-written the methods section and added a more robust selection processes to assess diver-asset responses using AIC and relaimpo *package in R to determine the* explained variance (R^2)

Colour coding and limits

Lines 227-234. The favourable condition targets for the Poole Harbour SPA are set out in the supplementary advice on qualifying features document available at https://www.gov.uk/government/publications/marine-conservation-advice-for-special-protection-area-poole-harbour-uk9010111 This sets out quantitative targets for amongst other things: the area of saltmarsh (424ha), the area of littoral sediment (1,359 ha) and the size of the wintering waterbird assemblage i.e. 25,091 birds.

Lines 233-234. Does this mean that for manila clam landings and bird numbers, the target level above which levels were deemed favourable was simply the mean of the values at the start and end of the time series? In the case of the birds, favourable condition in reality is likely to be defined by the target of 25,091 +/- some fixed % of that value.

Figure 3. There needs to be an explanation in the text of the reason why so many grey line breakpoints do not appear in obvious places and why some are far wider than others. If it does not clutter the images too much, in some cases it would help to indicate with data points the times at which each driver/asset etc was actually measured. I do not fully understand the colour-coding. Surely it is wrong to assess the fishing pressure from 2000 - 2005 to be "green" when clearly this was the period in which overfishing was occurring? Arguably fishing pressure, being much reduced now, might be coded green rather than red. Why is riparian river flow classed as green until 1971 and yellow thereafter? Why is subtidal sediment classed as red during the period of change but not before or since? Why are wildfowl and

wader numbers classed as green in the middle period and yellow at start and end. I guess the latter is because of the use of the start/end mean as being the target and that that mean is exceeded (apparently) only in the middle years.

We have removed the colour coding from figure 3

Bird data

The document at the link above notes that "Five year peak mean at time of classification was 25,091 individuals (1992/93 to 1996/97) (English Nature, 2000) and the most recent five year peak mean (2009/10 to 2013/14) was calculated to be 26,374 (Holt et al., 2015)". That latter figure is totally different to that plotted in Figure 3 and does not suggest there has been any marked decline in the size of the assemblage since the early 1990s.

BUT in this case I question the bird count data. The WeBS online dataset yields the following figures for Poole Harbour between 2011/12 and 2015/16: 21,662, 23,272, 22,807, 24,673 and 21,264. These are way in excess of what is plotted here and suggest no change since mid-1990s.

Lines 481-482 state that wader numbers have declined since Poole Harbour was designated an SPA in 1999. Based on all the count data on the WEBS online database this does not appear to be the case.

We have checked our bird data and it did not as the reviewer says correlate with the numbers provided above. We have amended the data based on the WeBS online dataset and it now yields similar population trends.

Other

L247 'without plausible mechanism' – this is a real problem to me. Biology is implausible. All the great and interesting stories of biology are implausible from Darwin's earthworms burying landscapes to the golden salamander changing from fully aquatic to running several km over the desert. Crabs undermine saltmarsh, bivalves armour the bed, worms both armour and disaggregate the bed, birds disarmour the bed and raise sediment, shrimps clear the water and aggregate sediment (in huge volumes), algal mats armour the bed, bivalves seive the water and remove algal spores, the estuaries are full of system engineers reinforcing and destroying the physical landscape, including the water itself, above, below and intertidally, they are all potentially related to each other and to system physical characteristics. The real insights come from understanding the implausible stories, not removing them. I am suspicious that these areas produced statistically significant results which undermine the utility of the methods. I was going to suggest the addition of some totally unrelated timeseries just to test this - I think you should include some - the birth rate in Sweden is often used as a cross check in this way.

We have removed the selection criteria for variables in the GAMS analysis. Instead of testing all the possible mechanistic relationships separately, we conducted multi-

model inference to determine the statistical contribution of each driver variable to each NC asset. This should now produce a more statistically robust estimate of pressure-state interactions. We also now consider other possible drivers (in our discussion) that may have affected the NC assets but were not included in this analysis (due to a lack of data). E.g. disease and Manila clam.

Results

Edits

Line 356 and 486 should be 1970s/1980s

Amended

Line 336 – typo 1989 should read 1889?
Removed when results re-written

STARS

L313 "These effects may be compounded by the observed almost six fold rise in river flow levels since the 1960's, which may act to convey more nitrogen into the harbour." …or flush it out quicker. Here we have a number of speculative statements, without back-up from this or other studies. More nitrogen, more algal mats – or they might be limited by some other thing, "likely due to land use changes," etc. These should be stripped out, or backed up with primary sources. Mainly because in the future somebody else may cite these as facts in a peer review paper when that are just musings - even if they appear self-evident - this is a scientific paper; they need to be evidenced.

Statement removed

Table 5. AS noted above there are quantitative targets for the areas of littoral sediment and saltmarsh and the numbers of waders and waterfowl.

Table 5 removed from analysis

GAMS

L445 Figure 5. Panel b is a worry. All these figures need to have much clearer labels. Riparian water flows look more or less linear over the timeseries, yet cause (correlate to) big swings in manila clam landing. What does this mean? It makes me think the method is not working well, perhaps it is highlighting any smooth monotonically increasing variable in combination with one with one abrupt transition and giving false weight to the relationship with the spectacular graph, would this be very similar for any monotonically increasing variable in place of river flow - number of licenced pleasure boats, etc.?.

L 465 I disagree. What evidence is there that these are tipping points, as exhaustively defined above – irreversible system changes, I do not see any evidence for that. It looks to me like the manila clam were overfished, and were not able to recover.(oh… that is stated in L487) L473 No, this is just correlation it does not imply causation.

