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Characterizing driver-response relationships in marine pelagic ecosystems for improved ocean management

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Abstract

Scientists and resources managers often use methods and tools that assume ecosystem components respond linearly to environmental drivers and human stressor. However, a growing body of literature demonstrates that many relationships are non-linear, where small changes in a driver prompt a disproportionately large ecological response. Here we aim to provide a comprehensive assessment of the relationships between drivers and ecosystem components to identify where and when non-linearities are likely to occur. We focus our analyses on one of the best-studied marine systems, pelagic ecosystems, which allowed us to apply robust statistical techniques on a large pool of previously published studies. In this synthesis, we (1) conduct a wide literature review on single driver-response relationships in pelagic systems, (2) use statistical models to identify the degree of non-linearity in these relationships, and (3) assess whether general patterns exist in the strengths and shapes of non-linear relationships across drivers. Overall we found that non-linearities are common in pelagic ecosystems, comprising at least 52% of all driver-response relationships. This is likely an underestimate, as papers with higher quality data and analytical approaches reported non-linear relationships at a higher frequency – on average 11% more. Consequently, in the absence of evidence for a linear relationship, it is safer to assume a relationship is non-linear. Strong non-linearities can lead to greater ecological and socio-economic consequences if they are unknown (and/or unanticipated), but if known they may provide clear thresholds to inform management targets. In pelagic systems, strongly non-linear relationships are often driven by climate and trophodynamic variables, but are also associated with local stressors such as overfishing and pollution that can be more easily controlled by managers. Even when marine resource managers cannot influence

ecosystem change, they can use information about threshold responses to guide how other stressors are managed and to adapt to new ocean conditions. As methods to detect and reduce uncertainty around threshold values improve, managers will be able to better understand and account for ubiquitous non-linear relationships.

Keywords: thresholds, tipping points, pressure, stressor, food web, management, generalized additive models, non-linearities

Introduction

Ecosystem regime shifts, or 'tipping points', represent abrupt shifts in ecosystem structure and functioning that can dramatically alter human-derived benefits from the system (Scheffer et al. 2001, 2009). A burgeoning literature over the past decade shows these tipping points to be common in terrestrial (Folke et al. 2004, Higgins and Scheiter 2012, Brando et al. 2014), freshwater (Carpenter 2003) and marine (Hughes 1994, Hughes et al. 2010, Daskalov et al. 2007) systems. To better anticipate and manage for these shifts, recent research has focused on understanding the mechanisms of regime shifts (Beaugrand 2004; Daskalov 2007, Perry et al. 2013), identifying early warning signs (Scheffer et al. 2009, Carpenter et al. 2011, Dakos et al. 2010, 2012, Litzow et al. 2013), and considering ecological thresholds in management, policy and law (Samhouri et al. 2010, 2011, Kelly et al. 2014a, b). Efforts to understand mechanisms of regime shifts often seek to identify the components of the ecosystem that exhibit disproportionately large changes (i.e., non-linear responses) when an ecosystem regime shift occurs, and pinpoint external drivers correlated with these changes (e.g., Collie et al. 2004, Beaugrand 2004, Alheit et al. 2012). Yet despite the awareness of non-linearities within ecosystems, many methods used to investigate ecological responses to environmental drivers and anthropogenic stressors (herein collectively referred to as drivers) are inadequate for detecting non-linear relationships and therefore linear responses are often a default assumption (e.g., Gil 2013, Ban et al. 2013).

Strong nonlinear or threshold responses in these systems indicates ecological boundaries that may serve as critical reference points for managers to avoid or target when making decisions (Briske et al. 2006, Suding and Hobbs 2009, Selkoe et al. in press). The costs associated with incorrectly assuming linearity when an ecological response is actually non-linear can be large.

For instance, instead of an incremental increase in fishing pressure causing an incremental decrease in fish abundance, the fish stock might collapse and impact other ecosystem components and processes. Similarly, a gradual increase in anthropogenic nutrient loading in marine and aquatic ecosystems may elicit sudden increases in eutrophication and hypoxia events. Such ecological surprises can have broad ecological, social and economic consequences that may be difficult to reverse. For instance, the collapse and limited recovery of Atlantic cod in the northwest Atlantic Ocean had profound effects on ecosystem structure (Frank et al. 2005, 2011, Steneck et al. 2013) and the livelihoods and economies of coastal communities (Steneck et al. 2011), and eutrophication and formation of harmful algal blooms in coastal systems worldwide have threatened water quality, human health and animal life (Gunderson 2001, Johannessen et al. 2011, Glibert et al. 2014). The serious consequences that strong non-linear responses potentially create for ecosystem health, economies, cultures and public health motivated us to assess their prevalence in marine ecosystems.

A practical and feasible starting point for elucidating non-linearities in complex ecosystems is to catalogue the strengths and shapes of uni-variate driver-response relationships. Regressing ecological responses against hypothesized explanatory variables can reveal whether the changes occur in a linear, curvilinear or highly non-linear fashion, even if it is unclear whether the explanatory variables are true drivers or proxies for true drivers, or whether curvilinear relationships truly represent non-linear threshold dynamics. Curvilinear relationships may be considered non-linear from a statistical sense even if they do not exhibit threshold dynamics. From a complex systems perspective, non-linear threshold dynamics can cause systems to abruptly transform into new states that can be difficult to reverse and may, in some cases, exhibit hysteresis, where recovery does not immediately ensue when conditions preceding

the transformation are re-created (Scheffer et al. 2001). Curvilinear relationships may exist without such transformation, but still represent challenges to management in which a key driver-response relationship switches, e.g., from positive to negative. It is unclear how many of the curvilinear relationships identified in the literature could potentially exhibit threshold dynamics. Because both non-linear and curvilinear relationships can lead to unexpected management outcomes, from here on we collectively refer to them as non-linear.

