

LETTER

Spatial patterns and predictors of trophic control in marine ecosystems

Abstract

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A key question in ecology is under which conditions ecosystem structure tends to be controlled by resource availability vs. consumer pressure. Several hypotheses derived from theory, experiments and observational field studies have been advanced, yet a unified explanation remains elusive. Here, we identify common predictors of trophic control in a synthetic analysis of 52 observational field studies conducted within marine ecosystems across the Northern Hemisphere and published between 1951 and 2014. Spatial regression analysis of 45 candidate variables revealed temperature to be the dominant predictor, with unimodal effects on trophic control operating both directly ($r^2 = 0.32$; $P < 0.0001$) and indirectly through influences on turnover rate and quality of primary production, biodiversity and omnivory. These findings indicate that temperature is an overarching determinant of the trophic dynamics of marine ecosystems, and that variation in ocean temperature will affect the trophic structure of marine ecosystems through both direct and indirect mechanisms.

Keywords

Bottom-up, consumer control, diversity, resource control, temperature, top-down.

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INTRODUCTION

The ocean supports some of the most diverse and productive ecosystems on the planet. Ocean ecosystems support fisheries valued at ~ US\$ 240 billion annually (Dyck & Sumaila 2010) and provide the seafood that is the primary source of protein for 6.5% of the global population (FAO 2014). Developing effective management strategies for marine ecosystems is therefore of great applied importance. A necessary prerequisite to achieving this objective is a thorough understanding of the factors that govern the dynamics of marine ecosystems. Resource supply ('bottom-up' control) and consumer pressure ('top-down' control) are known to be critical determinants of marine ecosystem structure and function. For example, research indicates that ecosystems operating under strong consumer control may be more sensitive to fisheries exploitation than those under resource control (Petrie *et al.* 2009). However, there is little consensus on how and why these types of trophic control vary. Several hypotheses based on mathematical theory, small scale experiments and observational field studies (McQueen *et al.* 1986; Shurin *et al.* 2002, 2012; Borer *et al.* 2005) have been advanced to explain patterns of trophic control within ecosystems. While insightful, the support for, and generality of these hypotheses has not yet been systematically evaluated in large open marine ecosystems. Regional-scale studies suggest that temperature, species diversity and exploitation pressure could play roles in influencing trophic control in marine ecosystems (Worm & Myers 2003; Frank *et al.* 2006, 2007; Myers *et al.* 2007; Petrie *et al.* 2009). However, how trophic control is organized at larger spatial scales

remains unclear, and the full spectrum of hypotheses advanced to explain such patterns have yet to be evaluated. Here, we undertake such an initiative using all relevant published observational field studies.

Trophic control is difficult to quantify, largely because it cannot be directly observed. Short-term or small-scale studies may employ gut content or biochemical tracer analyses, or experimental methods to estimate trophic control. However, these approaches are impractical in quantifying trophic control for the full spectrum of species, and over large spatial or temporal scales. Moreover, experimental approaches may not accurately reproduce the complexity and realism of natural systems. One way to overcome these obstacles is to develop statistical state indicators of trophic control that are based on the strength of association between spatial or temporal gradients in the abundance of consumers and their prey. Numerous state indicators of trophic control have been developed, yet the correlation coefficient calculated from time-series of population abundance, has perhaps become the most widely used metric to assess the type and strength of trophic control. This approach has been used to quantify trophic control within marine (Micheli 1999; i.e. Worm & Myers 2003; Frank *et al.* 2005, 2006), terrestrial (i.e. Post *et al.* 1999) and freshwater (i.e. Carpenter & Kitchell 1993) environments and is commonly featured in contemporary ecological textbooks (Moloney *et al.* 2011). Within this framework, strong positive correlations indicate resource control, as both populations are driven by factors regulating productivity, and strong negative correlations indicate consumer control, as predators suppress the abundance of their prey (Micheli 1999; Worm & Myers

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2003; Frank *et al.* 2005, 2006, 2007; Myers *et al.* 2007; Petrie *et al.* 2009). Weak correlations imply weak or possibly oscillatory patterns of trophic control. This indicator has also been interpreted in the context of dynamic community stability, with weak or positive correlations representing the canonical ecosystem state (Di Lorenzo *et al.* 2013) and negative correlations representing an ecosystem at disequilibrium (Strong 1992; Frank *et al.* 2006).