Lines 332-333 states that the decline in subtidal sediment area (ie the depth of the Wareham channel??) declined in a non-linear Type IV fashion. No explanation is given as to why this is classed as a Type IV tipping point positive feedback loop rather than a standard non-linear response. The same comment applies to lines 356-357.

Line 337 – why is the clear change of direction in saltmarsh extent in 1924 described here as "passing a threshold" not highlighted by a grey bar in Figure 3?

Lines 344-345. It is hard to understand how it can be said that "quantitative understanding of the contribution of material to the sediment budget of the harbour is poor" when the capital dredge by PHC in the early 2000s was based on very detailed modelling by IH or Haskoning of the harbour's sediment budget.

Lines 396-405. There needs to be an explanation (in the introduction or discussion) as to what the likely causative mechanisms are between the various drivers and assets/benefits. For example I can think of no reason why there should be a linkage between manila clam landings and the depth of the Wareham channel (subtidal sediment). Why are the thresholds between clam landings and sediment depth and riparian water flows considered to be Type IV – a positive feedback loop? References to clams should strictly refer to clam landings. Text referring to eg "recovery to numbers below their initial population density" needs re-worded – this is all about clam landings not clam population density.

Line 407 Says that saltmarsh area INCREASED with increasing river flow. I do not understand this. Fig 6 shows a negative relationship and Fig 3 shows that since 1965, when river flow records begin and have been steadily increasing since then, saltmarsh has been in steady decline.

Lines 409-10 Here it says that saltmarsh area exhibited a linear trend with increasing macro algal mats (condition). This is what Fig 6 shows but again table 3 highlights this as a GAM fitted with a significant threshold response, a smoothing term and 7 knots. I suspect I am totally failing to understand the analyses – in which case I will not be the only one. Far better explanation is needed.

Line 414. Somewhere, the linear relationships between nitrates, phosphates, temperature and saltmarsh area need to be discussed. Although the focus is thresholds, non-linear relationships merit equal consideration.

Lines 423-424. Why is the threshold in the relationship between wader/wildfowl numbers and saltmarsh area a tipping point? What is meant by "pre-population levels of c10,000 individuals"? Why should there be a negative linear relationship between bird numbers and clam landings other than coincidence?

Figure 5. Why does the range of manila clam landings in each sub-plot differ? Landings data are available every year from 1989-2015. The plot of landings v fishing pressures has NO landing values between 300 and 100 yet the plots with riparian water flows and subtidal sediment do,

Figure 6. Why should saltmarsh area increase with increasing subtidal sediment depth?

Lines 470-472. Say that all three intertidal mudflat variables, saltmarsh area and bird numbers decreased over the time series. But algal mats (area), and algal mats (condition) both increased over much of the time series and bird numbers (apparently) increased and then decreased (though I think that is wrong).

Table 5 indicates that in some cases the thresholds identified in the analyses were classed as Type III or Type IV (tipping point) but in no case is an explanation provided as to what the positive feedback mechanism is in these cases which justifies this distinction.

> *To answer all the comments above relating to the GAM's analysis, the results section has been completely re-written and the GAM's analysis re-run with the outcome of more robust/plausible results. As such all of these points have been addressed. We have also gone into substantial detail on the possible mechanistic feedbacks that may have caused such changes in the time series data (in the discussion). Many of the relationships of concern in the comments here are no longer significant relationships.*

Discussion and conclusions

-Reviewer 1

Line 531 should be NGOs

> *We have removed this reference from the discussion*

L489 "The reduction in licensed boats has led to a reduction in fishing pressure" No this does not follow. Are these boats licensed for anything else? The original licenses may not have been used (this is highly likely after the crash – they were probably held unused waiting for recovery) - what gear is being used? What access is allowed? How big are the boats? Steel hull or GRP, fridges on board, etc etc etc. fishing changes. No the GAM does not show a strong positive feedback mechanism. It would not falsify that hypothesis – this is bad scientific philosophy. L496 again: "also influenced t…" Not true. The model does not provide falsification of that hypothesis – but it does not suggest influence through correlation – this is just plain wrong. This discussion needs significant shortening and sharpening with proper reference to scientific statements (in the precise meaning of that term outlined by Karl Popper in The Logic of Scientific Understanding).

Lines 494- 495. Says that causes of manila clam mass mortalities are poorly understood. I find that hard to believe having in the past trawled through a massive literature on manila clam cultivation, disease, population dynamics etc etc. Here it also says that subtidal sediment depth "also influenced the Poole Harbour manila clam population status". What possible explanation is there for that "influence"?

Lines 489-491. It is not clear to me why the reduction of the number of fishing boats and fishing pressure exerted by the fewer boats on the remaining clam stock constitutes a strong positive feedback mechanism. I could understand that if fewer clams leads to more boats and more boats lead to even fewer clams leading to even more boats and thence clam extinction that would be a positive feedback loop.

Lines 541-543 suggests that in order to restore the manila clam population to deliver the benefit flow that it once did, restoration targets should look beyond simply setting (more stringent) fishing pressure targets. However, in respect to the other drivers identified in this paper eg riparian water flows, subtidal sediment depth and temperature – what reasonable targets might be set and on what causative basis? Surely fishing pressure is far and away the only thing that really matters in this case?