Understanding when and where strong non-linearities occur enables use of critical points or thresholds for precautionary target-setting in an ecosystem-based management context (Samhouri et al. 2010, Large et al. 2013, 2015a). Non-linear population dynamics and functional relationships underlie the calculation of reference points used to regulate fisheries (e.g., maximum sustainable yield, Maunder 2008), recover endangered species (e.g., minimum viable populations, Morris and Doak 2002) and control environmental contaminants (e.g., exposure-response relationships, Suter (2007)). For instance, Cury and others (2011) identified a threshold value of forage fish biomass needed to sustain the long-term productivity of seabird populations using data from seven different ecosystems. Their empirically-derived estimate of "one third for the birds" (1/3 of maximum long term forage fish biomass) can serve as a general principle for guiding management decision making around forage fish catch limits to ensure the sustainability of predator populations. However, such ecological thresholds, particularly generalizable ones, have not yet been commonly identified. Empirical evidence of functional relationships and non-linearities may guide the functional form and inclusion of stressor-response linkages in models used to assess marine resources and set management targets. Furthermore, understanding uni-variate driver-response relationships is an important precursor to understanding and managing the interacting effects of multiple drivers on ecosystem components, for which far fewer data

exist. For example, assessments of cumulative human impacts on ecosystems (e.g., Halpern et al. 2008) would be greatly improved with a greater understanding and incorporation of potential single-stressor non-linear relationships (Halpern and Fujita 2013).

Here, we systematically collected uni-variate driver-response relationships from peer-reviewed literature; identified the prevalence, strength, and shapes of the relationships; and assessed whether general patterns exist in the shapes and strengths of driver-response relationships. While many studies of uni-variate driver-response relationships exist in the literature, synthetic insights are challenged by the variety of methods and statistical techniques used to quantify them. Some of the most powerful methods used to decipher the shapes of relationships between drivers and ecological components are regression-based techniques, and therefore we were particularly interested in reviewing these studies. As a case study, here we focus on a single, well-studied system, the pelagic zone, to quantify where, when and why linear and non-linear relationships are found.

Methods

Literature search, selection criterion, and data extraction

We conducted a wide literature search of driver-response relationships in marine pelagic ecosystems published in peer-reviewed literature through year 2013 using the Web of Knowledge bibliographic database. We first searched the database using keywords related to pelagic ecosystems and non-linear system dynamics (e.g., regime shifts, thresholds, tipping points) and then conducted a new search to include keywords related to specific drivers in these systems (e.g., climate, pollution, fishing). The second iteration of the literature search ensured that we captured both linear and non-linear driver-response relationships published in peer-

reviewed literature. A comprehensive list of the keywords used in both searches is provided in Appendix A (Table A1).

Several criteria were used to determine which studies to include in our analyses. First, the paper must have been based on an empirical field study in marine pelagic ecosystems. Mesocosm and laboratory experiments and modeling studies were not included. We note that if studies on demersal species came up in our literature search they were included in our database because demersal species are vulnerable to the same biophysical and human drivers as pelagic species. Second, the authors must have identified the functional form of the relationship, i.e. linear, non-linear (curvilinear and threshold responses), between a driver and ecosystem component. Third, the authors must have used statistical analyses, such as uni- and multivariate regression or correlation techniques, to determine whether the relationship was linear or non-linear. If a paper did not meet this last criterion, but the raw data were published in the paper, we extracted the data and ran our own multivariate analysis, fitting Generalized Additive Models (GAMs; Wood 2006) with and without a smooth term (non-linear and linear model formulation, respectively) to the driver-response data. The best-fit model, and thereby the form of the relationship, was determined based on the Akaike Information Criterion (AIC; Hastie and Tibshirani 1990), i.e., the model with the lowest AIC value was deemed the best-fit model. Raw observations that were presented in figures rather than tables were digitized from electronic (PDF) versions of manuscripts using the ImageJ on-screen measuring tool (Schneider et al. 2012). All analyses using GAMs were done using the mgcv package in R (version 3.0.2, 9/25/2013).

Database

We created a database of the published single driver-response relationships that were deemed significant based on p values ≤ 0.05 or were included in best-fit models identified through model selection. Multiple summary statistics were recorded (when available) in the database in an effort to explore variation in driver-response relationships in the present study and to be made available for researchers for future studies. The summary statistics included published or derived shapes of the relationships (linear, non-linear or specific functional forms), sample size, quantitative estimates of ecological thresholds, p values, R^2, deviance explained, correlation and regression coefficients, and model covariates (if multivariate model).

While we were mainly interested in single driver-stressor response relationships, many published studies often included multivariate models. In those cases, we collected statistical information on the partial effects of individual drivers on ecological responses. In addition, authors often log-transformed their data to meet statistical assumptions of normality or equal variances, and in such cases we included these relationships in our database. In the papers that met our selection criteria, there were no studies in which the authors' intent was to linearize the relationships of interest through transformations. When possible, we digitized, back-transformed and refit models to accessible data using GAMs as described above, although there were no instances in which back-transformation of the data changed the findings from the original studies. Further, we were mainly interested in the influence of time-variant drivers on ecological responses, and therefore time-invariant physical drivers, such as depth, latitude and longitude were not included in our database. We also minimized the potential for spatial and temporal pseudo-replication (non-independence of data) within studies in the following manner: 1) when authors reported findings across different spatial scales, e.g., regional and global, we recorded their results for regional scales only to avoid repeated measurements in the same vicinity, and 2)

if authors reported results for an individual time unit (e.g., one year) and across an entire time period (e.g., all years combined), we included the results for the individual time unit only. In studies that included multiple species, we considered each species as an independent measurement.

In addition to summary statistics, we collected ancillary data on study characteristics to explore the variation in driver-response relationships and to identify the most robust papers with respect to statistical methods. The ancillary data in our database include: ecosystem type (enclosed bay or sea, coastal pelagic, continental shelf and continental slope/oceanic), local region, ocean basin, temporal scale of study, functional level (i.e., individual, population, community) and species trophic level (TL 1-4) of ecological response, primary productivity ($mgC/mg^2/day$) and the statistical methods used by the authors. Estimates of species trophic level and primary productivity were obtained from the Sea Around Us Project (http://www.seaaroundus.org/).

We created a subset of data from papers that we deemed to be the most statistically robust for our analysis. We defined statistically robust papers as those in which the authors tested hypotheses of linear versus non-linear relationships, or at the very least provided evidence of fitting both linear and non-linear models to their data. Papers were also included in this subset if we were able to extract raw observations and fit GAMs to the data. We compared the prevalence of non-linear relationships in the subset of driver-response pairs to the prevalence in pairs from all of the studies to determine if inconsistencies in the analytical approach among papers might influence our results. We also used the subset of data in our analyses below to explore variation in the degree of non-linearity in the driver-response relationships and to characterize the shapes of those relationships.