Here, we evaluate the geographic patterns of trophic control across marine ecosystems using published observational field studies which reported the correlation (hereafter r_{TC}) between abundance time-series of marine consumers and their prey as an indicator of trophic control. We then use this newly constructed database to evaluate the factors that best explain the geographic variation in r_{TC} . Factors of interest were identified according to the leading hypotheses proposed to explain variability in trophic control (Tables 1 and S2).

MATERIALS AND METHODS

Data

We identified published studies that reported correlations (r_{TC}) between time-series of annually-averaged marine consumers and their prey as a basis for investigating the type and strength of trophic control. Relevant studies were compiled over several years using the ISI Web of Science, Google Scholar, and SCOPUS. Only those studies in which the time-series of consumers and prey (in units of abundance, biomass, or concentration) spanned at least 5 years and the linear relationship (r_{TC}) between consumers and their prey was reported were used for the analysis (Table S1). We extracted the reported r_{TC} values, the identity, trophic level and taxonomic resolution of consumers and their prey, the geographic location, spatial extent and length of the time-series over which the r_{TC} values were derived. For each extracted r_{TC} , we also calculated the bathymetry (m) and distance to the nearest coastline (km). The fractional trophic level of the consumer and prey species was obtained from published studies and Fishbase (Froese & Pauly 2004).

Our analysis of the predictors of trophic control was informed by published hypotheses that sought to explain the type and strength of trophic control. These include biodiversity, temperature, omnivory, perturbation, ecosystem productivity, turnover of primary producers, food quality, habitat heterogeneity and trophic position (Tables 1 and S2). Guided by these hypotheses, we identified 45 biophysical variables which may explain patterns of trophic control across marine ecosystems (Tables 1 and S2; Figs S3–S5). We also included additional variables which may influence the relationship between the biophysical variables and r_{TC} . These variables include the spatial scale of the study, average latitude and average year of the study, the ocean basin in which the study was conducted, the difference between the trophic level of the consumers and prey, and whether the trophic effects operate at the species or community level. A complete description of these specific hypotheses, as well as details of the data set and analysis methods and workflow can be found in the Supplementary Information (SI; Table S2, and Figs S1, S3, S4 and S5).

Table 1 Factors hypothesized to explain variation in trophic control, and their indicators (See SI for data sources and attributes, and list of references)

Hypothesis	Indicator(s)
Temperature	Temperature (0–200 m) Temperature variability
Diversity	Cumulative normalized Cumulative Oceanic Cumulative Coastal Oceanic shark Shark Euphausiid Coastal fishes Cephalopods Pinnipeds Seagrasses Mangrove Tunas and billfishes Squids Cetaceans Foraminifera
Perturbation	Exploitation pressure Hypoxia Velocity of temperature change Magnitude of temperature change Human impact index Pollution index UV index
Omnivory	Consumer omnivory Ecosystem omnivory
Production or biomass	Chlorophyll Zooplankton Net primary production Chl : NPP ratio Phytoplankton cell size
Primary producer turnover	Frequency of picophytoplankton
Food quality	Frequency of diatoms Bathymetry
Habitat features	Distance from coast
Trophic position	Trophic level Trophic aggregation
Additional factors	Spatial scale Latitude Year Trophic separation Ocean basin

A single database was created by spatially matching the biophysical variables with each r_{TC} based on the minimum geographic distance separating them (SI contains details). We used this distance-based method rather than matching r_{TC} values and environmental values on a cell-to-cell basis in order to account for the different spatial resolution of the environmental variables. Biophysical variables located > 1000 km from any r_{TC} value were removed prior to the analysis. The median distance between r_{TC} values and the associated environmental variables was 62 km. The full database is available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4gt21>.