In response to the four comments above: We have clarified the type of fishing pressure in our methods section re-analysed these results of fishing pressure vs manila clam and re-written the entire discussion section. We still found fishing pressure to have contributed to the decline in mania clam landings BUT also provide new evidence that other factors such as disease and socio-economic factors may also be responsible. Subtidal sediment depth was no longer significant. We also discuss potential feedback mechanisms between the variables.

Lines 477-478 Notes that Poole harbour may not be able to meet its conservation objectives. The most recent condition assessment of the Poole Harbour SSSI indicates that almost one quarter of the SSSI by area is already in an unfavourable declining state. See *summary condition* link at:

https://designatedsites.naturalengland.org.uk/SiteDetail.aspx?SiteCode=S1000110&SiteName=poole&countyCode=&responsiblePerson=&SeaArea=&IFCAArea=

We have removed this reference from the discussion.

Lines 436-439. There is no explanation for the way in which tipping points (ie changes driven by positive feedback mechanisms) were identified as distinct from other ecological thresholds and no explanation given as to what those plausible feedback loops are.

We have re-written this discussion to now discuss the potential feedback mechanisms for all variables.

Lines 514-515. Discusses early warning indicators. It would be very useful to discuss what some of those early warning indicators might be.

We have removed the reference to early warning indicators from the paper as they were not the main focus of this research.

Lines 537-539. Given the need for resource managers to set targets to reduce pressures such as eutrophication, etc, it would seem to me to be appropriate for this paper to try to present what some of those targets might be in order to avoid thresholds or tipping points being reached. Without that we are little further forward.

We have added discussion on potential thresholds that may be useful for management based our GAM's.

Lines 544-546. I am not at all convinced by the assertion that there is a trade-off to be made between bird numbers and saltmarsh area.

We have removed this conclusion

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 calm fisheries of the harbour
- Restoration targets need to consider multiple drivers not just recognisable drivers

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

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

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 generalized 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/benefit flows of the harbour; mudflat area, Manila clam landings 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, which declined by -95% over a period of 4 years. Generalized additive models identified the contribution of macroalgal mats, sediment shoaling and river flows to historic changes in mudflat area, saltmarsh area and wader/wildfowl numbers. The relatively recent cessation in the Manila clam fishery of the harbour was partly attributable to increased fishing pressure although other factors such as disease are also likely to have contributed. 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 & Möllmann, 2015), few previous studies have examined their occurrence in transitional systems such as estuaries and harbours (although see Hewitt *et al.,* 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 systems (McLusky & Elliott, 2004). 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 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 Donahue *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 (Donahue *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 (Donahue *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, natural capital 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 (Figure 1 (I)). In addition, we hypothesize that the relationship between anthropogenic drivers (or pressures) and natural capital status may also demonstrate a threshold response or a tipping point (Figure 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 (Figure 1 (V-VII)). If an environmental driver intensified over time, then it could produce a threshold response in natural capital 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.