Degree of non-linearity

We quantified the strength of non-linearity in driver-response relationships using the effective degrees of freedom (EDF) of Generalized Additive Models (GAM). The EDF is a summary statistic of GAM and it reflects the degree of non-linearity of a curve (Wood et al. 2006). An EDF equal to 1 is equivalent to a linear relationship, $1 < EDF \leq 2$ is considered a weakly non-linear relationship, and $EDF > 2$ implies a highly non-linear relationship (Figure 1; Stenseth et al. 2006, Litzow and Ciannelli 2008, Zuur et al. 2009). As the EDF increasingly exceeds 2, the degree of non-linearity progressively increases. The driver-response relationships with $EDF > 2$ are those that are most likely to have at least one inflection point and exhibit threshold responses.

Estimates of EDF were often reported in papers in which the authors used GAMs to model driver-response relationships. If the EDF was not reported or authors used a regression technique other than GAMs, we generated approximate estimates by fitting GAMs to digitized data, including raw observations and model predictions. We sequentially fit GAMs with a decreasing number of knots (i.e., locations in spline curves where piecewise polynomial curves are joined (Wood 2006)) to the data until we identified a model that had the lowest number of knots and still maintained the shape of the published relationship, as determined by visual inspection. By reducing the number of knots we constrained the flexibility or 'wiggliness' of the curve, which resulted in a lower and more conservative estimate of EDF (for example see Appendix B, Fig. B1). If the authors used linear regression or correlation techniques, we assigned an EDF of 1 to significant linear relationships. We note that in many studies the authors reported significant linear and non-linear relationships.

Variation in degree of non-linearity among relationships

We used regression trees (Brieman et al. 1994, De'ath and Fabricus 2000, Hastie et al. 2013) to explore variation in the degree of non-linearity across driver-response relationships in relation to a suite of explanatory variables. We applied regression trees to the subset of data extracted from statistically robust papers; however, many combinations of driver metrics and ecological components lacked sufficient replication to draw conclusions about trends. Therefore, we only included the major driver-response pairs from the subset of data with sample sizes (i.e. number of individual relationships) > 5 (Appendix C, Table C1). In addition, we focus these analyses on the four major ecological responses (shown in Table 2), which have more than one driver-response pair and/or come from more than one study. Tree models were fitted using binary recursive partitioning (rpart package (Therneau et al. 2014) in R version 3.1.1. 10/7/2014), which repeatedly splits the response variable along coordinate axes of explanatory variables into groups that are as homogenous as possible in terms of their deviance (e.g., sum of squares) until no further reduction in deviance is obtained. In our analysis, the response variable is estimates of EDF and the potential explanatory variables biological attributes of the relationships and study systems (i.e., driver, ecological response, primary production rate in study system, and functional and trophic level of ecological response), and study characteristics (i.e., publication year, sample size, i.e. number of observations, and temporal scale of the study). To find the best tree, we first constructed the largest tree possible using all potential explanatory variables. We then pruned the trees to a size that had the smallest estimated error and was the best estimated predictive single tree using the cost-complexity pruning parameter determined with ten-fold cross validation (De'ath and Fabricus 2000, Therneau et al. 2014). The total

variance explained by the best single tree was calculated as R^2 = 1- relative error. The quality of each split was assessed by 'improvement'; the proportion of the total sum of squares explained by the tree at each node (Therneau et al. 2014).

Shapes of relationships

We categorized the shapes of highly non-linear driver-response relationships (shown in Table 2) using expert consensus-based visual inspection. Many of the papers selected for our study provide model fitted curves and residuals of the relationships between the metrics of drivers and ecological responses, but do not present raw observations. This prevented us from quantitatively estimating functional forms of most metric-response relationships in our database, and therefore we adopted a qualitative approach. We created five categories of potential shapes of metric-response relationships based primarily on Bolker's (2007) qualitative descriptions of functions used for ecological modeling. We then independently assigned metric-response relationships to one of the five shape categories. The potential shapes of relationships included: single maximum or minimum and hump-shaped (i.e., dome-, U- shaped and Ricker); splines (i.e., ≥ 2 maximum or minimum); decreasing, increasing or saturating (i.e., negative and positive exponential, Michaelis-Menten); sigmoid (i.e., logistic); and threshold (i.e., threshold and piecewise models best fit the data – not based on visual inspection) (see Figure 2 for illustrations of shapes). Shapes were included in our final assessment of metric-response relationships if at least four of the five co-authors who participated in this analysis agreed on the shape. Otherwise, the shapes were categorized as 'no-consensus'.

Results

Using our search and selection criteria, we identified 75 studies of driver-response relationships in pelagic ecosystems, producing 728 estimated relationships that focused on a wide range of trophic levels (plankton to large pelagic predators), drivers and response variables (see Table S1 in Supplement 1). To aid interpretation of patterns, we combined driver-response data into broad groupings of major drivers: climate, pollution, exploitation, and trophodynamic (Table 1). Sample sizes within categories were uneven; climate drivers were the best represented, followed by trophodynamic drivers, pollution, and exploitation (Table 1). Response variables were grouped into 17 different categories of ecological components that ranged from individual- to population- to ecosystem-level responses (Table 1).

Across all four major drivers, the ecological response was non-linear in 52% of all relationships identified in the existing literature (ranged from 48% to 53% among drivers, Figure 3). However, excluding the studies with the least robust statistics led to a higher estimate of non-linear responses in all four driver groups (Figure 3). The subset of robust papers comprise ~70% of the original papers (55 studies, 592 relationships) and are shown in the Table S1 in Supplement 1. Adding this filter had greatest effect on results for the trophodynamic driver category (increased from 51% to 61% non-linear), followed by climate (53% to 59%), pollution (48% to 53%), and exploitation (51% to 53%; Figure 3).

The published and derived estimates of degree of non-linearity indicate that when driver-response relationships are non-linear they are most often strongly non-linear. For example, more than 90% of all non-linear relationships associated with pollution and exploitation had EDF >2. Similarly, 70% of all non-linear relationships with climate as the driver had EDF >2. For the trophodynamic driver, approximately 50% of the non-linear relationships were highly non-linear and the remainder were weakly non-linear, i.e. $1 < EDF \leq 2$, or no estimate of EDF was available

(Figure 3). Further, the higher prevalence of non-linear relationships in the subset of robust papers compared to all papers is mainly driven by an increase in the percentage of highly non-linear relationships. This was found for all four drivers (Figure 3). Thus, papers in which authors investigated the potential for both linear and non-linear responses not only detected a higher amount of non-linear driver-response relationships, but also a greater percentage of strongly non-linear responses.