Analyses

First- and second-order weighted linear univariate and multivariate spatial regression models and structural equation

models (SEMs) were used to explain spatial patterns in r_{TC} . Ideally, to statistically account for the uncertainty of r_{TC} values these regressions would be weighted by the inverse of the r_{TC} variances. However, r_{TC} variance estimates for the majority of the studies in our database were either not reported or, in some cases, were potentially biased by a failure to account for temporal autocorrelation in the time-series. For this reason, we based our regression weights on the number of measurements (years) used to calculate each r_{TC} value. The presence of discrete or stepwise effects was explored using regression trees, while nonlinear effects and their possible interactions were explored using generalized additive models. Where relationships were nonlinear, r_{TC} was estimated as a second-order function of the predictor. All ordinary least-squares (OLS) linear model assumptions (*i.e.* independence, linearity and normality) were verified by analysis of the model residuals.

A multivariate model (MVM) was developed to identify the combination of predictors explaining the greatest proportion of the variability in r_{TC} , and to predict patterns of trophic control for locations beyond the geographic domain of the database. The MVM was estimated using information theoretic (IT) multi-model inference (Fig. S13; SI contains details). Rather than relying on a single model, multi-model analyses allows for an ensemble set of plausible candidate models to be ranked and integrated using information theory, thereby incorporating the uncertainty of the individual models. The performance of the multi-model approach was also assessed using backward stepwise model selection. Prior to estimating the MVMs, we assessed the degree of dependence or collinearity among predictors by calculating the variance inflation factor (VIF) for all predictors (Dormann *et al.* 2013). The predictors responsible for high VIFs were identified by calculating the Pearson correlation coefficient between all model predictor combinations (Figs S7, S8). To reduce collinearity prior to the analysis, highly collinear predictors were removed from the analysis until all VIF values were < 5 . The decision of which collinear variables to omit was based on sequential regression analysis (Dormann *et al.* 2013). To statistically account for the relationships between model predictors, while estimating the effects of predictors on r_{TC} , we used SEMs. SEM coefficients were estimated from the correlation matrix using the reticular action model method (SI contains details).

The MVM was then used to predict r_{TC} at locations outside the geographic domain of the trophic database. To accomplish this, global spatial gradients of all predictors retained by the MVM were extracted or calculated (Fig. S19). All predictors were spatially interpolated so that they were available at the same locations on a global $1^\circ \times 1^\circ$ grid. All predictions were restricted to the range of biophysical predictor variables contained in the trophic database; no extrapolations were made outside the range of any of the predictor variables (Fig. 2).

RESULTS

Database summary

The database contained 155 r_{TC} values reported in 52 peer-reviewed studies (Fig. 1) and was derived from time series

sampled between 1951 and 2011 (Table S1 contains list of references). These r_{TC} values originated from studies conducted in the Atlantic (58%), Pacific (27%) and Arctic (15%) oceans north of $25^\circ N$, and involved species ranging from phytoplankton to cetaceans (Fig. 1a,b). The availability of r_{TC} values was greatest in continental shelf (< 200 m depth) and temperate locations (40° – $60^\circ N$). Virtually all r_{TC} values originated from ecosystems classified as medium or highly impacted by human activities (Halpern *et al.* 2008) and in which directed exploitation pressure on upper trophic level fishes was high (Fig. S2).

Spatial patterns of trophic control

The type and strength of trophic control (r_{TC}) operating within marine ecosystems was variable spatially (Fig. 2a). Within the spatial domain of our analysis, trophic control varied according to latitude. Strong consumer control was prevalent in high latitude ecosystems, particularly in the Northwest Atlantic, Arctic and North Pacific Oceans (Fig. 2a). Resource control was prevalent in lower latitude ecosystems, such that studies conducted below $\sim 45^\circ N$ almost exclusively reported resource control. The Northeast Atlantic Ocean was an exception to this general pattern. There, trophic control varied little with latitude, and resource control was widely reported within ecosystems at latitudes ranging from 40° to $65^\circ N$ (Fig. 2a).

Predictors of trophic control

Average upper ocean temperature (0–200 m) was consistently the strongest predictor of trophic control (Table 2 and Fig. 2a, b, c), and alone explained 32% of the variability in r_{TC} ($P < 0.0001$). The temperature effect remained strong even when all significant predictors were included in the MVM (Fig. 2c). The direction and strength of trophic control was best predicted as a quadratic function of temperature. Resource control dominated at temperatures between $\sim 5^\circ C$ and $20^\circ C$ and consumer control dominated at both low ($< 5^\circ C$) and high ($> 20^\circ C$) temperatures ($P < 0.0001$).

