



Original Articles

Quantifying ecosystem responses to environmental and human pressures in the marine ecosystem off the west coast of Vancouver Island

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ABSTRACT

One necessity of ecosystem based management is an understanding of the shape and functional forms of ecosystem responses to environmental and human pressures. Both nonlinear and linear relationships may provide leading indicators of ecosystem change and inform reference points for ecosystem approaches to management. The objectives of this study were to 1) determine functional forms of pressure-response relationships, 2) identify non-linear relationships, and 3) quantify potentially relevant management thresholds for the west coast of Vancouver Island marine ecosystem in British Columbia, Canada. To do this, a multi-model approach was applied to mechanistically linked indicators of pressures and responses. Both single pressure-response and multivariate relationships were examined. Results indicate that 1) nonlinear and linear relationships were not prevalent with the percentage of occurrence (6–12%) similar to other regions, 2) ecological responses (both linear and nonlinear) were more commonly associated with environmental pressures than human pressures, 3) gradient forest analysis generally produced similar results as single pressure-response models and identified additional nonlinearities, 4) dynamic factor analyses (DFA) reduced the numerous pressure and response indicator to a few trends, however, the process may have resulted in a loss of information, and 5) possibly due to this loss of information, gradient forest and single pressure-response analyses on DFA trends produced different results. Quantifying how pressures affect ecosystem components can provide advanced knowledge about changes in ecosystem productivity, structure, and function which can inform science advice and management strategies. Mechanistically linked pressure-response relationships should be explored further with multi-model ensembles to better inform ecosystem-based and climate-ready approaches to marine management.

1. Introduction

Ecosystem approaches to management require an understanding of how ecosystems respond to environmental and human pressures. Considerable research in marine systems has focused on characterizing pressure-response relationships (Litzow et al. 2013; Fay et al. 2013; Hunsicker et al. 2016), particularly to identify abrupt changes in ecosystem responses (Scheffer et al. 2001; Peterson and Schwing 2003; Collie et al. 2004; Folke et al. 2004; Perry and Masson 2013). There are documented examples of mechanistically-linked shifts in multiple ecosystem components (Daskalov et al., 2007) and synergistic and antagonistic effects of multiple pressures (Hughes 1994; Crain et al.

2008; Piggott et al. 2015). Nonlinear relationships have been recognized as potential drivers of, and used to identify thresholds for, such abrupt shifts in ecosystem responses (Hunsicker et al. 2016; Kelly et al. 2015). Thresholds may provide leading indicators of change and inform reference points for ecosystem approaches to management (Samhouri et al., 2010; Large et al. 2013; Samhouri et al. 2017; Satterthwaite et al. 2012; Fu et al., 2020). Detecting thresholds in variable or noisy ecosystem time series data however, is difficult (Hillebrand et al., 2020).

The prevalence of nonlinearities and thresholds in ecosystems varies among published studies. While some studies indicate that nonlinear pressure-response relationships are common or dominant in ecosystems (Scheffer et al. 2001; Hunsicker et al. 2016), other studies indicate they

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are not prevalent (Fu et al., 2020; Hillebrand et al. 2020) or that linear relationships dominate (Litzow and Hunsicker, 2016). Recent research indicates that detecting thresholds is not always possible, given the variance in time series (Capon et al. 2015; Hillebrand et al. 2020), the length or temporal resolution of the time series (Litzow and Hunsicker, 2016), or the range of values (Fu et al., 2020). As Dudney and Suding (2020) point out, however, it is important to understand and quantify functional shapes of pressure-response relationships (both linear and nonlinear) for an array of ecosystem components. This knowledge can thereby inform future research and potential ecosystem reference points.

Reference points in fisheries management have commonly been single-species based; however, ecosystem reference points are drawing more attention and beginning to be implemented (Dolan et al. 2016; Guo et al. 2019). Ecosystem-based approaches to management are promoted by various organizations (e.g., Canada's Oceans Strategy (DFO, 2002); and the U.S. National Oceanographic and Atmospheric Administration's Magnuson Stevens Fishery Conservation and Management Reauthorization Act). There has, therefore, been considerable research into identifying ecosystem indicators (e.g., Boldt et al. 2014; Bundy et al. 2017), assessing the state of marine ecosystems (Boldt et al. 2020), identifying regime shifts (Perry and Masson, 2013), and incorporating ecosystem considerations in fisheries and oceans management (e.g., DFO 2016). Identifying ecosystem reference points necessitates the identification and understanding of the functional shape of pressure-response relationships.

The objectives of this study were to 1) determine functional forms of pressure-response relationships, 2) identify non-linear relationships, and 3) quantify potentially relevant management thresholds for the west coast of Vancouver Island (WCVI) marine ecosystem in British Columbia (BC), Canada. To address these objectives, a Driver-Pressure-State-Impact-Response (DPSIR; Elliott 2002) approach was used to identify indicators for this region and mechanistic hypotheses were developed to link pressures to indicator responses (both directly and indirectly). Both single pressure-response relationships as well as multivariate relationships were examined. A multi-model inference framework (Samhoury et al., 2017) was applied to this region, with the goal to improve understanding of the WCVI and identify indicators of ecosystem change which could be used to inform an ecosystem-based approach to fisheries management.

2. Methods

2.1. Study area

The west coast of Vancouver Island (WCVI) is a highly productive upwelling area that supports some of British Columbia's (BC's) largest fisheries (Ianson et al., 2010) including fisheries for pelagic fish, such as, Pacific herring (*Clupea pallasii*), Pacific hake (*Merluccius productus*), Pacific salmon (*Oncorhynchus* spp.), and Pacific sardine (*Sardinops sagax*); groundfish fisheries for Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), lingcod (*Ophiodon elongatus*), Pacific halibut (*Hippoglossus stenolepis*), Pacific spiny dogfish (*Squalus acanthias*) and other flatfish and rockfish species; and trap/trawl fisheries for Pandalid shrimp (*Pandalus* spp.). The WCVI includes the northern extent of the California Current upwelling zone (Ware and McFarlane 1989; McFarlane and Beamish 1992; Beamish and Bouillon 1993) and experiences seasonal (spring-summer) upwelling (Ianson et al., 2010). The periods of transition between the upwelling and downwelling seasons occur in February-April and October-November (Ware and McFarlane, 1995). Annual variation in the timing, duration, and magnitude of the spring upwelling, along with El Niño and marine heat wave events, may produce varying degrees of match or mismatch between biological processes and environmental conditions (Mackas et al. 2001; Hourston and Thomson, 2019) which in turn impact other ecosystem components (phytoplankton, zooplankton, fish, and marine mammals). For example,

changes in zooplankton species composition in the northern California Current system, such as alternations of boreal, subarctic, and southern copepod species, occur with changes in circulation patterns and water temperatures. These copepod communities (boreal, subarctic, and southern) have different body sizes and fat content that can translate to different qualities of food available to predators (Mackas et al., 2001; Keister et al., 2011). As a consequence, zooplankton biomass anomalies are correlated with salmon marine survival, sablefish recruitment, herring growth, and sardine production (Mackas et al., 2007) and could cascade to higher trophic levels (e.g. marine mammals, the proportion of predatory fish, the trophic level of the community, etc.). Predation and competition are other biological processes that may play a role in the WCVI ecosystem for some species, such as Pacific herring (Schweigert et al., 2010; Godefroid et al., 2019). Warm years can result in increased hake abundance which negatively affects herring year class strength, since hake are predators of herring and also competitors for euphausiid prey (Mysak, 1986; Ware and McFarlane, 1986). Bottom-up processes, however appear to be important drivers in this ecosystem, since resident fish yield was found to be correlated with phytoplankton and zooplankton production in BC (Ware and Thomson, 2005).