Closer inspection of the driver-response relationships published in the set of robust papers indicates that the response of ecological components to individual metrics of major drivers (with sample sizes >5) is quite variable (Table 2, based on 43 papers and 443 relationships). Non-linearity was most common for response relationships involving species biomass / abundance and species growth / body condition while the other two response metrics, area occupied / distribution and recruitment overwhelming showed linear relationships to the drivers. All four ecological components exhibited non-linear responses to large-scale climate patterns (Table 2). We also found greater evidence for non-linearity than linearity in some other metric-response relationships for which bycatch, reproduction, landings and community composition were the response variables (Appendix C, Table C2). Many combinations of the driver metrics and ecological components lacked sufficient replication in the literature to draw conclusions about their trends.

Variation in degree of non-linearity

Sorting studies by EDF using regression tree analysis suggested that the type of ecological response and driver group were the two most important biological variables explaining variation in degree of non-linearity. The analysis also revealed that older studies and

brief studies were associated with unusually high EDF. Specifically, a small number of studies that were published prior to year 1999 (mean EDF = 6.31; 3 papers and 22 relationships) or with duration less than one year (mean EDF = 6.03, 2 papers and 11 relationship) clustered together (Appendix C, Fig. C1; R^2 =0.58, cross validation error = 0.46, n=416, cost-complexity pruning parameter = 0.03). To remove the influence of these extreme values on model outcome, we re-fit the tree model to a reduced data set that did not include these relationships. The best fit model of the reduced data showed that the strength of the splits, and thus variable importance, were strongest for ecological response and driver followed by study sample size and trophic level of the response (R^2 = 0.45, cross validation error = 0.32, n=381, cost-complexity pruning parameter = 0.05; Figure 4). Those relationships in which species biomass / abundance or growth / body condition were the ecological responses had a higher mean estimate of EDF than area occupied / distribution and recruitment relationships. The mean EDF was also higher for species biomass / abundance and growth / body condition relationships in which pollution was the driver than for relationships in which climate, fishing and trophodynamic were drivers. These findings correspond with the patterns gleaned from Table 2. Study sample size was also an important variable explaining variation in degree of non-linearity when pollution was the driver. For the remaining drivers, trophic level of the response variable mattered most (Figure 4).

Shapes of relationships

The four major ecological responses for which there were adequate sample sizes showed evidence of threshold relationships between single drivers and responses (Figure 2). The strongest evidence was found in relationships in which species biomass / abundance was the ecological component. The papers included in our study indicate that all four drivers elicited

threshold responses in species biomass / abundance, although this was most often found in those relationships in which pollution was the driver, and specifically, oxygen was the metric (Figure 2). The following shapes were also identified through visual inspection and were equally evident in relationships between the four drivers and species biomass / abundance: single maximum and minimum; spline; and saturating / decreasing / increasing. It is possible that these relationships also exhibit inflection points and threshold responses, however there are few studies (8 out of 75) in our database in which authors attempted to quantify threshold values for driver-response relationships through formal analysis (e.g., changepoint analysis, derivatives, threshold GAMs). For the remaining ecological responses (growth / body condition, area occupied / distribution, recruitment), single maximum and minimum and spline shapes were most evident in relationships with climate drivers while saturating / decreasing / increasing shapes were more often observed in relationships that included trophodynamic drivers, particularly density dependence (Appendix C, Table C3). Sigmoid curves were only noted once and were the least common shape assigned to driver-response relationships, however sigmoid and spline shapes were the most challenging to distinguish based on visual inspection alone.

Discussion

We provide a quantitative assessment of the prevalence, strength and shapes of non-linear relationships in pelagic marine ecosystems. Our synthesis of driver-response relationships from existing literature indicates that: 1) non-linear driver-response relationships are common and are likely underestimated in the peer-reviewed literature, 2) strong non-linearities are most common in relationships in which species biomass, abundance, growth and body condition are the ecological responses, and/or when pollution is the driver and 3) increased use of robust methods

to detect nonlinearities and threshold responses will likely uncover further evidence for threshold driver-response relationships. Together, our findings suggest that it is safer to assume that driver-response relationships are non-linear, rather than linear, and that certain driver-response relationships in pelagic marine ecosystems have the potential to exhibit threshold response.

Understanding when linear and non-linear responses occur can advance our ability to anticipate future conditions and better inform management strategies. Linear relationships indicate that incremental increases in a driver provoke incremental changes in ecosystem components, and thus, related management decisions are determined simply by which particular ecological outcome a decision-maker prefers. On the contrary, when relationships are non-linear, incremental increases in driver levels can cause unexpected and large changes (positive and negative) in ecological components, allowing for more data-driven target setting by managers, and limiting options for fine-tuning to a desired state. Understanding such non-linear changes critically informs what management actions can maximize ecological, social or economic benefits (Kelly et al. 2014a, b). Despite the large amount of research dedicated to understanding driver-response relationships, we found it difficult to identify general patterns in the shapes of these relationships and predict non-linear changes, even within the same or similar ecosystems. For instance, a multi-year study on the influence of environmental conditions on North Sea herring abundance and distribution demonstrates that driver-response relationships in a single study system can vary substantially among years (Maravelais 1997). Another study from the eastern Bering Sea indicates that the response of jellyfish to environmental variables is quite variable between neighboring sub-regions (Brodeur et al. 2008). Nevertheless, a consistent finding of our study is that non-linearities are more common than linear responses among all four drivers in the most robust studies and in the most well-studied driver-response relationships (i.e.,

where species biomass, abundance, growth and condition are the ecological responses). We suggest that it is more prudent to use default assumptions of non-linear responses rather than linear responses in fisheries and ecosystem models and management to more accurately guide target-setting through identifying and avoiding, if possible, undesirable non-linear ecosystem shifts. While many of the non-linear relationships were driven by climate and may be outside the control of managers (though are still critically important), there are also non-linear relationships with drivers that managers can influence (e.g., pollution).

Many of the non-linear relationships in the literature were identified as strongly non-linear, indicating that they are potentially prone to inflection points and threshold dynamics. Using regression trees, we found that species biomass, abundance, growth and condition showed the most evidence of strongly non-linear responses to all four drivers in our study. On average, the strongest non-linearities were between these ecological responses and pollution drivers, primarily oxygen. This result is largely attributed to a three-year study that examined the influence of dissolved oxygen on the catch-per-unit-effort (proxy for abundance) of 10 demersal species in the northern Gulf of Mexico (Craig 2012). Threshold models offered the best fit when each species was evaluated independently in each year of the study. Avoidance thresholds are to be expected given the lethal and sub-lethal behavioral and physiological thresholds of dissolved oxygen concentrations on marine species. The effect of oxygen on the biomass of small pelagic fishes in coastal systems, i.e., sardines and anchovies, has been shown to be highly non-linear as well (Bertrand et al. 2011).