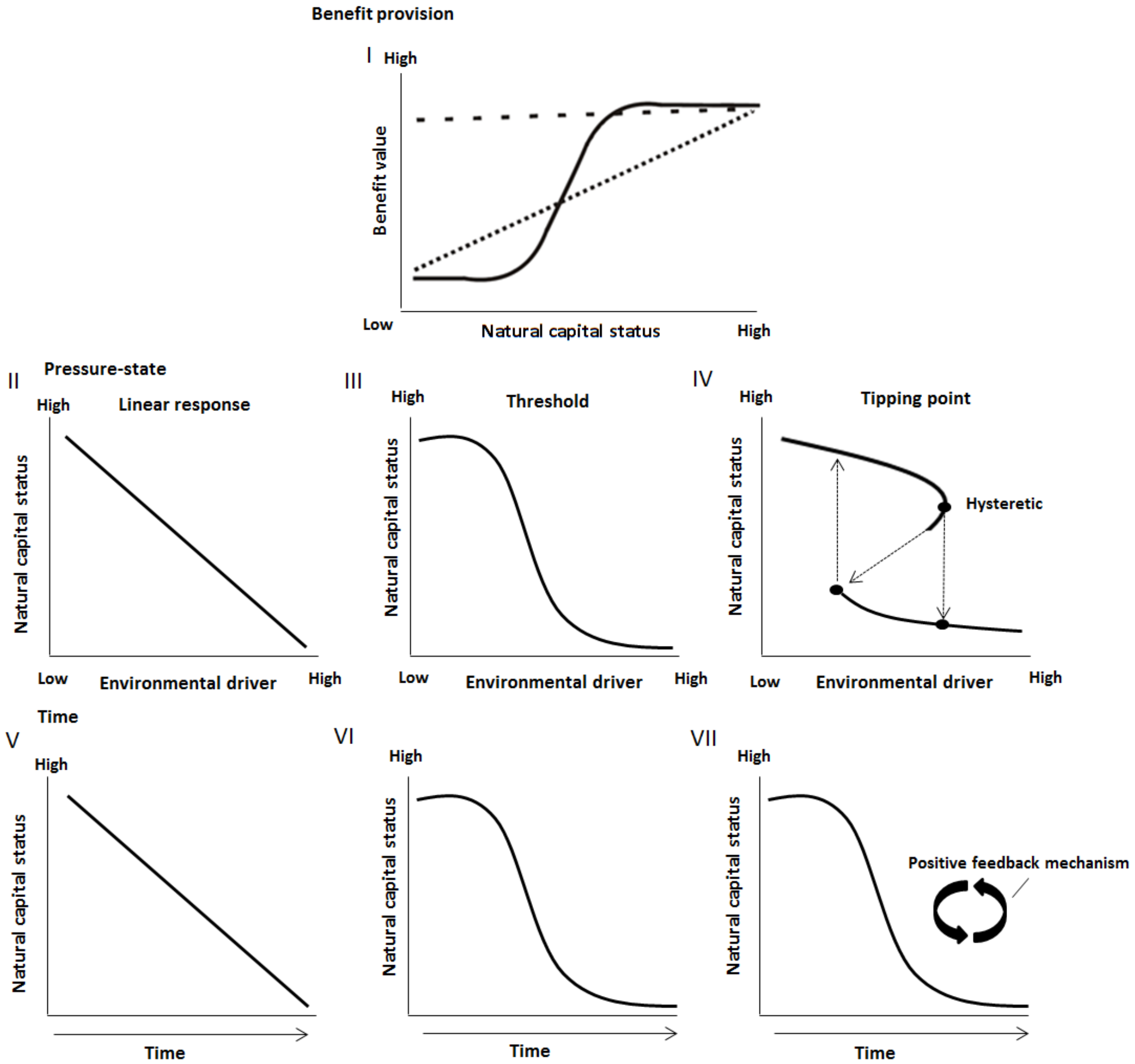

Figure 1: (I) Alternative forms of forms of natural capital asset–benefit relationships, as hypothesized by Mace *et al.* (2015). The solid black line illustrates how the value of benefits might change in response to variation in the status or condition of natural assets, which could be caused by environmental degradation. The dashed line shows a threshold response (or tipping point). Panels (II-IV) show the relationship between natural capital 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).

3 Methods

3.1 Details of study area: Poole Harbour

Poole Harbour is a large natural harbour of nearly 4,000 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 (Figure 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, 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 at their peak 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.

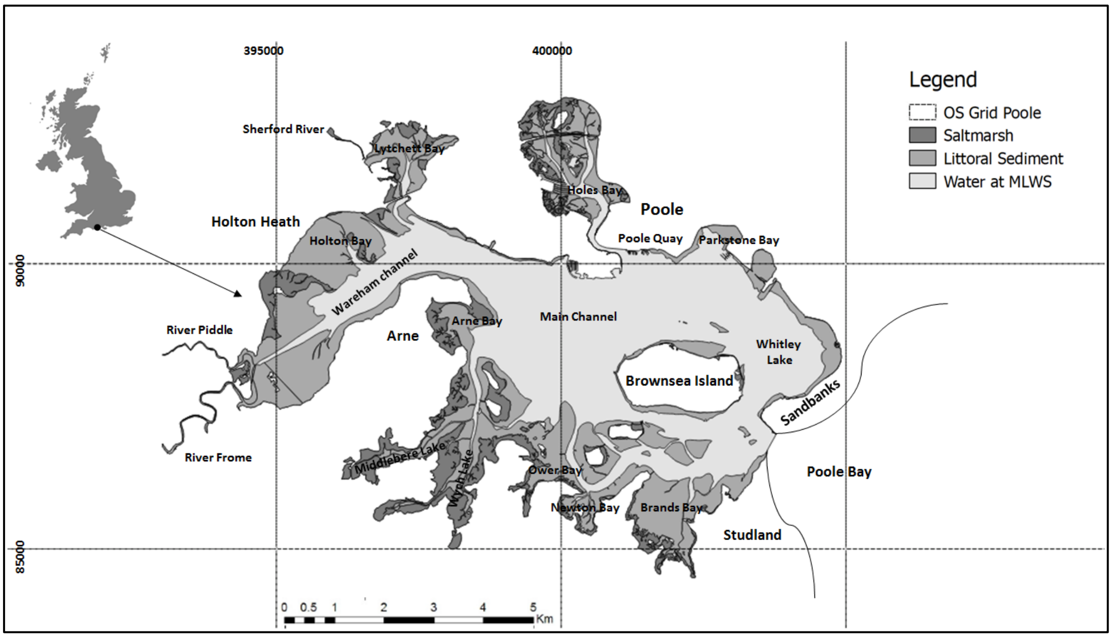

Figure 2 Map of Poole Harbour ©Crown Copyright and database right (2010) Ordnance Survey Licence Number 1000022021. Open water, Saltmarsh & Sediment data from East Dorset Habitat map© Environment Agency, 2010.

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 benefit flows provided by the landings of the Manila clam (*Ruditapes philippinarum*) into Poole Harbour were chosen based on its significant commercial importance.

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: 44207) 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.

Table 1: Proxies used for assessing natural capital assets (stocks) and benefit flows 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).	1980-2015	Environment Agency field data. (Bryan *et al.,* 2013).
Saltmarsh (area)	Nutrient cycling and coastal protection (Regulating), marine invertebrate habitat (Supporting/Habitat)	Trends in saltmarsh area (ha) in Poole Harbour derived from OS maps and aerial photography analysis.	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.
Measures of Benefit (Flows)	**Potential Goods**	**Indicator**	**Time series**	**Data source**
Manila clam (*Ruditapes philippinarum*)	Seafood (Manila clam) (Provisioning)	Total reported catch (tonnes).	1989-2015	Poole Harbour Commissioners (PHC); Defra Landing Statistics.

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. Clams are removed from the seabed using a pump scoop dredge which is towed along the seabed by small (under 10 m) fishing vessels.	1989-2015	Poole Harbour Commissioners (PHC); Defra Landing Statistics
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.	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 ($\mu g\ l^{-1}$)	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^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 (°C)	1980-2015	Cefas Coastal Temperature Network Station 23: Channel Coastal Observatory from 2011.