2.2. Indicators

To select indicators for this study, we used methods typically applied in ecosystem assessments; however, a full ecosystem assessment was not the objective of this study. Assessing ecosystems requires defined and place-based ecosystem management goals and objectives (DFO, 2007; Boldt et al., 2014; Bundy et al., 2017), and consultation with First Nations and stakeholders to integrate ecological, social, economic, and governance perspectives (McLeod et al., 2005; Levin et al., 2014). To date, Fisheries and Oceans Canada has not developed ecosystem management goals for the WCVI. Bundy et al. (2017) faced a similar problem for the Scotian Shelf bioregion on Canada's Atlantic coast. They adopted the 'healthy ecosystems' goal from a nearby ecosystem and outlined ecosystem attributes for the Scotian Shelf bioregion, with fishing as the main pressure. We followed a similar approach and included environmental pressures to address attributes/objectives identified by Bundy et al. (2012) and that are relatively common among other efforts that have defined management objectives (e.g., Gislason et al. 2000; Jamieson et al. 2001; Zador 2013). These attributes include: 1) maintain structure and function, 2) maintain stability and resistance to perturbations, 3) conserve biodiversity, 4) maintain resource potential, and 5) incorporate/monitor effects of climate change and fisheries.

An Indicator Selection Guidance Framework (Bundy et al., 2017) for state of the ocean reporting, based on the DPSIR (Elliott, 2002) framework, was used to select indicators for analyses (Table 1). When deriving this initial set of indicators, consideration was given to including adequate spatial and temporal coverage (Doren et al. 2009; Birk et al., 2012), different levels of biological organization (Adams and Greeley, 2000; Elliott, 2011), key functional groups (Rombouts et al., 2013), and essential ecosystem characteristics, attributes, or processes (Harwell et al., 1999; Fulton et al., 2005). The set of selected indicators was consistent with core indicators identified by previous studies (Shin et al., 2010a; Shin et al., 2010b; Link et al., 2010; Lucey et al., 2012; Takahashi and Perry, 2019).

To select indicators, we started with the full list of indicators in Bundy et al. (2017) plus those indicators listed in Takahashi and Perry (2019). Indicators were qualitatively screened using published criteria (Rice and Rochet, 2005; Boldt et al., 2014; Bundy et al., 2017) and to align indicators with pressures or ecosystem attributes (theoretical basis, mechanism) (Table 1). Indicators were then screened for measurability (i.e., data availability for the study area) and to identify the longest consecutive time period for the majority of indicators.

Indicators of climate and physical environmental pressures include those core indicators recommended by Takahashi and Perry (2019), where data existed. Broad-scale climate indicators of sea surface

Table 1

Drivers, objectives, pressures (A), responses (states and impacts) (B), indicators, and sources for the west coast of Vancouver Island and broader basin-scale ecosystem time series. Those indicators in bold font were included in further analyses; other indicators were excluded because they were highly correlated ($r \geq 0.8$) either among pressure or among response indicators (see Table 2).

(A) Drivers and Pressures								
Component	Driver	Objective	Pressure	Pressure Indicator	Source			
Environment	Atmospheric pressure and greenhouse gas	Monitor effects of climate change	SST change	Pacific Decadal Oscillation (PDO_Annual)	a			
			Large-scale circulation	North Pacific Gyre Oscillation (NPGO)	b			
			SST change	Multivariate ENSO Index Version 2 (MEI_Annual)	c			
			SST change	Local sea surface temperature (SST_satellite)	d			
			Nutrient availability	Upwelling magnitude	e			
			Nutrient availability	Spring transition timing	e			
Human	Seafood demand	Monitor effects of fisheries	Fishery removals (landings)	Total landings (Tot_Landings)	f			
			Ecosystem function change	Trophic level of landings (TL_Landings)	g			
			Ecosystem function change	Intrinsic vulnerability index (IVI)	g			
			Ecosystem function change	Catch of foraging groups: benthivores, planktivores, zoopiscivores, piscivores	f			
			Ecosystem function change	Catch of habitat groups: demersals, pelagics	f			
			Ecosystem function change	Ratio of pelagics to demersals catch (C_Pel_Dem)	f			
			(B) Responses - States and Impacts					
			Component	Objective and Impacts	Response Indicator	Source		
Ecosystem	Maintain structure and function	Copepods southern biomass anomalies	h					
	Maintain structure and function	Copepods boreal biomass anomalies	h					
	Maintain structure and function	Copepods subarctic biomass anomalies	h					
	Maintain structure and function	Trophic level of surveyed species (TL_SurveyedComm)	i					
	Maintain structure and function	Steller sea lion abundance	j					
	Maintain structure and function	Mean length (Mean_Len)	g					
	Maintain stability and resistance to perturbations	Mean lifespan	g					
	Conserve biodiversity	Proportion predatory fish (Prop_PredFish)	i					
	Maintain resource potential	Biomass of surveyed species (Tot_B_Survey)	i					
	Maintain resource potential, structure, function	Survey biomass of foraging groups: benthivores, planktivores, zoopiscivores, piscivores	i					
Maintain resource potential, structure, function	Survey biomass of habitats groups: pelagics, demersals	i						
Maintain resource potential, structure, function	Ratio of pelagics to demersals survey biomass (B_Pel_Dem)	i						

Source:

- a. <http://research.jisao.washington.edu/pdo/PDO.latest.txt>; Mantua et al. 1997.
- b. Di Lorenzo et al. 2008.
- c. National Center for Atmospheric Research Staff (Eds). Last modified 20 Aug 2013. "The Climate Data Guide: Multivariate ENSO Index." Retrieved from <https://climatedataguide.ucar.edu/climate-data/multivariate-enso-index>.
- d. "https://www.ncdc.noaa.gov/oisst. Data.set Citation: Banzon et al. 2016, Reynolds et al. 2007.
- e. Hourston and Thomson 2019.
- f. Maria Surry, Shelee Hamilton, Leslie Barton, Mary Thiess (DFO).
- g. Caihong Fu (DFO).
- h. Moira Galbraith, Kelly Young, Ian Perry (DFO); Galbraith and Young (2018).
- i. Brenda Waddell, Ian Perry, small mesh multispecies survey (DFO).
- j. Olesiuk 2018.

temperature change included the Pacific Decadal Oscillation (PDO, annual; Mantua et al., 1997), multivariate ENSO Index (MEI, annual; <https://climatedataguide.ucar.edu/climate-data/multivariate-enso-index>), and the local sea surface temperature (SST) as measured by satellite for the WCVI area (<https://www.ncdc.noaa.gov/oisst>; Banzon et al., 2016; Reynolds et al., 2007) (Table 1). The North Pacific Gyre Oscillation (NPGO) was used as an indicator of large-scale circulation (Di Lorenzo et al., 2008) and the magnitude and timing of upwelling in spring were used as indicators of nutrient availability (Hourston and Thomson, 2019).

Indicators of human pressures (Table 1), such as fishery removals and ecosystem function change, were derived from commercial landings data available in BC for Fisheries and Oceans Canada (DFO) statistical areas 24/124, and 25/125 (Fig. 1). Human pressures can have direct and indirect (via trophic interactions) impacts on ecosystem responses (e.g., fish biomass, trophic level of the community, proportion of predatory fish; Fu et al., 2019; Fu et al., 2020). Human pressure indicators included total landings, trophic level of the landings, catch of foraging groups (benthivores, planktivores, zoopivores (defined as animals that consume

zooplankton, shrimp, and fish), and piscivores; based on Lucey et al. 2012), catch of habitat groups (pelagics, demersals, and the ratio of pelagics to demersals), and the intrinsic vulnerability index (IVI; Cheung et al., 2007). Release data (number or weight of fish released and not landed) from commercial fisheries were not consistently recorded prior to 1996, therefore, were excluded from analyses.