For the remaining driver groups (climate, fishing and trophodynamics), the following metrics had the strongest non-linear effects on species biomass and abundance: temperature, large-scale climate patterns, salinity, predator or prey biomass, and fishing effort. Relationships

with climate metrics are likely defined by strong non-linearities, as species respond to oscillatory or cyclical patterns of the environment. Increasing fishing effort and changes in trophic control are also known to have strong non-linear impacts on marine population dynamics, e.g. fishery collapses and trophic cascades (Hutching and Reynolds 2004, Dulvy et al. 2004, Daskalov et al. 2007, Anderson et al. 2008). For example, in a study from the Baltic Sea, where the top predator cod collapsed due to overfishing, the authors' showed that the planktivore sprat regulates zooplankton dynamics once sprat abundance reaches a threshold level. When sprat abundance is below the threshold, zooplankton is regulated by hydrological conditions rather than predation pressure (Casini et al. 2009). In addition, we found that the influence of temperature, winds, salinity, predator or prey biomass and density dependence on species growth and condition were strongly non-linear. This was expected given the extensive knowledge about how environmental conditions influence physiology of marine organisms and how competition for food and space regulate population growth and body condition. For example, another study from the Baltic Sea found that sprat also regulates herring growth once sprat abundance surpasses a certain threshold (Casini et al. 2010) due to an increase in inter-specific competition. Sprat is the main food competitor of herring. Below the threshold level of sprat abundance, the main driver of herring growth variation is salinity, which acts on the abundance of herring's main copepod prey (Casini et al. 2010). Further, a study from the Bering Sea identified a threshold value of predator population abundance that once crossed caused a large change in the predator's spatial distribution (Ciannelli et al 2012). At high abundance levels, geographical expansion can equalize habitat suitability and individuals' fitness over a species spatial domain (Fretwell and Lucas 1970). The authors' findings corroborate previous work that points out that species distributions can undergo abrupt shifts in response to small changes in a driver (Turner 2005).

Functional level (i.e. individual, species / stock, community / ecosystem) did not explain any of the variation in degree of non-linearity in the regression trees. One may expect the ecological responses within these functional levels to behave differently because they integrate across different spatial and temporal scales. We found that the percentages of non-linear and linear relationships among three functional levels were similar; however, sample sizes of the relationships grouped by functional levels varied greatly (Appendix C, Table C4), which might mask potential differences. Surprisingly, however, we found that trophic level influenced the strength of non-linear responses. As lower trophic levels are thought to be more sensitive to system perturbations than higher trophic levels (e.g., Benson and Trites 2002), we expected to see stronger non-linearities associated with species lower in the food chain. However, our regression tree model showed that on average the strongest non-linearities were associated with the highest trophic levels (TL = 4), in those relationships in which species biomass, abundance, growth, and condition were the ecological responses and climate, fishing and trophodynamics were the drivers. This finding should be interpreted with caution because it may be largely explained by study methodology. For example, two studies accounted for most of the driver-response relationships associated with the highest trophic levels and the GAMs used in these studies appear to over-fit the data, i.e., the response curves do not look biologically plausible. When we removed each of the two studies from the analysis trophic level was no longer an explanatory variable. More studies on driver-response relationships of top predators may help determine if our finding is an artifact of study methodology, although in general interpreting trophic level patterns is complex (see Shannon et al. 2014); for example, there is uncertainty in allocating species to a single trophic level, and exploitation history may influence species' responses to stressors. A main criticism of GAMs is the tendency of model over-fitting, and as a

result it is becoming standard practice for authors to restrict the flexibility of the response curves to ensure that model results are indeed plausible. Until the standard becomes more widespread inconsistencies in study methodology will influence comparisons across studies. We note, however, that in published studies where over-fitting may have resulted in high EDFs (e.g., > 5) it is likely that response curves would still have EDFs > 2 and be considered strongly non-linear even if the authors had constrained the flexibility of the model.

Identifying shapes of highly non-linear relationships can reveal driver (stressor) levels where abrupt changes in ecological components are prone to occur. Our characterization of the shapes of non-linearities suggests the potential for single or multiple inflection points and thresholds in several single driver-response relationships, which has important implications for managing marine systems (see Selkoe et al. 2015). For instance, the many non-linear response shapes supports the need for greater precaution in setting management targets, as in many cases changes along some regions of the driver levels could have greater effects on ecological components than changes in other regions. Knowledge of where those regions exist can help define a precautionary buffer for setting management targets that can reduce risk of adverse ecological outcomes (Selkoe et al. 2015). Our study documents those relationships where scientists and managers might look for non-linearity and where further investigation of response shapes and refinement of thresholds estimates are warranted. Without access to original datasets and without knowing if a study captures a wide range of driver levels (including e.g., anomalies), it is difficult to get a complete picture of the functional form of the relationships and where along the scale of driver levels threshold regions may occur. Laboratory and mesocosm experiments may be helpful in this regard to identify thresholds across wider range of driver levels, but often cannot capture the complexity of ecosystems and multi-driver contexts.

More empirical studies aimed at quantifying threshold values in driver-response relationships will strengthen their utility for precautionary target-setting (i.e., identifying where a threshold change in the ecological response is undesirable and setting management targets to limit the associated driver). Until recently threshold detection methods (e.g., changepoint analysis and STARS) have mostly been applied to identifying shifts in ecological time-series data rather than driver-response relationships. However, as more powerful, flexible and accessible methods to detect non-linearities and thresholds are developed, we are seeing a growing number of detectable thresholds in driver-response relationships that could help inform target-setting (e.g., McClanahan et al. 2011, Cury et al. 2011, Large et al. 2013, 2015a,b, Karr et al. 2015, Gove et al. 2015). With increasing use of these robust statistical methods, we expect there to be accumulating evidence of strong non-linear relationships and threshold dynamics in pelagic ecosystems and other marine systems as well. An important avenue for future work will be to apply nonlinear methods to a suite of original datasets to further investigate whether common shapes and threshold levels in certain driver-response relationships can be detected. Thresholds common across analogous systems could be used to develop robust sets of reference points across decision-making contexts. In addition, given the temporary nature of many empirical relationships, more studies should test the robustness of the driver-response relationships and evaluate how interacting variables influence the shape of the relationships and where thresholds occur.