Positive relationships were observed between r_{TC} and all biodiversity indices evaluated. The strongest effects were related to shark diversity ($r^2 = 0.29$; $P < 0.0001$) and to normalized cumulative biodiversity ($r^2 = 0.14$), higher biodiversity being associated with enhanced resource control (Table 2 and Fig. 2d,e). Trophic control was best predicted as a unimodal function of both shark and cumulative biodiversity. However, unlike the effects of temperature, resource control prevailed even in the regions where diversity was highest (Fig. 2e). Our analyses also suggested that the cumulative effects of biodiversity and temperature on r_{TC} were additive rather than multiplicative; the strongest consumer effects occurred at locations where both temperature and biodiversity were at the lowest (Fig. S17).

The trophic level of the consumer-prey pair also had a significant effect on r_{TC} . The strength of consumer control dissipated downward through the food web (Table 2; Fig. 2f,g) such that predator-prey pairs higher in the food chain exhibited greater consumer control than those at lower trophic levels.

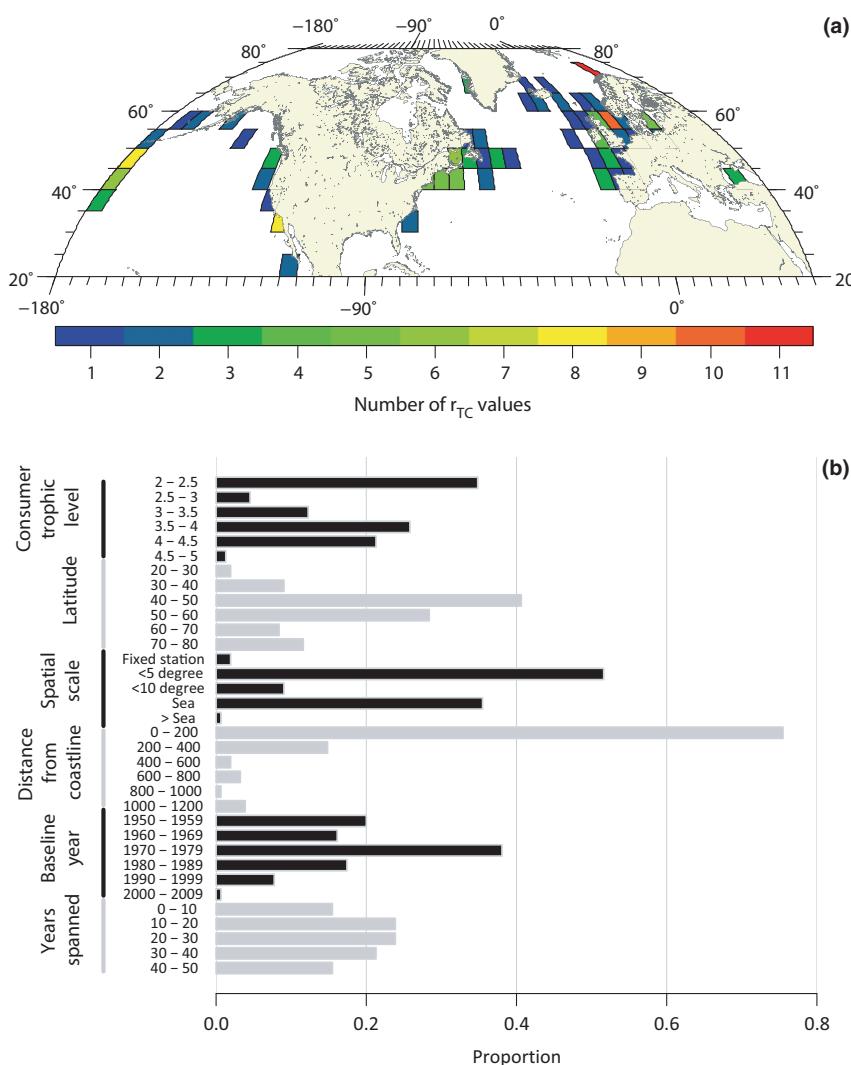


Figure 1 Summary of trophic database. (a) Spatial distribution of studies for which r_{TC} values were extracted. Colours depict the number of r_{TC} values available. White areas contain no data. (b) Proportion of the r_{TC} values as a function of the consumer trophic level, latitude, spatial scale, distance from the nearest coastline, baseline year of the time-series, and years spanned by the time-series.