Indicators of fish community were derived from DFO's fishery-independent, multi-species, small mesh bottom trawl survey conducted in late April or May each year in an area off WCVI (statistical areas 124 and 125, matching the spatial domains for the commercial fishery data) since 1973. Indicators from these data included: total surveyed biomass, biomass of foraging groups (benthivores, planktivores, zoopivores, and piscivores; based on Lucey et al. 2012), biomass and ratio of habitat groups (pelagics, demersals, and the ratio of pelagic to demersal biomass; de Leiva Moreno et al., 2000, Coll et al., 2010, Fu et al., 2012), proportion of predatory fish, mean length, and mean lifespan (Table 1).

Zooplankton biomass and community composition data for this marine ecosystem were available from 1986 (Galbraith, and Young, 2018). Indicators included the biomass anomalies of southern, boreal,

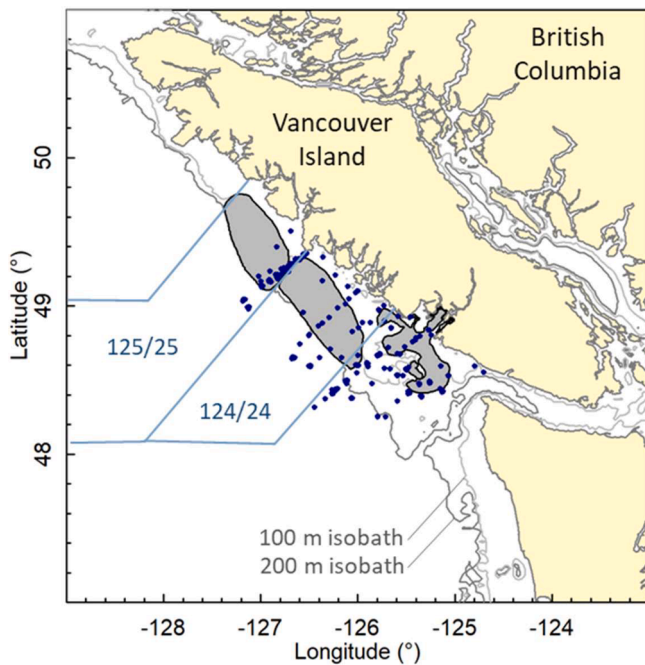


Fig. 1. Fisheries and Oceans Canada's multi-species, small mesh bottom trawl survey area (grey shaded areas), zooplankton stations (blue dots), and Pacific Management Areas 124/24 and 125/25 on the west coast of Vancouver Island, British Columbia, Canada. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and subarctic copepods (e.g., Mackas et al., 2001). Steller sea lion abundance data were available every 2 to 5 years during 1982–2013 (Olesiuk, 2018).

A final screening of indicators was conducted to reduce some redundancy. Within each of the three groups of indicators (environmental pressures, human pressures, ecosystem responses), indicators with correlations < 0.80 were selected to reduce the number of highly correlated indicators. Of the indicators with correlations ≥ 0.80 , we selected indicators that were more generalized. For example, within response indicators, if the biomass of one or more foraging groups were correlated with total biomass, only the indicator of total biomass was retained. Also, if an indicator was correlated with multiple indicators within the same group (environmental pressures, human pressures, or responses), it was excluded. For an ecosystem assessment, a lower correlation value might be considered; however, given that the objective of this study was to evaluate where nonlinear relationships may exist, we selected a relatively high correlation value to find a balance between inclusion of all potential relationships, and tractability and redundancy in the indicator list (some redundancy was acceptable for the analyses used in this study).

2.3. Analyses

2.3.1. Single pressure-response relationships

Single pressure-response relationships (environment and human drivers of ecosystem responses) were examined. Four models were developed for each pressure-response relationship: general additive mixed models (GAMM), linear models with autocorrelation (LMAC), general additive models (GAM), and linear models (LM). Model selection procedures were the same as outlined in Samhouri et al. (2017): a log-likelihood ratio test was used to compare GAMMs (with autocorrelated error structure) vs GAMs (with normal error structure); a value < 0.05 indicated temporal autocorrelation existed and model evaluation was carried out using GAMM vs LMAC. Akaike's Information Criterion (corrected for small sample sizes; AIC_c) and estimated degrees of

freedom (edf) were used to identify the best model between GAMMs and LMACs or between GAMs and linear models. As in Samhouri et al. (2017), supportive evidence for nonlinear models (vs. linear models) was based on these criteria: i) estimated degrees of freedom ≥ 2 (Zuur et al., 2009), ii) difference in AIC_c values ≥ 2 (Burnham and Anderson, 2002), and iii) for GAMs vs. linear models, a lower generalized cross validation score (GCV; Wood, 2004). The "mgcv" (Wood, 2000) library in R (R Core Team, 2017) was used to run the GAM models with thin plate splines and with knots constrained to 5 to reduce overfitting. Data were $\log_{10}(+1)$ -transformed if residuals appeared to deviate from a normal distribution (see Table A1). For presentation of indicator trends (Fig. 2), indicators were standardized (zero mean and unit variance); however, indicators used in single pressure-response models were as-listed in Table A1.

For nonlinear pressure-response relationships, thresholds were identified as the pressure value at which the sign of the second derivative changed (Fewster et al., 2000; Bestelmeyer et al., 2011; Large et al., 2013; Samhouri et al., 2017). The most likely value of the threshold (and 95% confidence interval (CI) of the smoothing function) was determined using bootstrapping of residuals (allowing for autocorrelation). In the resultant pressure values, the value at which the second derivative was most different from zero was defined as the inflection point (Samhouri et al. 2017). The magnitude of the response change due to crossing the threshold was estimated as in Samhouri et al. (2017), based on the proportional difference in response values above or below the threshold.

2.3.2. Gradient forest

Gradient forest analyses (Ellis et al., 2012) were used to identify thresholds in response variables along gradients of environment and human pressures (Large et al., 2015). Gradient forests are built upon random forests by integrating individual random forests over the different response variables to capture complex relationships between potentially correlated pressures and multiple response variables (Ellis et al., 2012). The overall importance of each pressure was determined using the R^2 value. Cumulative ecosystem responses to pressures were calculated and, as in Samhouri et al. (2017), for those pressures that increased the R^2 by ≥ 0.01 , thresholds were identified based on a range of pressure values. Analyses were conducted using the R package gradientForest (Ellis et al., 2012). One response indicator (Steller sea lion abundance) did not have a continuous time series so was excluded from gradient forest analysis. Where nonlinearities between individual pressures and responses were identified, shapes and thresholds were compared to the results of single pressure-response analyses where a non-linear relationship was also identified as the best-fit model.

2.3.3. Dynamic factor analysis

Multivariate Dynamic Factor Analyses (DFA; Zuur et al., 2003; Holmes et al., 2012) were used to identify common trends in (i) each of the three sets of indicators: environment pressures, human pressures, and ecosystem responses, with no covariates, (ii) ecosystem response DFA trend(s) with either the environment DFA trend(s) or the human DFA trend(s) as a covariate(s), and (iii) ecosystem response DFA trend(s) with both environment and human DFA trends as covariates.

Dynamic factor models were applied with these error covariance matrices: identity, diagonal and equal (time series have the same variance), equal variance and covariance, diagonal and unequal (each time series has a unique variance), and unconstrained (different variance and covariance). Initial conditions for all models were set with a minimum of 200 iterations and maximum of 100,000 iterations. AIC_c values were used to identify the best model, of those that converged. Dynamic factor models were applied using the R package MARSS (Holmes et al., 2012; Holmes et al., 2018).