We encountered multiple challenges to gleaning patterns in the strengths and shapes of non-linear driver-response relationships through a synthesis of existing literature. First, while there is a large literature on a wide diversity of driver-response relationships, there are still considerable gaps in the literature and many relationships are understudied. For example, only 4

of the 18 ecological responses in our database had adequate data to be included in formal analyses, which precluded us from making generalizations across a broader set of drivers and ecological responses. Second, it is difficult to distinguish between linear and weakly non-linear relationships without large sample sizes and thus non-linear relationships may go unreported if this is not considered by authors when developing study designs. Third, similar to other literature synthesis studies on driver (stressor)-response relationships (e.g., Ban et al. 2013), the methods and statistical techniques used to examine these relationships varied substantially among studies, making it difficult to identify common metrics for making comparisons among them. To mitigate this challenge, we limited our pool of published papers to those in which authors used regression-based techniques to decipher the strength and shapes of relationships. However, authors often did not formally test whether the relationships were linear versus non-linear, and therefore the number of robust papers that we could use in our analyses was even more limited. If more authors had made their data accessible, we could have overcome some of these challenges by applying consistent, analytical methods to original data sets to quantify strengths, shapes and thresholds of driver-response relationships. At the very least, greater use of model selection to determine whether linear or non-linear functions fit data best and consistent reporting of standard summary statistics (e.g., EDF, confidence intervals, standard errors) for all models in a confidence set could improve our ability to characterize driver-response relationships in marine ecosystems.

Despite these challenges of elucidating the driver effects in complex pelagic systems, this study demonstrates the need for more robust, non-linear analyses to characterize the nature of driver-response relationships and threshold dynamics. Improved understanding of non-linearities in single driver-response relationships can inform how managers set management targets to

achieve desired ecological outcomes and maintain ecosystem services. Moreover, non-linear analyses can help characterize how multiple drivers interact and inform decision criteria to better manage for these interactions. Ecological surprises - including non-linear changes - often result from synergistic or interactive effects of multiple drivers. Where and when one or more drivers cause a non-linear ecosystem response in isolation, their combined effects with other drivers will almost certainly also be non-linear, with varied consequences for ecosystems and the societies that depend on them. To provide a broad overview of the prevalence and strength of nonlinearities we needed to use published studies and a uni-variate approach was most practical for synthesizing the results of the studies. Multi-variate relationships and synergistic/antagonistic effects would be better assessed through analysis of original data sets from data-rich systems. One could then systematically analyze the influence of different variables on stressor-response relationships. Elucidating critical points or thresholds in ecological responses to multiple stressors is a promising area of research for managing marine resources (e.g., Large et al. 2015b), as is the application of non-linear dynamic models to characterize non-linearities, identify causal drivers, and forecast ecosystem conditions (e.g., Hsieh et al. 2005, Sugihara et al. 2012, Glaser et al. 2014, Ye et al. 2015). Considering non-linearities in management decisions, given their prevalence in the environment, is critical for successfully mitigating and responding and adapting to ecosystem change.

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Ecological Archives

Appendix A: Supplementary information on Web of Knowledge search terms used to collect peer-reviewed publications on driver-response relationships in marine pelagic ecosystems.

Appendix B: Supplementary information on how Generalized Additive Models (GAMs) were fit to published model predictions to estimate effective degrees of freedom.

Appendix C: Supplementary results: sample size of each metric-response pair in the subset of statistically robust papers, percentages of non-linear and linear relationships between additional metrics of drivers and ecological responses, enumeration of additional shapes of highly non-linear driver-response relationships, percentages of non-linear and linear relationships by major functional level, regression tree of the degree of non-linearity of major metric-response relationships, including extreme values.

Supplement 1: List of papers, study regions, drivers, stressors, metrics, ecological responses and estimated degree of non-linearity associated with each driver-response relationship included in the study.

Table 1. Broad categories of drivers, metrics of drivers, and ecological responses of the single driver-response relationships in peer-reviewed publications that met our selection criteria (see methods). The bold and italicized numbers indicate the number of relationships and publications for each driver, respectively. References for the publications are provided in the Supplement 1.

Drivers	Climate	Pollution	Exploitation	Trophodynamic
	341, 69	**109**, *10*	**68**, *10*	**210**, *49*
Metrics	Currents, Ice, Inflow, Large-scale climate patterns, Phenology, Precipitation, River flow rate, Salinity, Sea surface height, Temperature, Thermocline depth and strength, Turbulence, Upwelling, Winds	Nutrient loading, Oxygen, Total organic carbon, Water clarity	Fishing effort, Fishing mortality, Landings and catch	Density dependence, Feeding, Growth and body condition, Nutrients, Predator and prey biomass and abundance, Predator and prey occurrence, Prey quality, Primary production and productivity, Recruitment and year class strength, Reproduction
Ecological responses	Area occupied and distribution, Bycatch rates, Community composition and diversity, Consumption:Landings, Growth and body condition, Habitat composition, Landings and Landings composition (proxy for abundance), Nutricline depth, Oxygen levels, Phenology, Prey composition, Primary production and productivity, Recruitment, Reproduction, Species biomass and abundance, Species richness, Survival			

Table 2. The percentages of non-linear (NL) and linear (L) relationships between metrics of major drivers and ecological responses identified from the subset of robust papers. Only metric-response relationships with sample sizes (N) > 5 are shown. See Appendix A, Table A2 and Supplement 1 for full list of metric-responses. Bold numbers indicates metric-response relationships for which there was equal or greater evidence of non-linear than linear responses. Species biomass, N= 235; growth and condition, N = 67; area occupied, N = 99; recruitment N = 43; total N = 444.