Of the seven perturbation indices evaluated individually (SI; Tables 1 and S2), only exploitation pressure exhibited a significant effect on r_{TC} (Table 2 and Fig. 2h,i). Consumer control tended to be strongest in ecosystems subjected to higher exploitation rates. Exploitation effects on r_{TC} were strongest at high trophic levels, dissipated downward through the food chain, and impacted minimally on the plankton (Fig. S12a). However, despite these strong univariate effects, after accounting for the covariance between exploitation and temperature within the MVM or SEM, the effects of exploitation on trophic control were not significant (Table 2 and Fig. 3).

Coincident omnivory estimates were available for 74 r_{TC} values. At locations where average ecosystem omnivory was high, stronger resource control prevailed ($r^2 = 0.21$; $P < 0.0001$; Table 2 and Fig. 2j,k). Ecosystem omnivory remained a strong predictor of r_{TC} even after the effects of additional significant predictors were taken into account (Table 2 and Fig. 2k). An additive effect of omnivory and shark diversity was also observed, with resource control

predominant in ecosystems in which both omnivory and biodiversity were high and *vice versa* (Fig. S12b). Despite the significant influence of omnivory on r_{TC} , the incomplete number of coincident matchups precluded the inclusion of this variable in the final MVM or SEM.

Weaker, but statistically significant effects of primary producer cell size and turnover rate on trophic control were also evident (Table 2; Fig. S9). Trophic control shifted towards greater consumer control with increasing phytoplankton cell diameter (a measure of food quality). Ecosystems characterized by rapid primary producer turnover also exhibited greater consumer control (Table 2).

Direct and indirect effects of temperature on trophic control

Structural equation models were used to test the effect of multiple predictors on r_{TC} while accounting for the indirect effects of temperature on other predictors. Although, some univariate predictor effects on r_{TC} were nonlinear (Figs 2c, e), the