Gradient forest analysis was used also to look for nonlinear relationships among DFA trends in the ecosystem (as response variables) along gradients of environment and human pressures (DFA trends of environment and human pressures). Single pressure-response models

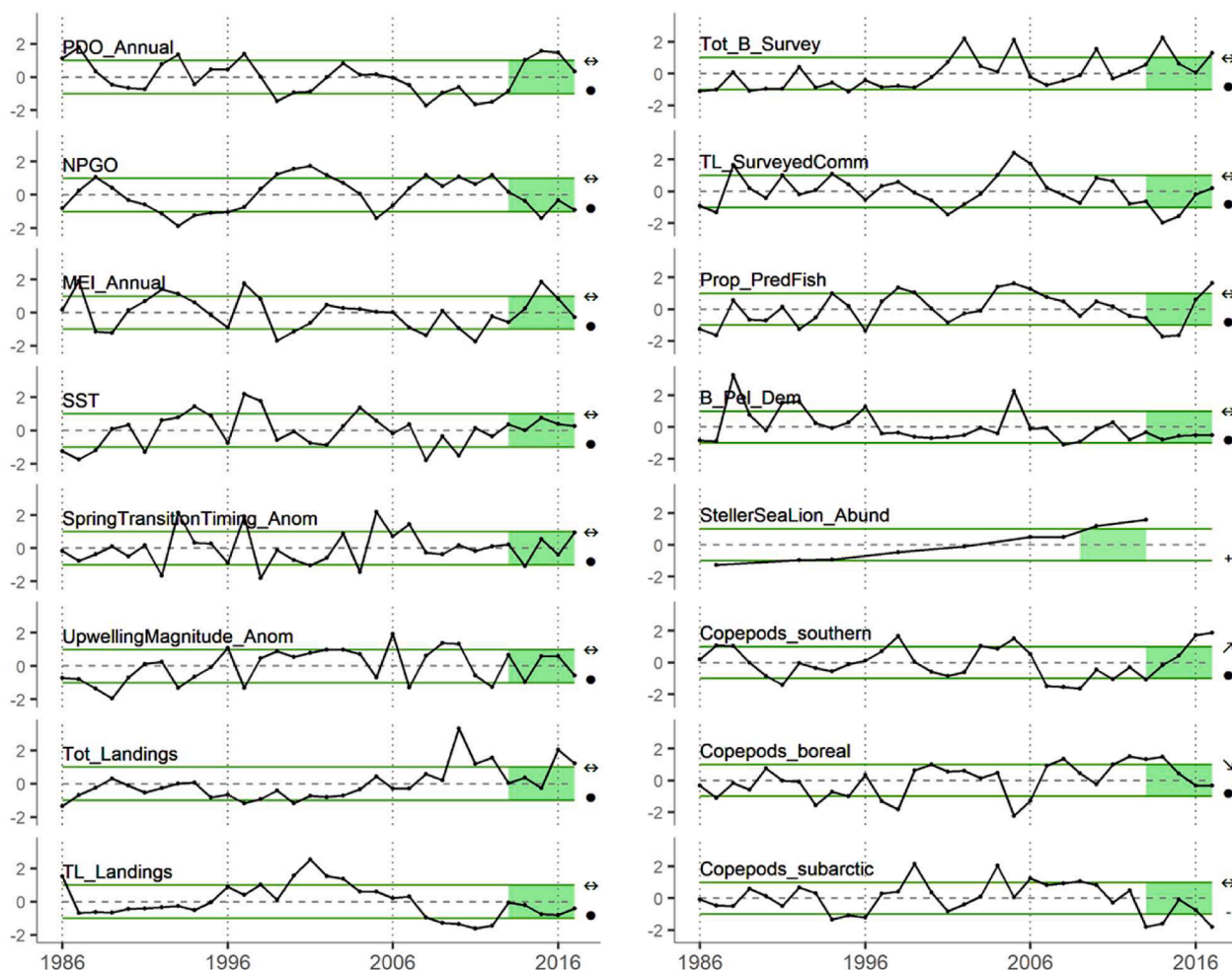


Fig. 2. Standardized time series of environment and human pressures (left) and ecosystem responses (right) included in analyses for the west coast of Vancouver Island, British Columbia, Canada, 1986–2017. Solid horizontal lines are +/- one standard deviation; the last five years of the times series are highlighted in green. Symbols to the right of graphs indicate trend (top) and status (bottom). Trend symbols indicate whether the trend in last five years was significantly increasing (upwards pointing arrow) or decreasing (downwards pointing arrow), or neither (horizontal arrow), where there are > 2 years of data available within the last five years. Status symbols indicate if the mean value for the last five years was greater than one standard deviation above (+) or below (-) the long-term mean or within the standard deviation of the long-term mean (filled circle). See Table 1 for acronym definitions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(GAMM, LMAC, GAM and linear models) were used to examine relationships between DFA trends (e.g., between pressure DFA trends and response DFA trends).

3. Results

3.1. Indicators

A list of indicators was identified for the west coast of Vancouver Island (WCVI) ecosystem, based on the selection criteria, with the most important being data availability (Table 1). The longest common time period for which data were available for this region was 1986 – 2017. Of these indicators, several were highly correlated ($r \geq 0.8$; Table 2); therefore, only one indicator was selected from highly correlated groups of indicators. For example, within the group of ecosystem response indicators, the survey biomass of both demersal and pelagic habitat groups were highly correlated with total survey biomass. In addition, the biomass of benthivores (the primary survey target species) was highly correlated with total survey biomass. The biomass of habitat and foraging groups were, therefore, excluded from further analyses. Similarly, both the mean length of the surveyed fish and mean lifespan of surveyed fish were highly correlated with the trophic level of the

Table 2

Pairwise correlations between indicators listed in Table 1, where $r \geq 0.8$. Only those indicators in bold font (here and in Table 1) were included in further analyses.

Indicator	Indicator	r
Mean_lifespan	Mean_Len	0.935
TL_SurveyedComm	Mean_Len	0.961
TL_SurveyedComm	Mean_lifespan	0.886
B_Benthivore	Tot_B_Survey	0.834
B_Demersal	Tot_B_Survey	0.896
B_Demersal	B_Benthivore	0.977
B_Pelagic	Tot_B_Survey	0.809
B_Pelagic	B_Piscivore	0.914
C_Zoopiscivore	Tot_Landings	0.885
C_Pelagic	Tot_Landings	0.987
C_Pelagic	C_Zoopiscivore	0.864
C_Pel_Dem	Tot_Landings	0.921
IVI	TL_Landings	0.894

surveyed community, so were excluded from further analyses (Table 2). Within the group of human pressure indicators, the catches of some habitat and foraging groups were correlated with total landings, so only total landings were considered further. The Intrinsic Vulnerability Index

(IVI) was highly correlated with the trophic level of landings, so only trophic level of landings was included (Table 2).

Ecosystem indicators for the WCVI show varying trends during 1986–2017 (Fig. 2). The most notable trends were increases in small mesh multispecies survey biomass, total landings, and Steller sea lion abundances, as well as declines in subarctic copepods since the 1990s, and declines in the trophic level of the landings from the early 2000s to approximately 2012 (Fig. 2).

3.2. Single pressure-response relationships

Best fit models were examined for 64 single pressure-response relationships (Table 3 and Appendix Table A1). Of these, model fits were significant ($p < 0.05$) with an $R^2 > 0.2$ for five linear (8%) and four nonlinear GAM (6%) models. All significant (and $R^2 > 0.2$) linear and nonlinear relationships were between ecosystem response indicators and environmental pressures. For example, boreal copepod biomass anomalies were linearly related to two environmental pressures (Pacific Decadal Oscillation (PDO; negative linear relationship) and North Pacific Gyre Oscillation (NPGO; positive linear relationship)). Also Steller sea lion abundance was negatively linearly related to the PDO and multivariate ENSO Index (MEI), and positively linearly upwelling magnitude. There were no significant relationships between ecosystem responses and human pressures.