		Ecological responses											
		Species biomass			Growth and condition			Area occupied			Recruitment		
Drivers	**Metrics**	% NL	% L	N	% NL	% L	N	% NL	% L	N	% NL	% L	N
Climate	Large-scale climate patterns	**67**	**33**	**18**	-	-	-	**55**	**45**	**11**	**86**	**14**	**7**
	Salinity	**100**	**0**	**10**	**83**	**17**	**6**	21	79	19	-	-	-
	Temperature	**73**	**27**	**53**	**63**	**38**	**16**	42	58	31	43	57	28
	Winds and upwelling	**63**	**38**	**8**	**64**	**36**	**11**	-	-	-	-	-	-
Tropho-dynamic	Density dependence	**71**	**29**	**7**	**60**	**40**	**15**	**50**	**50**	**8**	-	-	-
	Predator and prey biomass	**63**	**38**	**40**	**64**	**36**	**11**	-	-	-	38	63	8
	Recruitment	29	71	7	-	-	-	-	-	-	-	-	-
	Nutrients	-	-	-	**50**	**50**	**8**	-	-	-	-	-	-
Pollution	Water clarity	22	78	9	-	-	-	-	-	-	-	-	-
	Oxygen	**100**	**0**	**41**	-	-	-	0	100	30	-	-	-
Fishing	Fishing effort, landings and catch	**50**	**50**	**42**	-	-	-	-	-	-	-	-	-

Figure legends

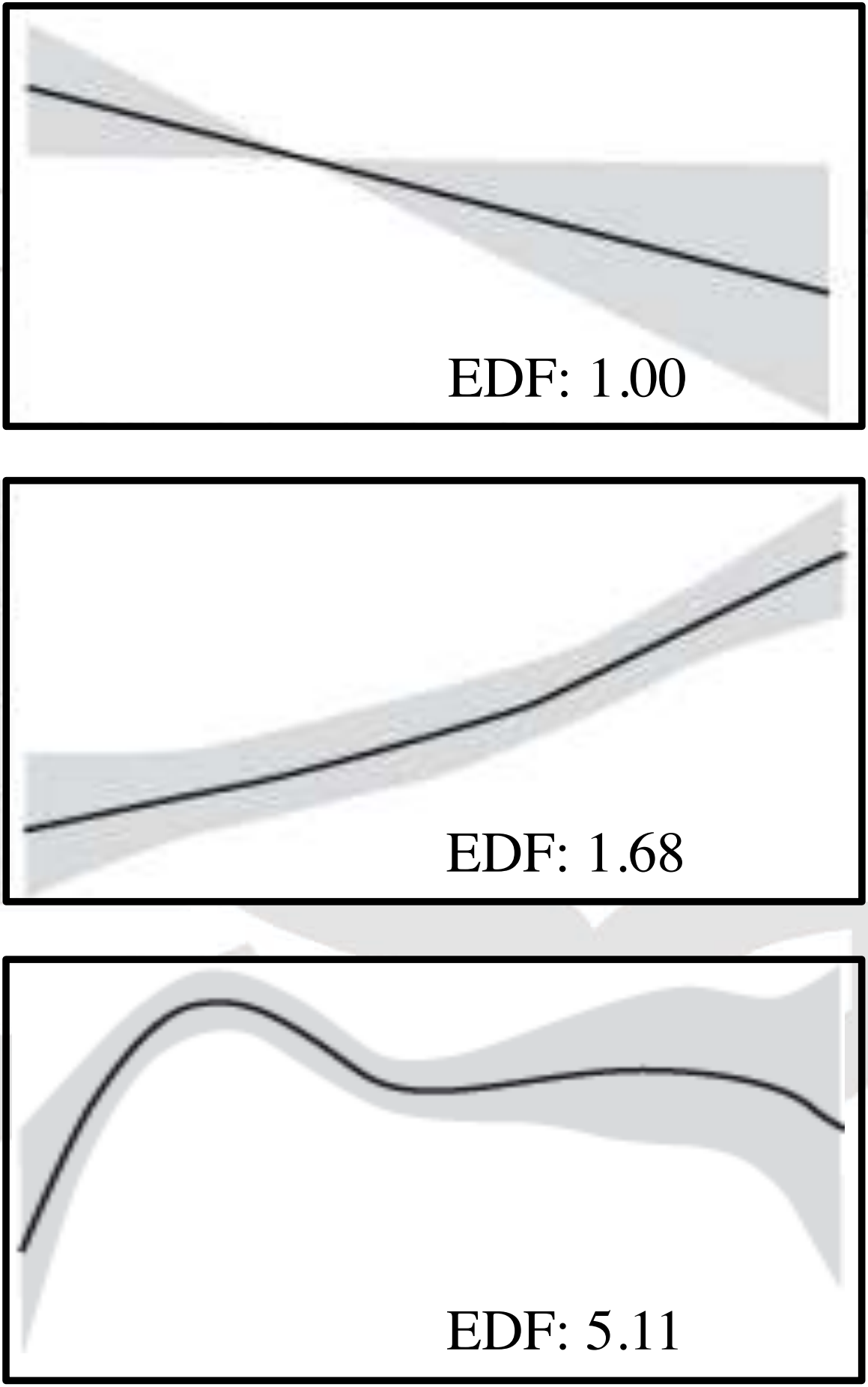
Figure 1. The effective degrees of freedom (EDF) estimated from Generalized Additive Models were used as a proxy for the degree of non-linearity in stressor-response relationships. An EDF of 1 is equivalent to a linear relationship (A), an EDF > 1 and ≤ 2 is a weakly non-linear relationship (B) and an EDF > 2 indicates a highly non-linear relationship (C) (Zuur et al. 2009). Highly non-linear relationships are those that are most likely to have inflection points and exhibit threshold responses.

Figure 2. Enumeration of the shapes of highly non-linear driver-response relationships determined through expert consensus-based visual inspection of model fitted curves. The categories of shapes include: single maximum or minimum and hump-shaped; splines; sigmoid, saturating (sat), decreasing (dec), or increasing; and threshold (i.e. threshold and piecewise models best fit the data). NC = no consensus. Total sample size = 121.

Figure 3. The percentages of relationships that are linear (black), weakly non-linear (light grey), highly non-linear (dark grey), and non-linear to an unknown degree (lightest grey) for the major driver types (top panel; climate, n=341; exploitation, n=68; trophodynamic, n=210; and pollution, n=109, total n=728) and for a subset of studies with robust statistical design (bottom panel: climate, n=294; exploitation, n=66; trophodynamic, n=138; pollution, n=94, total n=592). Unknown non-linearity represents cases where either the authors did not publish the EDF or there were no data available to derive an estimate of EDF.