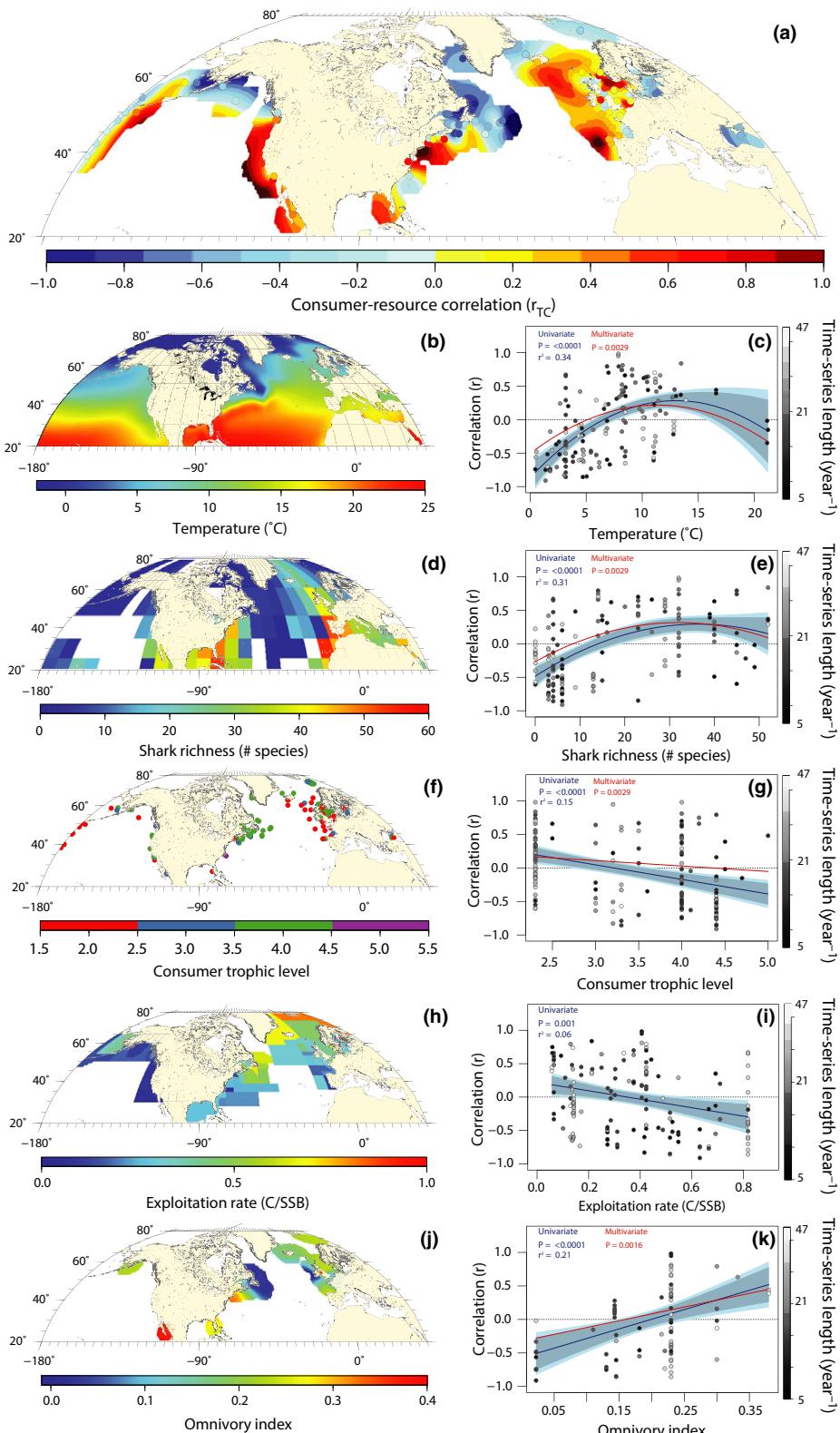


Figure 2 Predictors of trophic control across marine ecosystems. (a) Geographic patterns in trophic control. Coloured points are the individual r_{TC} values, and colour shading represents spatial interpolations of those values. Yellow and red denotes resource control ($+r_{TC}$) and blue denotes consumer control ($-r_{TC}$). (b–g) The left columns depict spatial gradients in predictor variables and the right columns depict univariate relationships between the predictors and r_{TC} . Spatial gradients (left column) and relationships (right column) are plotted for (b–c) Surface temperature (°C); (d–e) shark species diversity; (f–g) Trophic level; (h–i) Exploitation rate; and (j–k) Omnivory index. For the right-hand columns, the shading intensity depicts the length of the time-series used to calculate the r_{TC} values. The blue lines are the best fitting univariate linear regression fits, and shading represents the 99 and 95% confidence limits for the fitted trends. The red regression lines are estimated from the best-fitting MVM.

Table 2 Results from univariate and multivariate regression models

Predictor	Fixed effects models			Mixed effects models				N	Effect
	Slope	P-value	r^2	Slope	P-value	r^2			
Univariate models									
Temperature	0.175	< 0.0001	32.1	0.176	< 0.0001	30.3	155	+	
Temperature ²	-0.007	< 0.0001		-0.007	0.0015				
Shark diversity	0.044	0.0002	28.9	0.044	< 0.0001	27.2	155	+	
Shark diversity ²	-0.001	< 0.0001		-0.001	0.0021				
Omnivory	2.877	< 0.0001	20.1	2.725	0.0002	16.4	74	+	
Diversity	4.082	0.0636	14.2	2.470	0.1718	15.3	155		
Diversity ²	-4.17	0.0022		-0.840	0.7789				
Trophic level	-0.210	0.0000	13.6	-0.140	0.0329	5.1	155	-	
Turnover	9.980	0.0004	11.4	9.736	0.0087	12.9	155	+	
Turnover ²	-1.570	0.0007		-1.515	0.0135				
Exploitation	-0.388	0.0004	7.6	-0.758	0.0007	10.5	151	-	
Multi-model inference									
<i>Top-ranking multivariate model (AIC_w = 0.71)</i>									
Temperature	0.128	0.0001	47.2	0.131	0.0003	45.6*	155	+	
Temperature ²	-0.006	0.0006		-0.005	0.0025				
Shark diversity	0.036	< 0.0001		0.041	0.0002			+	
Shark diversity ²	-0.001	0.0004		-0.001	0.0037				
Turnover	-0.851	0.0010		-0.607	0.0736			-	
Cell diameter	-0.497	0.0006		-0.335	0.0624			-	
Trophic level	-0.081	0.0427		-0.063	0.2119			-	
<i>Multi-model averaged estimates (95% confidence set)</i>									
Temperature	0.136	0.0001	-					+	
Temperature ²	-0.006	0.0004							
Shark diversity	0.036	< 0.0001						+	
Shark diversity ²	-0.001	0.0004							
Turnover	-0.887	0.0007						-	
Cell diameter	-0.510	0.0004						-	
Trophic level	-0.082	0.0421						-	