Three significant nonlinear relationships included PDO as the pressure, with the proportion of predatory fish, southern copepod biomass anomalies, and the trophic level of the surveyed community as response variables (Fig. 3 and Table 3). The fourth nonlinear relationship was between boreal copepod biomass anomalies and spring transition timing (Fig. 3). The most likely thresholds identified for the proportion of predatory fish and the trophic level of the surveyed community occurred at the same value of the PDO (0.27), with similar 95% confidence intervals (-0.10–0.62 and -0.12–0.73, respectively), which was expected, since the two response variables are correlated ($r = 0.78$). The threshold for southern copepods had a similar PDO value of 0.37 (95% CI = 0.10–0.77). Additional thresholds were identified for the proportion of predatory fish (PDO = 1.52) and southern copepod biomass anomalies (PDO = -0.57). Generally, at values greater than approximately 0.27, both the proportion of predatory fish and the trophic level of the surveyed community decreased by about 12% and 1%, respectively. In contrast, at PDO values greater than -0.57, mean southern copepod biomass anomalies increased > 150% up to PDO values of 0.37, above which southern copepod biomass anomalies leveled off (increased by 3%). A threshold spring transition timing value of -0.98 (approximately the 73rd day of the year or March 14) was identified for boreal copepods, above which mean boreal copepod biomass anomalies decreased by 277% with later spring transition timing (Fig. 3 and Table 3).

Table 3

All best-fit single pressure-response models that were significant ($p < 0.05$) and had an $R^2 > 0.2$ (see Appendix Table A1 for all model results and Table 1 for acronyms), with R^2 , p-values, most likely threshold values (and ranges of values), and the mean magnitude of the response (percent).

Model	Response	Pressure	Linear slope	R^2	p-value	Thresholds (range)	Mean magnitude (%)
Linear	log(StellerSeaLion_Abund + 1)	log(MEI_Annual + 1)	-0.519	0.536	0.015		
Linear	StellerSeaLion_Abund	PDO_Annual	-2029	0.414	0.036		
Linear	log(StellerSeaLion_Abund + 1)	log(UpwellingMagnitude_Anom + 1)	0.496	0.598	0.009		
Linear	Copepods_boreal	NPGO	0.116	0.251	0.002		
Linear	Copepods_boreal	PDO_Annual	-0.138	0.228	0.003		
GAM	Copepods_boreal	SpringTransitionTiming_Anom		0.336	0.002	0.14 (-0.144 to 0.137)	-98
GAM	Copepods_southern	PDO_Annual		0.535	0.000	-0.178 (-0.087 to -0.051), 0.157 (0.083 to 0.14)	-57, 37
GAM	Prop_PredFish	PDO_Annual		0.316	0.004	0.543 (0.543 to 0.606), 0.835 (0.778 to 0.751)	152, 27
GAM	TL_SurveyedComm	PDO_Annual		0.319	0.003	3.804 (3.717 to 3.671)	27

3.3. Gradient forest

Gradient forest analysis identified three environmental pressures (and no human pressures) with a cumulative R^2 importance > 0.01, that may be associated with ecosystem thresholds (nonlinearities): PDO, spring transition timing, and sea surface temperature (SST) (Fig. 4). The main threshold responses included: southern and boreal copepod biomass anomalies and proportion of predatory fish in response to the PDO; boreal copepod biomass anomalies and proportion of predatory fish in response to spring transition timing; and boreal copepods biomass anomalies and proportion predatory fish in response to SST (Fig. 4). Overall, gradient forest analysis identified 7 nonlinear relationships out of a possible 57 (12%).

3.4. Dynamic factor analysis

Dynamic factor analyses (DFAs) were conducted on: 1) environmental pressures, 2) human pressures, 3) ecosystem responses, 4) ecosystem responses with an environmental covariate, 5) ecosystem responses with a human covariate, and 6) ecosystem responses with both environmental and human covariates. The three multivariate DFAs conducted on environmental pressures, human pressures, and ecosystem responses reduced those three sets of indicators to one trend each (Fig. 5). For the environmental pressures DFA, four environmental pressures loaded positively (and with a value > 0.2) and one (NPGO) loaded negatively on the single environmental trend, which varied considerably during 1986–2017 (Fig. 5). This indicates that NPGO had the opposite trend as the other four pressures (spring transition timing, SST, MEI, and PDO). Model fits were good for the NPGO and PDO ($r > 0.61$); model fits were not as good for the other environmental pressure time series, such as the upwelling magnitude ($r = 0.23$; Figure A1). This indicates that one trend is not necessarily representative of all observed environmental variability. The DFA on human pressures, produced one trend that peaked in the early 2000s and decreased to 2010 (Fig. 5). Total landings had negative loadings and trophic level of landings had positive loadings. These results reflect the increase in total landings and decreased trophic level of landings between 2000 and 2010 (Figs. 2 and 5). Model fits were good for both of the human pressure indicators ($r > 0.84$; Figure A1). Dynamic Factor Analysis on ecosystem responses produced one trend that decreased to 1991, increased to the early 2000s, decreased to 2010, and increased to 2017 (Fig. 5). Two responses had positive loadings (Steller sea lion abundance and southern copepod biomass anomalies) and one response (subarctic copepod biomass anomalies) loaded negatively on the trend (Fig. 5). Model fits were good for some responses (e.g., $r = 0.62$ for southern copepod biomass anomalies), but not good for others, such as the Proportion of Predatory Fish ($r = 0.07$) and Steller sea lion abundance ($r = -0.20$; Figure A1). Using covariates (human, or environment, or both human and