Figure 4. Regression tree of the mean response of the degree of non-linearity (i.e. EDF) of major metric response relationships (with sample sizes > 5, see Table 2) in relation to suite of explanatory variables. Bold and italicized font indicate mean estimate of EDF and sample

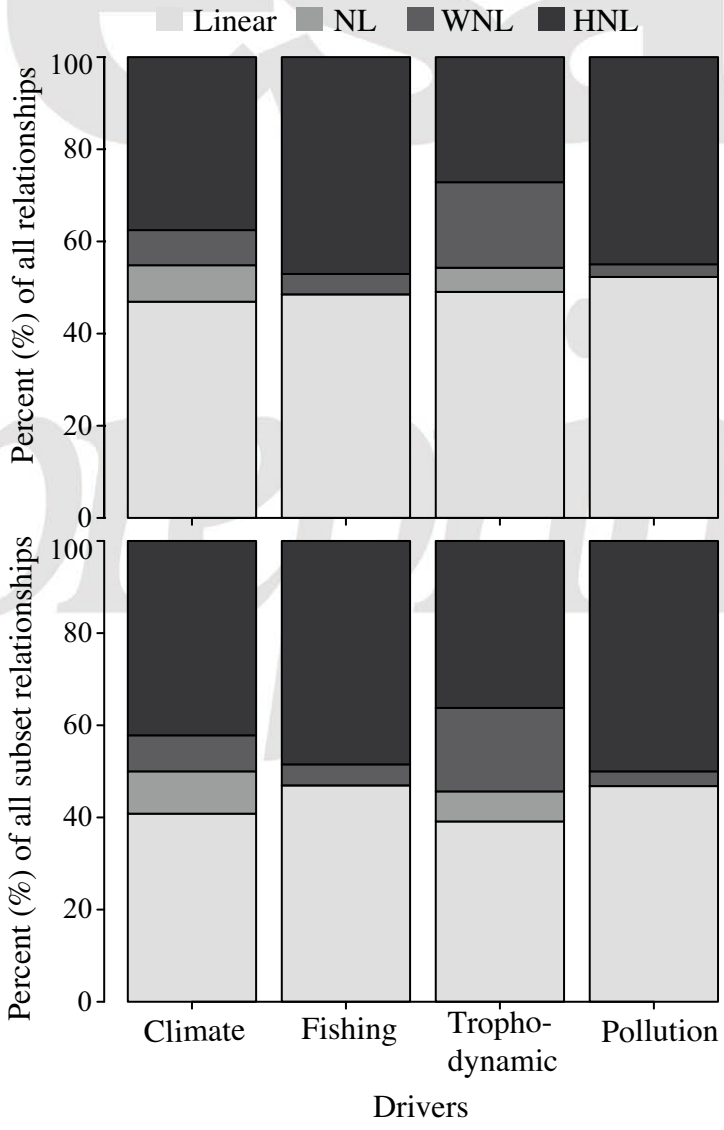
sizes, respectively. The cases to the left of the splits have lower mean EDF than those to the right of the splits. The strengths of the splits, and thus variable importance, are represented by their vertical lengths. $R^2 = 0.45$, cross validation error = 0.32, n=381, cost-complexity pruning parameter = 0.051

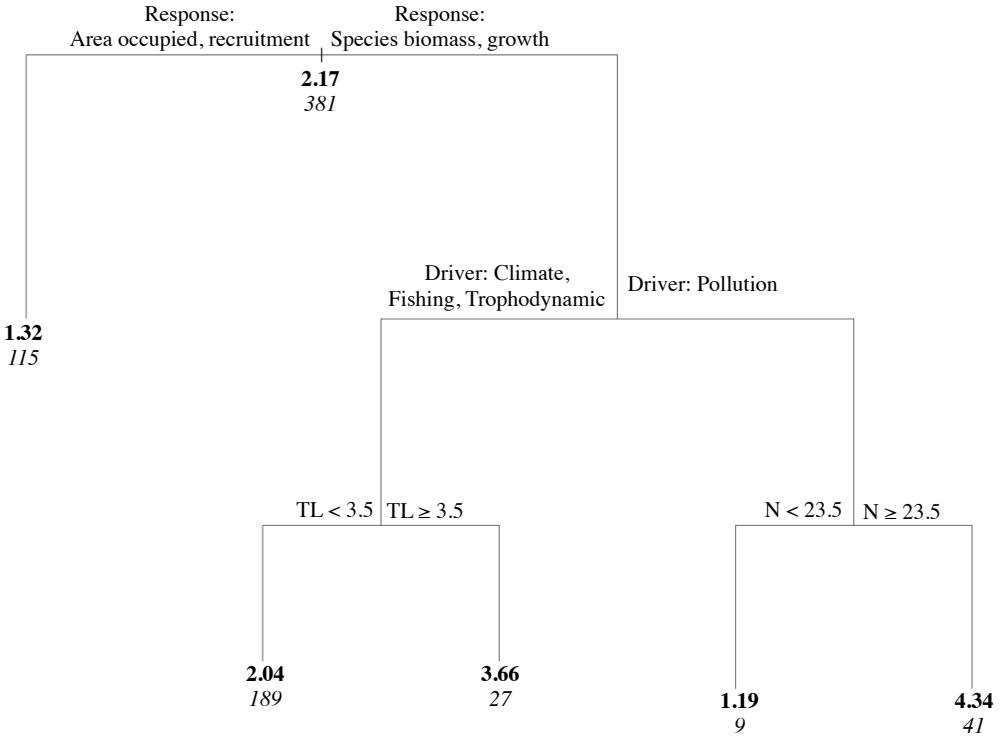

EDF: 1.00
EDF: 1.68
EDF: 5.11
Response
Stressor

Ecological response

Species biomass and abundance

Drivers	Metrics	Single	Spline	Sigmoid	Sat/dec	Threshold	NC
Climate	Climate patterns	-	3	-	1	2	-
	Salinity	2	-	-	3	-	5
	Temperature	7	7	1	7	3	11
	Winds	-	1	-	1	-	1
Tropho-dynamic	Density dependence	-	-	-	1	-	1
	Predator and prey biomass	2	2	-	1	11	1
	Recruitment	-	-	-	-	1	-
	Nutrients	-	-	-	-	-	-
Pollution	Oxygen	4	5	-	2	30	-
Fishing	Fishing effort and landings	1	-	-	3	1	-
	Total	16	18	1	19	48	19




Response:
Area occupied, recruitment
Response:
Species biomass, growth
2.17
381
1.32
115
Driver: Climate,
Fishing, Trophodynamic
Driver: Pollution
TL < 3.5
TL ≥ 3.5
N < 23.5
N ≥ 23.5
2.04
189
3.66
27
1.19
9
4.34
41