3.3 Data analysis

Based on criteria outlined by Collie *et al.* (2004), Bestelmeyer *et al.* (2011), Carpenter (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 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 (Table 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 & 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 & 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 optimization 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 & 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 (Groemping, 2007). 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 where 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 degradation in three of the four natural capital stocks and benefit flows: mudflat area, saltmarsh area and Manila clam landings (Figure 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 landings increased considerably between 1994 and 2004, but experienced strong abrupt shifts between 2002 and 2007 that have since reduced clam landings in the harbour to very low values. Results of the STARS algorithm (Table 3) suggest that the magnitude of the changes detected in 2004 and 2007 were the greatest of any variable tested (2.25 & 3.18 respectively). 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 2011-2015 (Appendix 1). Changes in nitrate concentrations and the water temperature both showed increasing trends over the multidecadal 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 2002 and 2007 can also be seen, coinciding with a decline in Manila clam landings (Figure 3).

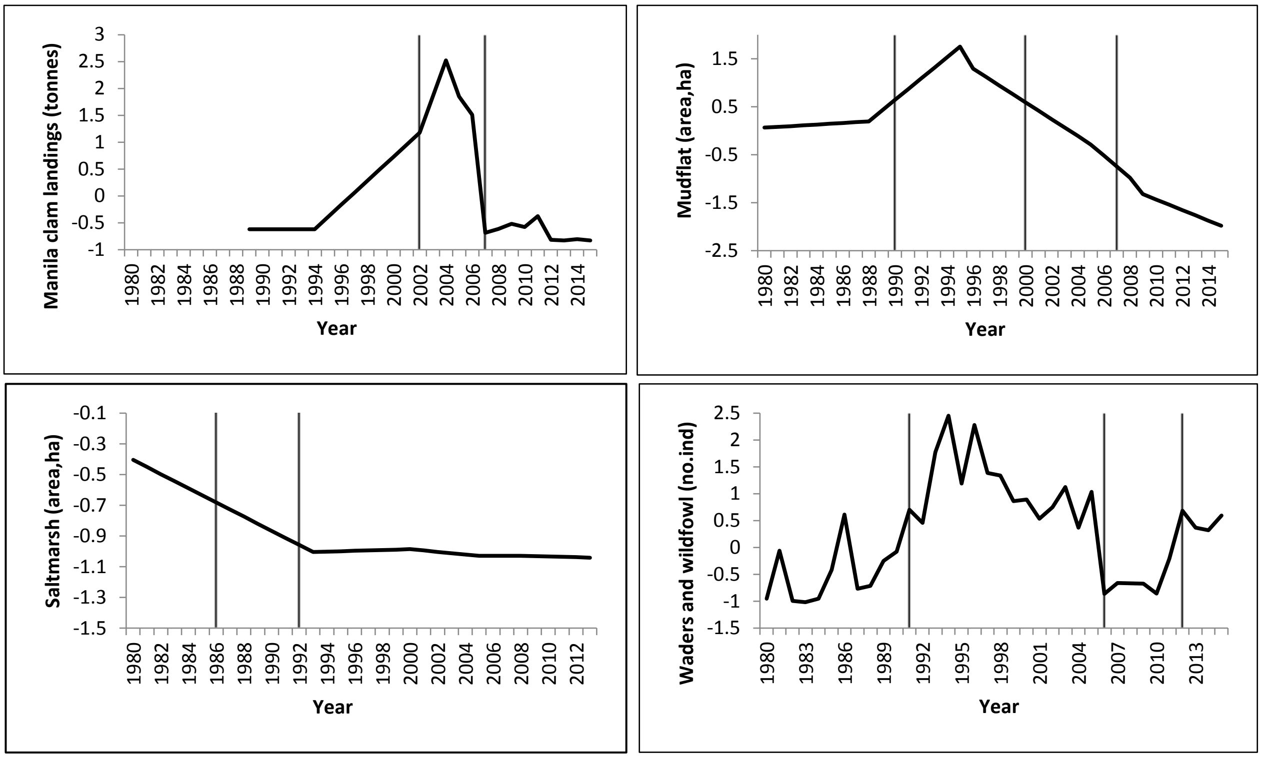

Figure 3: STARS threshold detection of the four normalised natural capital assets/benefit flows in Poole Harbour, Manila clam (tonnes harvested), mudflat area (ha), saltmarsh area (ha) and waders/wildfowl (no. individuals). The horizontal black line indicates the direction (positive or negative) of the trend representing a significant deviation from zero (i.e. the proxy mean over the time period).Vertical black lines represent statistically significant ($p \leq 0.01$) breakpoints for individual trends from sequential Student's t-tests.

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

Drivers/Natural capital stocks and benefit flows	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 landings	2002, 2007	2.25, 3.18
Mudflat (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

4.2 The relative contribution of multiple pressures to natural capital stocks and benefit flows

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

Table 4: p-values for all GAM models analysed. Significant models ($p \leq 0.01$) are shown in bold and with an (*).

	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	**0.0002***	N/A	N/A	0.159	0.824	N/A	0.370	0.436	0.495
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

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 (Figure 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 landings with a relative importance of 84%. Other variables were less important for all indices, ranging from 0.01 to a relative importance of 0.13 (see Figure 4).