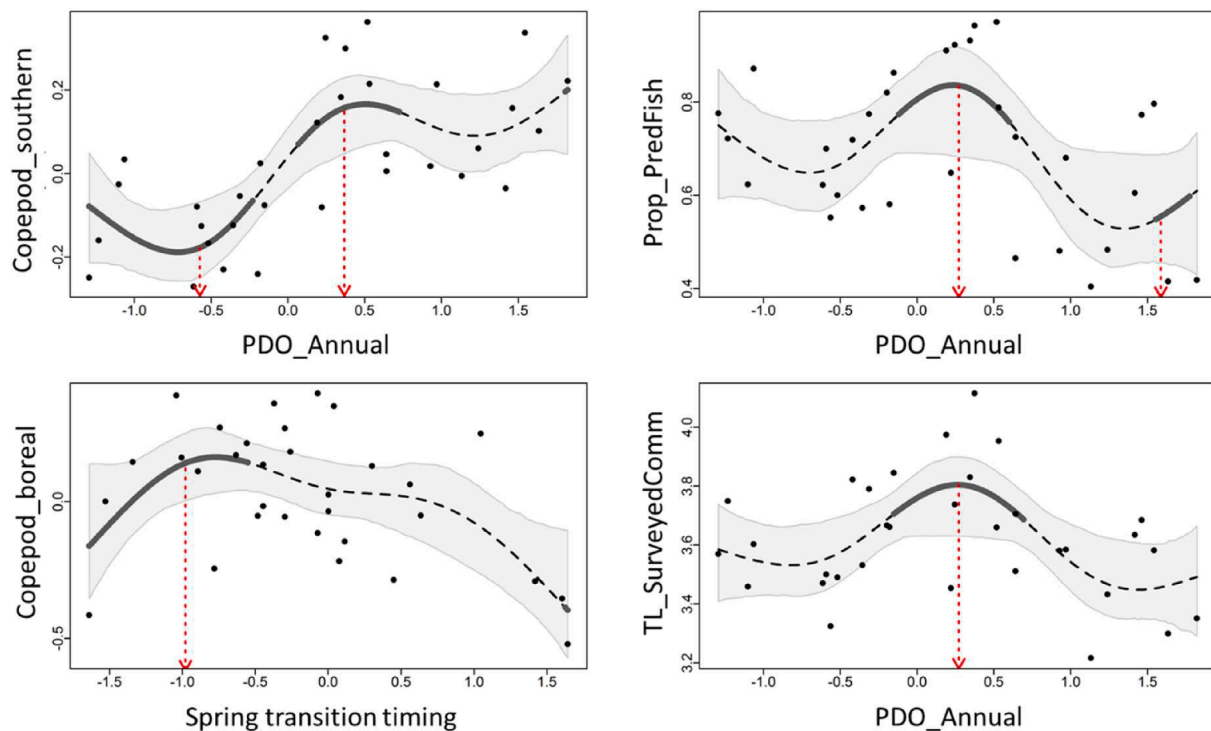


Fig. 3. Nonlinear relationships between environmental pressures and ecosystem responses identified using General Additive Models (GAMs). Dashed line is the GAM smoother, gray shaded area is the 95% confidence interval (CI), points are raw data, the thick solid line is the threshold range where the 95% CI of the second derivative of the GAM smoother line does not include 0, red dotted arrow indicates the best estimate of the threshold locations. See Table 1 for acronym definitions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

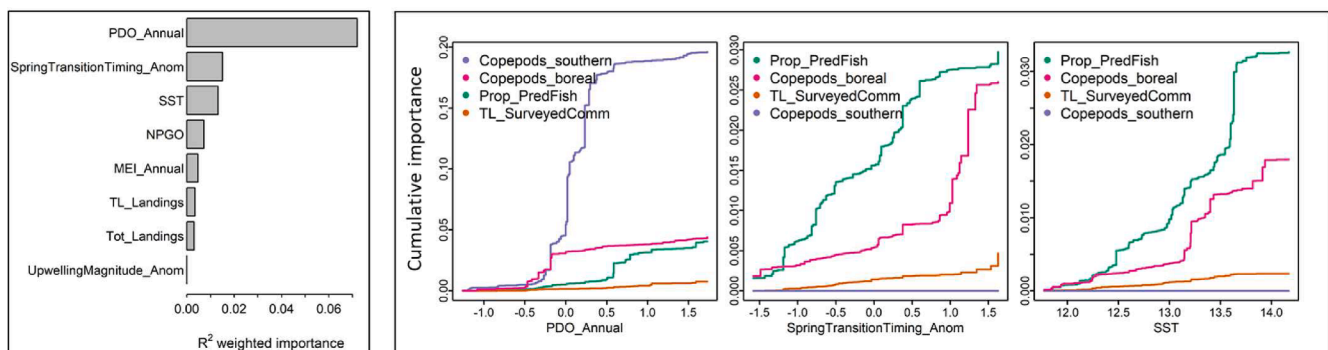


Fig. 4. Cumulative R^2 importance of six environmental and two human pressures on seven ecosystem response variables (see Table 1; Steller Sea lions were excluded due to missing data) during 1986–2017 on the west coast of Vancouver Island, identified through gradient forest analysis (left panel). Cumulative R^2 importance of ecosystem response variables as predicted by the best model (via gradient forest analysis), during 1986–2017 on the west coast of Vancouver Island (remaining three panels). Shown are the three pressures with R^2 weighted importance > 0.01. See Table 1 for acronym definitions.

environment) in the ecosystem responses DFA did not improve overall model fit (Figures A2-A4). The DFA model of ecosystem indicators without covariates had the lowest AICc (600.3). Of the three ecosystem response DFA models with covariates, the analysis with environmental pressure as a covariate had the lowest AICc (600.6) – but this was similar to the DFA model without covariates. The AICc for the model with human pressures was 624.2 and with both environmental and human pressures was 614.8. Despite the higher AICc value, the model with a human pressure covariate did appear to improve model fits to individual time series (e.g., Steller Sea Lion abundance, $r = 0.69$; Figure A3).

3.5. Comparative and secondary analyses

Results from single pressure-response relationships and gradient forest analyses were compared and secondary analyses were done on

trends identified with DFA. Results from the gradient forest analysis were similar yet not identical to those found through examination of single pressure-response relationships. For example, two of the three pressures identified through gradient forest analysis (PDO and spring transition timing) were also identified through single pressure-response relationships. The four responses with thresholds identified through gradient forest analysis were also identified in nonlinear single pressure-response relationships (boreal and southern copepod biomass anomalies, proportion of predatory fish, and trophic level of the surveyed community). For example, boreal copepod biomass anomalies had a threshold response to spring transition timing in both the gradient forest analysis and the single pressure-response GAM (Figs. 3 and 4). In some cases, there were differences between single pressure-response relationships and gradient forest results, such as, boreal copepod biomass anomalies which had a threshold response to the PDO, spring transition

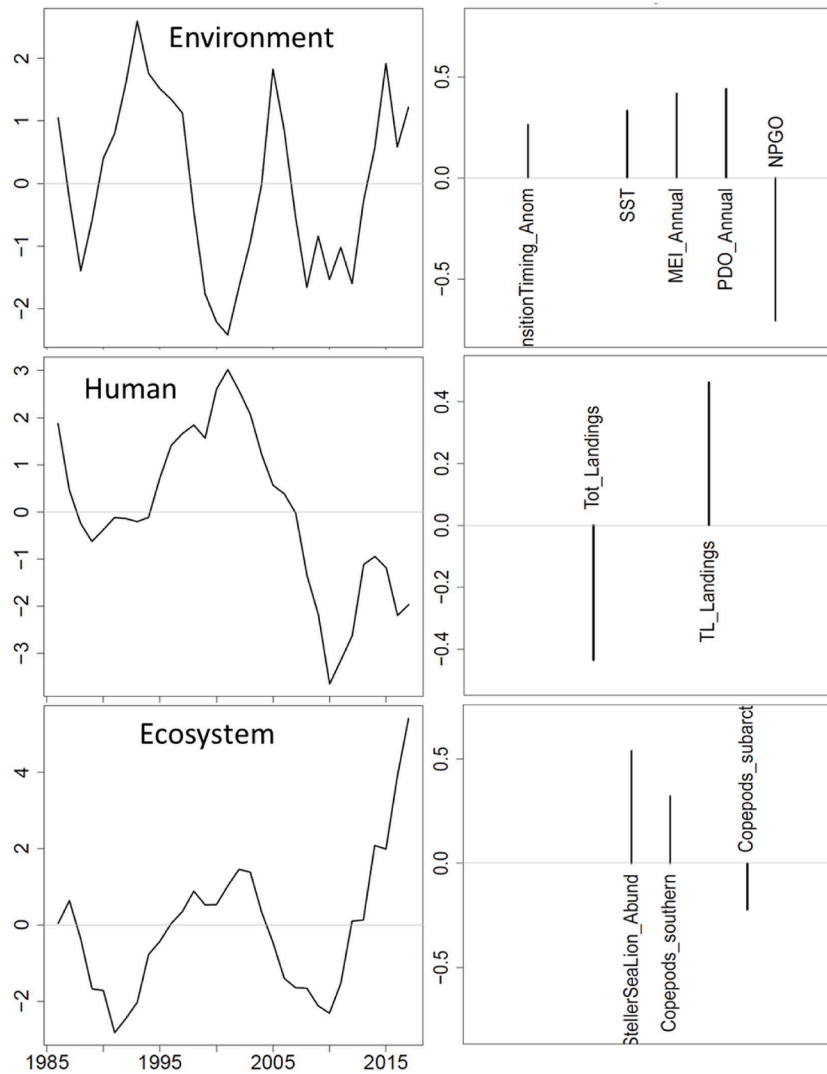


Fig. 5. Dynamic Factor Analysis (DFA) trends (left column) and factor loadings (right column) for environment pressures (top row), human pressures (second row) and for ecosystem indicator responses (bottom row). See Table 1 for definitions.