Effect and statistical significance of main predictors on trophic control are given. R^2 -squared values, and the number of measurements used are given for each model rather than for each predictor. Effect denotes the effect of increasing values of the predictor on the response. *Denotes the marginal r^2 value for mixed models.

estimated SEM effects are constrained to be linear. We removed three r_{TC} values derived from ecosystems in which water temperatures exceeded 20 °C to accommodate this constraint. This produced relationships that were approximately consistent with the SEM assumption of linearity. The SEM explained 38% of the variance in r_{TC} , indicative of strong covariation among the exogenous variables (temperature, trophic level and exploitation pressure), and the strong effects of temperature on the endogenous variables (shark diversity, turnover and cell size of primary producers; Fig. 3a). Phytoplankton cell diameter also had an effect on turnover, since small cells turnover faster than large. After controlling for the relationships between predictor variables, the influence of exploitation and the turnover and cell diameter of primary producers on r_{TC} was weaker. The SEM effects of shark diversity and trophic level, and temperature on r_{TC} were similar in direction and magnitude to the univariate effects and remained statistically significant.

Collectively, these analyses indicate that temperature is the primary determinant of spatial patterns in the type and strength of trophic control across marine ecosystems and that it operates both directly and indirectly, through its effect on other factors. The effect of temperature on r_{TC} also appears to be general, as significant effects were apparent both within

and across ocean basins (Fig. 3b), studies (Fig. 3c) and trophic levels (Fig. S15).

Global patterns of trophic control

The univariate regressions we report tested the influence of single predictors on r_{TC} , whereas the SEMs tested the linear effects among predictors and r_{TC} . The MVM analysis, in contrast, enabled us to estimate which combination of linear and nonlinear predictors best explained the observed geographic variation in r_{TC} . Within the multi-model analysis, there was marginal support for a single model ($w_i > 0.9$). However, the top-ranking model had an AIC weight of 0.71 and the 95% confidence model set contained only two models. The predictors retained by the top-ranking ensemble model were identical to those within the model selected via stepwise selection. The MVM parameter estimates were also largely insensitive to the use of multi-model averaging as opposed to traditional model selection (Table 2). Based on these results, the top-ranking MVM within the multi-model ensemble set was used as the basis for inference and prediction. The resultant MVM incorporated the following effects, listed in order of their perceived importance in explaining variability in r_{TC} , according to their respective P-values: temperature, shark diversity,