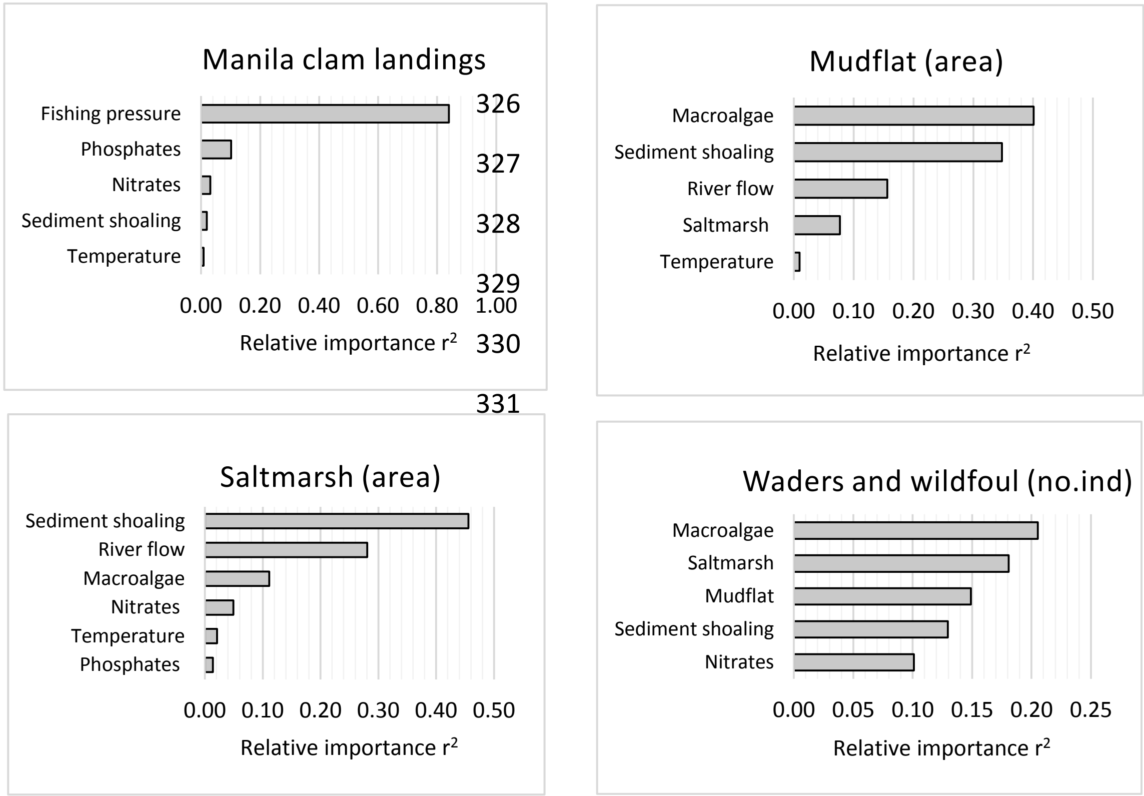

Figure 4: Relative importance of different pressures for each of the natural capital stock/flows. The proportion of variance explained by the final model was: Manila clam (100%), mudflat area (99.16%), saltmarsh area (86.90%) and waders/wildfowl (76.54%).

The full GAM analyses also allowed identification of relationships between natural capital status and significant pressures. Macroalgal mats showed evidence for negative nonlinear relationships (Figure 5) with three natural capital 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 landings in response to fishing pressure, suggesting a purely linear relationship between the variables. Overall, of the three proxies for natural capital stocks with nonlinear responses, all three showed evidence for thresholds in relation to more than one pressure.