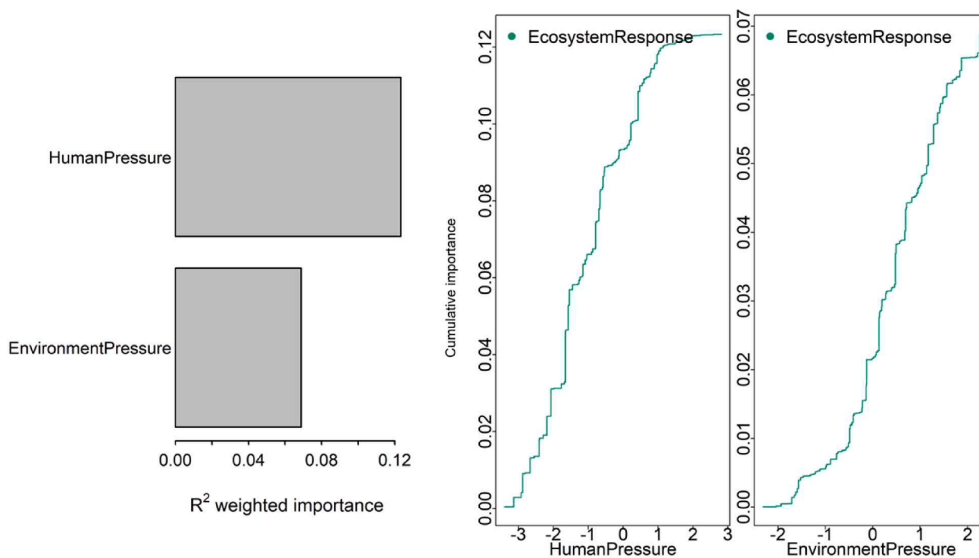


Fig. 6. Cumulative R² importance of two pressures (one environment and one human Dynamic Factor Analysis (DFA) trend) on one ecosystem response (one response DFA trend), during 1986–2017 on the west coast of Vancouver Island, identified through gradient forest analysis (left graph). Cumulative R² importance of one ecosystem response DFA trend as predicted by the best model (via gradient forest analysis), during 1986–2017 on the west coast of Vancouver Island (middle and right graphs).

timing, and SST in the gradient forest analysis, but only a significant nonlinear relationship with spring transition timing in the single pressure-response GAM (Figs. 3 and 4).

Single pressure-response relationships and gradient forest analyses were conducted on the trends identified with DFA. In these secondary analyses, the gradient forest analysis on DFA trends identified the human pressure DFA trend as having a R^2 weighted importance >0.01 , that may be associated with ecosystem thresholds (nonlinearities). This is different than results of the single pressure-response relationships and the gradient forest analysis on indicators (rather than on DFA trends), that found environmental pressures were nonlinearly related to ecosystem responses (Fig. 6). Also, the result is surprising since the ecosystem responses that loaded most on the ecosystem response DFA trend (Stellar sea lion abundance, and southern and subarctic copepods) would not be as directly impacted by the human pressures as, for example, total surveyed biomass. When single pressure-response relationships between DFA pressure trends (human and environment trends) and the DFA ecosystem response trend were examined, the best models were LMAC (lowest AICc values); however, neither of the models was significant (Appendix Table A1). Differences in results from these secondary analyses may be because DFA models did not fit well to some time series. The DFA trends, therefore, are not necessarily representative of all indicator time trends and by reducing multiple indicators to one trend, information may have been lost.

4. Discussion

We applied an indicator selection framework to identify mechanistically linked ecosystem response and pressure (human and environment) indicators, and explored the relationships between them. We applied single pressure-response models and multivariate methods to determine the shape of relationships, identify non-linear relationships, determine dominant pressures, and quantify thresholds. Our results indicate that 1) nonlinear and linear relationships were not prevalent in the west coast of Vancouver Island (WCVI) ecosystem indicators examined (i.e., 6–12% of relationships examined), similar to some previous studies (Samhouri et al., 2017; Satterthwaite et al., 2012), 2) ecological responses (both linear and nonlinear) were more commonly associated with environmental pressures than human pressures, 3) gradient forest analysis generally produced similar results as single pressure-response models and identified additional nonlinearities, but 4) multivariate dimension-reduction analyses (Dynamic Factor Analysis (DFA)) and secondary analyses on DFA trends (i.e., DFA trends analyzed using gradient forest analysis or single pressure-response models) resulted in the loss of information and different results.

When selecting indicators for an ecosystem assessment, management objectives need to be defined and selection criteria applied. The goal of this study was not a full ecosystem assessment but nevertheless, management objectives for other areas were adopted and indicators were selected based on a variety of screening criteria (Doren et al., 2009; Birk et al., 2012; Rombouts et al., 2013; Harwell et al., 1999; Fulton et al., 2005; Bundy et al., 2017) and the DPSIR (Elliott, 2002) framework, as well as previously identified core indicators (Shin et al., 2010a; Shin et al., 2010b; Link et al., 2010; Lucey et al., 2012; Takahashi and Perry, 2019). Indicator selection was limited by time series availability, highlighting the importance of long-term monitoring programs for ecosystem-based fisheries and climate-ready management (Groffman et al., 2006; Samhouri et al., 2017). Future research could explore inclusion of additional aggregate indicators (e.g., size spectrum, foraging guilds, fishing rate indicators).

In this study, nonlinear responses were not common in the single pressure-response relationships, consistent with other studies. Of the relationships examined, 6–12% were nonlinear and 8% were linear. The occurrence of nonlinearity is consistent with the findings of Fu et al. (2020), whose study was based on comparisons among 10 ecosystems around the globe, and with Samhouri et al. (2017) who found ~3–11%

of relationships were nonlinear in the California Current. This is also consistent with other studies which indicate that thresholds and regime shifts are not common (Capon et al., 2015; Donohue et al., 2016; Montoya et al., 2018; Hillebrand et al., 2020), but in contrast to studies that found many nonlinear relationships (Groffman et al., 2006; Hunsicker et al., 2016). Litzow and Hunsicker (2016) suggested that most observed ecosystem changes may be parsimoniously explained by linear responses to perturbation (76% of the studies they examined). This could be because: 1) thresholds may not be detectable at the current time- and spatial- scales of indicators, 2) the range of pressure indicators may not be wide enough for the ecosystem to have more chances to experience regime shifts (Fu et al., 2020), or 3) measurement variability in both response and pressure variables was not included in single-pressure response relationships (as recommended by Capon et al. (2015) and noted by Hillebrand et al. (2020)). Nonlinear relationships may not be common or easily detectable, however, they may prove to be valuable for further exploration as leading indicators of change that could inform reference points for ecosystem approaches to management.