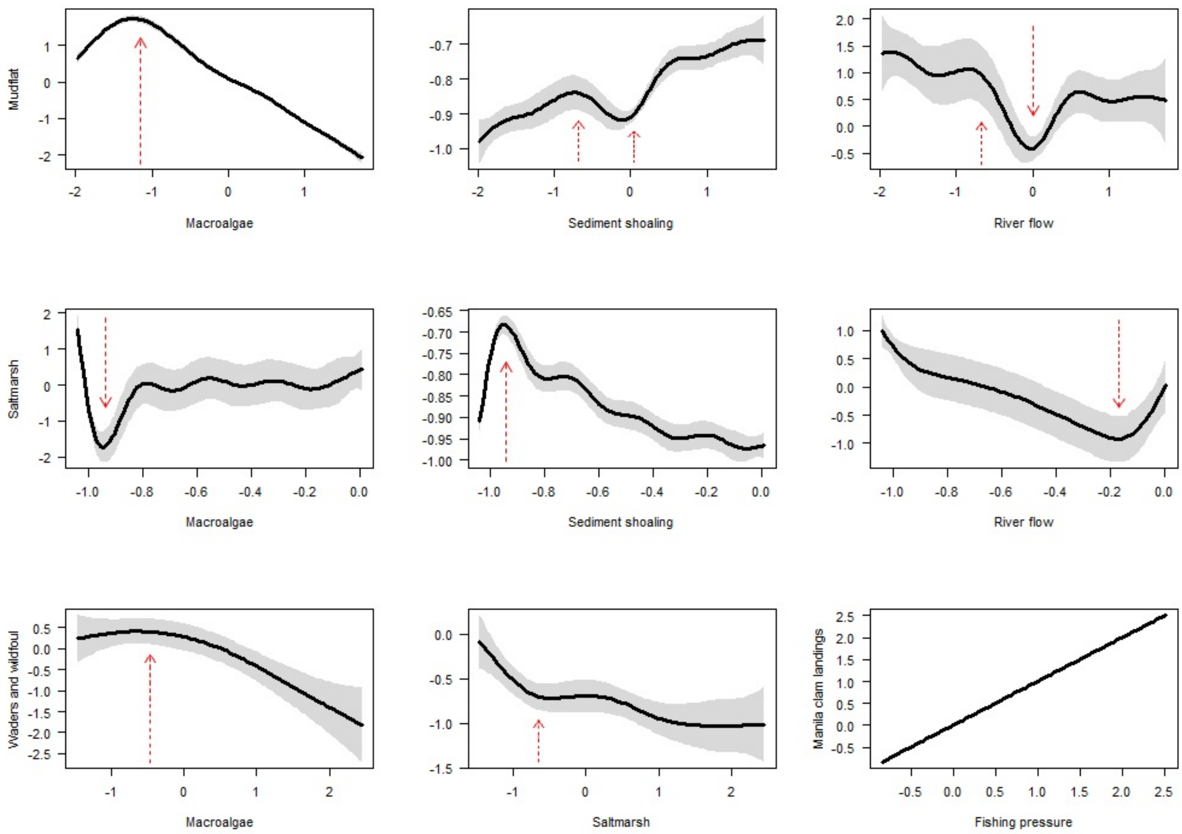

Figure 5 GAMs of the four normalised natural capital stocks/benefit flows response to pressures ($p \leq 0.01$), where the horizontal black line represents significant positive or negative trends, representing a significant deviation from zero (i.e. the mean). The grey polygon represents 95% confidence 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).

5 Discussion

In this study, we employed STARS and generalised additive models (GAMs) to identify trends and thresholds in NC-time series and NC-pressure relationships. Using this analysis we identified distinct points where four NC assets/benefit flows of the harbour (Manila clams, mudflat, saltmarsh and waders/wildfowl) have been substantially reduced in the past, and the potential drivers of that may have caused such changes. Although the STARS technique has been previously been used to identify thresholds in ecological time series data (Moellmann *et al.,* 2009; Conversi *et al.,* 2010), the present study is the first to employ this method to empirically identify thresholds within a NC or ES 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 & 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 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 Figure 1, STARS results here show saltmarsh area of the harbour to have declined linearly (Type V) between 1980-1988 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 with 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 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 & 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 (~800g m^{-2} wet weight), supporting a lowering of the current legislative threshold of 2 kg m^{-2} to 1 kg m^{-2}. As the condition of mudflats, wading birds and the extent of algal mats are sanctions under current legislation (JNCC 2004) for Poole Harbour, 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, an abrupt decline in landings of clams was observed between 2004 and 2007, since when values have not recovered. While these changes were the greatest in magnitude of the threshold responses observed in this study and fit the criteria outlined in Figure 1 for a tipping point transition (i.e. type VII), 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.

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, 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 Figure 1, I).

As suggested in the STARS analysis above, areas of macroalgal mats and saltmarsh were shown to have significant negative but mostly linear effect (II, Figure 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, Figure 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 & 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 & Pye, 2000), there is evidence that the loss of S*partina* 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 (Figure 5) suggest an abrupt threshold (III, Figure 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 S*partina* 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 landings. As expected, the relationship between fishing pressure and clam landings was entirely linear (II, Figure 1), suggesting there was no definitive threshold where reducing fishing pressure could prevent the collapse of clam landings. Nonetheless, 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 (Harris, 2016). This suggests that unless clam landings sizes are routinely policed or changed, landings may never return to pre-collapse levels. It is important to note that the trends here only exemplify the total stock taken from the harbour (i.e. the benefit flow) and we have not considered the actual free-living stocks that reside within the harbour. This is an important distinction to make because a number of other mechanisms could be responsible the abrupt shifts in landings seen in this study. For example, Manila clams cultured on the lease beds in the harbour have been subject to recurring bouts of mass mortalities (Bateman *et al.,* 2012). From the literature it is unclear what has caused such events but viral infection combined with low winter 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 (i.e. type VII, Figure 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 (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. Therefore, while the environmental conditions of Poole Harbour are currently favourable for Manila clam proliferation, different types of disturbance may have acted together to cause the abrupt decline in landings 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 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 now being reported in other locations around the world (Pretto *et al.,* 2014; Nam *et al.,* 2018).

The loss of a commercially attractive species such as Manila clam is also likely to have substantial repercussions on the wider ecology and economy of the harbour. For instance, there is evidence that the introduction of Manila 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). Although we could not test this relationship owing to a lack of long term wild stock data on Manila clam, it may be that the sharp fall in bird numbers in 2007 could have coincided with the equally large fall in Manila clams landings (which gives a rudimentary indication of stock levels in the harbour). Thus, it could be suggested that if the Manila clam fishery were to recover this would have the potential to provide an indirect benefit to several European shorebird populations. There is also evidence that when cultured at high densities Manila calms 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 to humans, DEFRA reported value (£) for total landings in the harbour estimate a drop in value from £1,000,000 in 2005 before the tipping point in 2007 to just £4148 in 2015 (see Appendix 2), suggesting there is a local economic interest in in ensuring that the clams do not disappear from the harbour. However, such benefits must also 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 *et al.,* 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). However, 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 (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 transitional protected systems such as harbours. The ecological thresholds that we have identified are driven by interactions among biophysical, ecological, and potentially 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 natural capital and/or multiple interacting drivers to create conceptual and dynamic modelling tools to support management decision-making.