In this study, the majority of significant single pressure-response relationships were associated with environmental pressures, such as the Pacific Decadal Oscillation (PDO), spring transition timing, North Pacific Gyre Oscillation (NPGO), and multivariate ENSO index (MEI), and all nonlinear responses were associated with two environmental pressures (PDO and spring transition timing). None of the single pressure-response relationships that included human pressures were significant, with an $R^2 > 0.2$. These results are supported by research within the mid- and southern portions of the California Current system, where the dominant pressures were large-scale oceanographic indices (PDO, NPGO, Northern Oscillation Index (NOI)) and the PDO was associated with nonlinear responses (Samhouri et al., 2017). In an adjacent ecosystem, the Strait of Georgia, Perry and Masson (2013) found that both human and environmental pressures, and both basin-scale and local-scale environmental pressures, were important. Other studies of the California Current and northern British Columbia (BC) also found that human pressures were associated with linear responses (Samhouri et al., 2017; Fu et al., 2019). Anthropogenic pressures were dominant in other studies of the California Current (Samhouri et al., 2017; Tam et al., 2017), northern BC (Fu et al., 2019), and the Northeast US continental shelf (Large et al. 2015). It is likely that identification of dominant pressures varies with the selection of indicators, scale of variables (i.e., measured on an annual basis and time series length), spatial scale (Heim et al., 2021), and ecosystems being examined. For example, the length of time series examined in this study was 32 years, compared to 19 in Samhouri et al. (2017); a recent update of the Samhouri et al. (2017) analysis, showed that by including additional years (time series length up to 48 years), fewer nonlinearities were identified (M. Hunsicker et al., unpublished). In this study, only 2 human pressures were considered, compared to, for example, 10 human pressures in Samhouri et al. (2017). Future analyses or full ecosystem assessments using additional human pressures (such as fishing rate indicators) might identify new pressure-response relationships. The dominance of environmental pressures in this study could be a result of the bottom-up nature of the upwelling-driven WCVI ecosystem, indicators examined, time series length, or the spatial or temporal scale of analyses (annual estimates of indicator values).

Using different modeling approaches can provide multiple sources of evidence for nonlinearities and pressure-response relationships (Samhouri et al., 2017). These approaches do not address nonstationarity and spatio-temporal variations in pressure-response relationships or non-additive responses to multiple pressures, for which future advances in analyses would be useful. Given that multiple pressures can act additively, synergistically, or antagonistically (Piggott et al., 2015), responses to multiple pressures are likely complex and therefore examining single pressure-response relationships may be too simplistic to characterize ecosystem responses (Montoya et al., 2018; Donohue et al., 2016). However, our results, using single pressure-response

relationships, were similar to those found using the multivariate gradient forest method. The four nonlinear responses identified with single pressure-response models were also identified using gradient forest analysis. In addition to these four, gradient forest analysis identified three additional nonlinear relationships. Gradient forest analysis, therefore, both confirmed single pressure-response model results while also identifying additional potential nonlinear relationships.

In this study, Dynamic Factor Analysis (DFA) trends were used as variables in both single pressure-response models and gradient forest analysis to see if nonlinearities could be observed in a reduced number of dimensions. Gradient forest methods identified nonlinearities between the human pressure DFA trend and the ecosystem response DFA trend. This does not support our findings from the single pressure-response and gradient forest analyses and may be due, in part, to poor DFA model fits to some time series (e.g., model fits to some of the environmental time series). Single pressure-response models on DFA trends did not identify any significant linear or nonlinear relationships, indicating that dimension-reducing analyses and DFA model fits may have resulted in a loss of information. For this reason, care should be taken when looking at dimension-reducing techniques alone, but there is value in using multiple analytical approaches, as used in this study, to allow for the verification of nonlinearities and discovery of additional information.

Both single pressure-response relationships and gradient forest analysis indicated that the proportion of predatory fish, trophic level of the surveyed community, and southern copepod biomass anomalies had threshold responses at similar values of the PDO. Increases in southern copepod biomass anomalies above a threshold value of PDO is consistent with other studies that show the alongshore current strength and sea surface temperatures (reflected by the PDO) affect copepod community composition on the west coast of North America (Mackas et al., 2007; Keister et al., 2011; Di Lorenzo et al., 2013). Changes to productivity (and indicated by the PDO) may have had cascading impacts on the proportion of predatory fish and the trophic level of the community (these are correlated indicators that both decreased above a threshold value of the PDO); although, Fu et al. (2020) found that lower productivity was associated with increased abundance of large fish and no change in the trophic level of the community. In this study, boreal copepod biomass anomalies had a threshold response to spring transition timing and a positive, linear correlation with the NPGO. Spring transition dates later than approximately March 14 (which is earlier than the average spring transition date of April 9) were associated with reduced boreal copepod biomass anomalies. Early spring transition timing has been associated with average to above-average upwelling-based coastal productivity (Hourston and Thomson 2019), which may have cascading impacts on boreal copepod biomass. The NPGO, another indicator of ocean climate-variability, has been linked to variability zooplankton abundance (Di Lorenzo et al., 2013). Finally, linear relationships were identified between Steller sea lion abundance and environmental variables, as has been found for other pinniped species in the California current: California sea lions were related to the MEI and SST (Melin et al., 2010) and Guadalupe fur seal emaciation was related to the PDO and copepods (D'Agnese et al., 2020). Tracking these pressure-response relationships will inform ecosystem assessments and ecosystem based approaches to fisheries management.

Many government organizations that manage fisheries, such as Fisheries and Oceans Canada, are now mandated to incorporate ecosystem considerations into fisheries management (Canada's Fisheries Act of 2019). Both linear and nonlinear relationships can provide advanced knowledge about changes in ecosystem productivity as a result of changes in pressures and this can inform science advice and management strategies when setting catch recommendations (Hunsicker et al. 2016; Samhouri et al., 2017). Both linear and nonlinear relationships in the WCVI marine ecosystem were associated with environmental pressures, which cannot necessarily be directly managed, yet can inform operating models in management strategy evaluations

and harvest control rules (Thayer et al., 2020). Mechanistically linked pressure-response relationships may provide auxiliary time series that can be directly incorporated into a stock assessment model (Maunder and Watters, 2003), be used as covariates to estimate recruitment in the past or future (Schirripa et al., 2013), or inform the use of time-varying natural mortality (e.g., Jiao et al., 2012) or catchability (e.g., Wilberg et al., 2010) in operating models. This type of study serves as a first step to identifying potentially important pressure-response relationships, and, although few relationships were found, these relationships could be explored at different spatial (Heim et al. 2021) and temporal scales pertinent to the species being assessed.

5. Conclusions

The application of multiple modeling approaches was informative in identifying and confirming pressure-response relationships, identifying non-linear relationships, and quantifying potential thresholds in the west coast of Vancouver Island marine ecosystem. Few nonlinear or linear relationships were identified in this study (6–12% of relationships examined), similar to other reviews and meta-analyses (Donohue et al., 2016; Capon et al., 2015) but in contrast to studies that found many nonlinear relationships (Groffman et al., 2006; Hunsicker et al., 2016). Gradient forest analyses and single pressure-response models, using indicator time series, generally produced comparable results; whereas, secondary analyses on Dynamic Factor Analysis (DFA) trends, produced different results – with a potential loss of information through dimension reduction of many indicators to, at times, singular trends. This implies that the detection of pressure-response relationships likely varies with selection and total number of indicators, spatial and temporal scale of variables, ecosystems being examined, and types of analyses used. Although not common in this study, nonlinear relationships could provide an early warning of changes in ecosystem productivity or communities. Mechanistically linked pressure-response relationships should therefore be explored further with multi-model approaches (Burthe et al. 2014), as part of an ecosystem-based and climate-ready approach to fisheries management.

CRedit authorship contribution statement

Jennifer L. Boldt: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft. **Elliott L. Hazen:** Conceptualization, Methodology, Software, Writing - review & editing. **Mary E. Hunsicker:** Conceptualization, Methodology, Software, Writing - review & editing. **Caihong Fu:** Conceptualization, Data curation, Methodology, Resources, Writing - review & editing. **R. Ian Perry:** Conceptualization, Data curation, Methodology, Writing - review & editing. **Xiujuan Shan:** Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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