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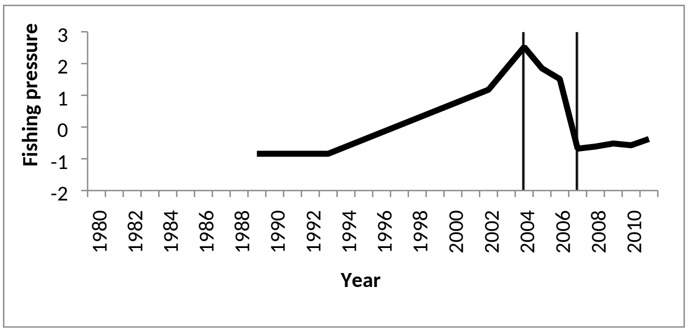
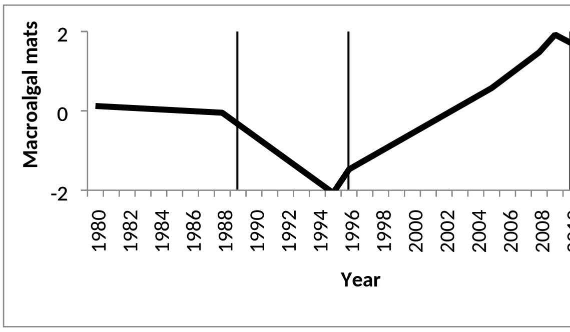
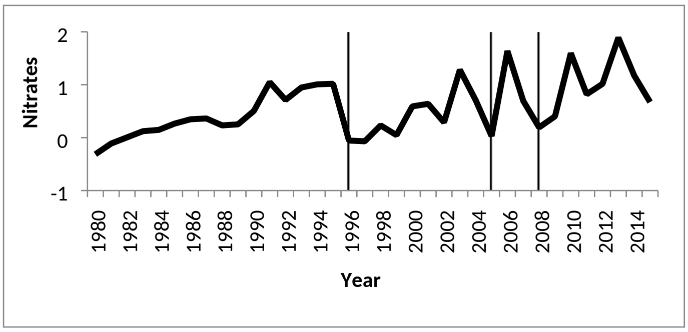
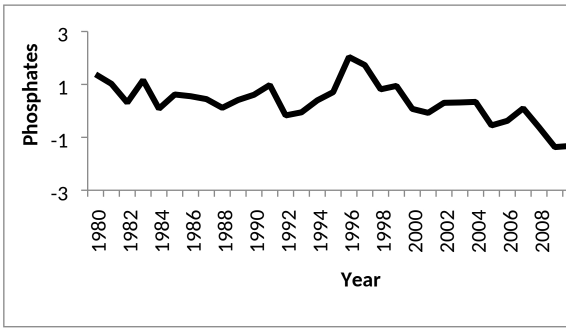
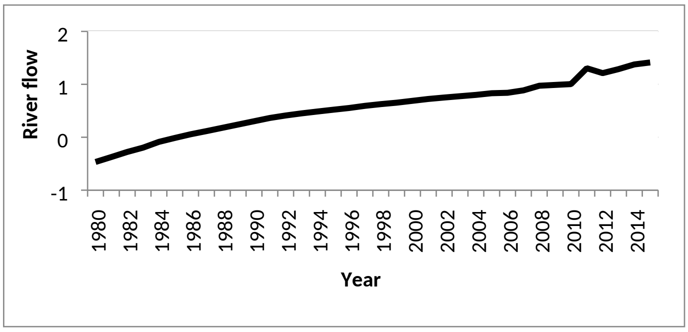
Appendix 1: Normalised time series of environmental drivers, in Poole Harbour for the period 1980-2015. From top to bottom: fishing pressure (no. boats), macroalgal mats (area (ha), nitrates (mg NO_3 N l^{-1}), phosphates (µg l^{-1}), riparian water flows (m^3 s^{-1}), sediment shoaling (m) and water temperature (°C). Vertical black lines represent statistically significant ($p \leq 0.01$) breakpoints for individual trends from sequential Student's t-test.

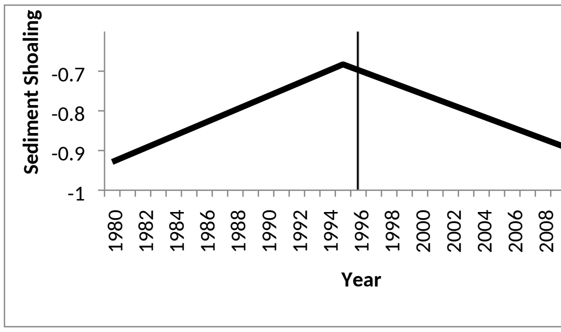


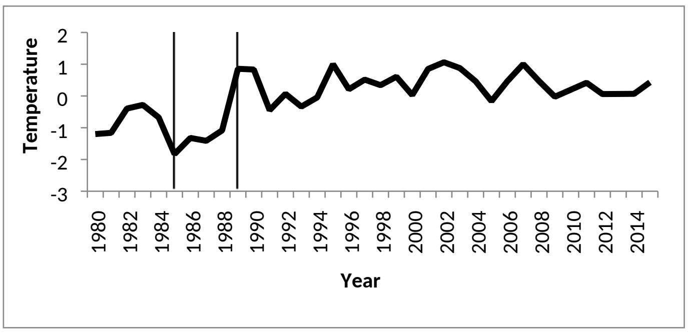












Appendix 2: The reported value of landings of Manila clams in tonnes from Poole Harbour between 2002 and 2015. Data from DEFRA UK sea fisheries annual statistics.