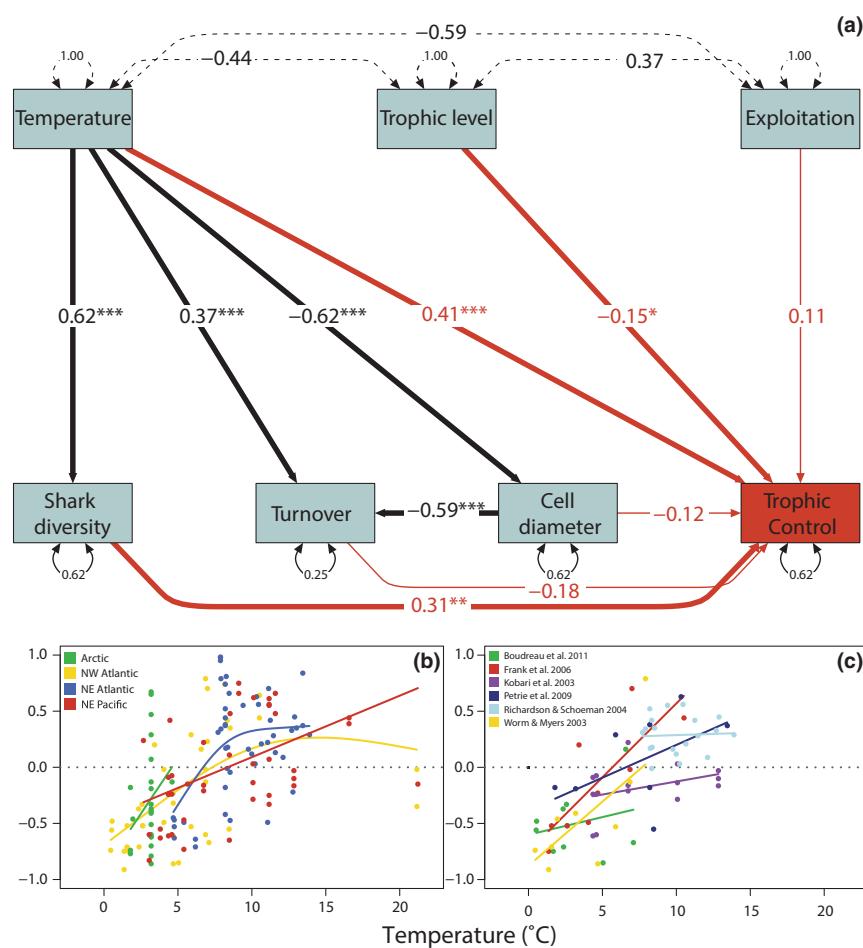


Figure 3 Effects of temperature on trophic control. (a) Structural equation model depicting the linear relationships between main predictors identified by the univariate models (Table 2 and Fig. 1). Solid lines depict effects of predictors on endogenous variables, dashed lines depict co-variation among exogenous variables, and statistically significant effects are shown as thick lines. Standardized path coefficients are given next to the path arrows with significances given as $*P < 0.05$ and $***P < 0.001$. Unexplained variances are denoted by closed circular arrows, and double-headed arrows depict covariance. Red arrows depict factors influencing trophic control. (b–c) Univariate relationships between temperature and the type and strength of trophic control (r_{TC}). Relationships are shown both within and across (a) ocean regions, and (b) studies. Colour of points and regression lines depict the ocean region (b) and study (c), respectively. For (c) only studies containing more than five r_{TC} values were used.

phytoplankton cell diameter, primary producer turnover and consumer trophic level (a combination of rates and traits). This model explained 47.2% of the observed variability in r_{TC} ($P < 0.0001$; Table 2).

The magnitude and direction of the MVM effects were broadly consistent with the findings of published studies that employed independent methods and data (SI and Table S2 for references), thus providing a stronger argument for causation. Given this coherence, the MVM was used to predict the direction and intensity of trophic control (\hat{r}_{TC}) at locations beyond the geographic domain of the trophic database (Fig. 4a). These predictions are not intended to be conclusive, but rather to provide a baseline hypothesis, using the available information from the data-rich Northern Hemisphere, as to what patterns of trophic control may look like across the vast areas of the seascape where data are currently lacking. Predictions of r_{TC} were only derived for locations at which the range of values for all five predictors fell within those over which the MVM was estimated. Predicted \hat{r}_{TC} varied strongly with

latitude (Fig. 4b), suggesting that resource control prevails at lower latitudes (50° S to 35° N) whereas consumer control prevails at higher latitudes ($> 50^{\circ}$ S and $> 35^{\circ}$ N; Fig. 4b). Average predicted \hat{r}_{TC} also varied with distance to the nearest coastline (Fig. 4c). Consumer control ($\hat{r}_{TC} < 0$) prevailed in ecosystems located < 250 or > 900 km from the coast, and weak trophic control (average $\hat{r}_{TC} \sim 0$) prevailed in ecosystems located 250–900 km from the coast.

DISCUSSION

Predictors of trophic control

Based on our evaluation of 45 biophysical variables, we conclude that upper ocean temperature is the strongest single factor explaining the observed spatial patterns of trophic control across marine ecosystems. Temperature was found to have both direct and indirect effects on trophic control, through its influence on biodiversity, average phytoplankton cell size and

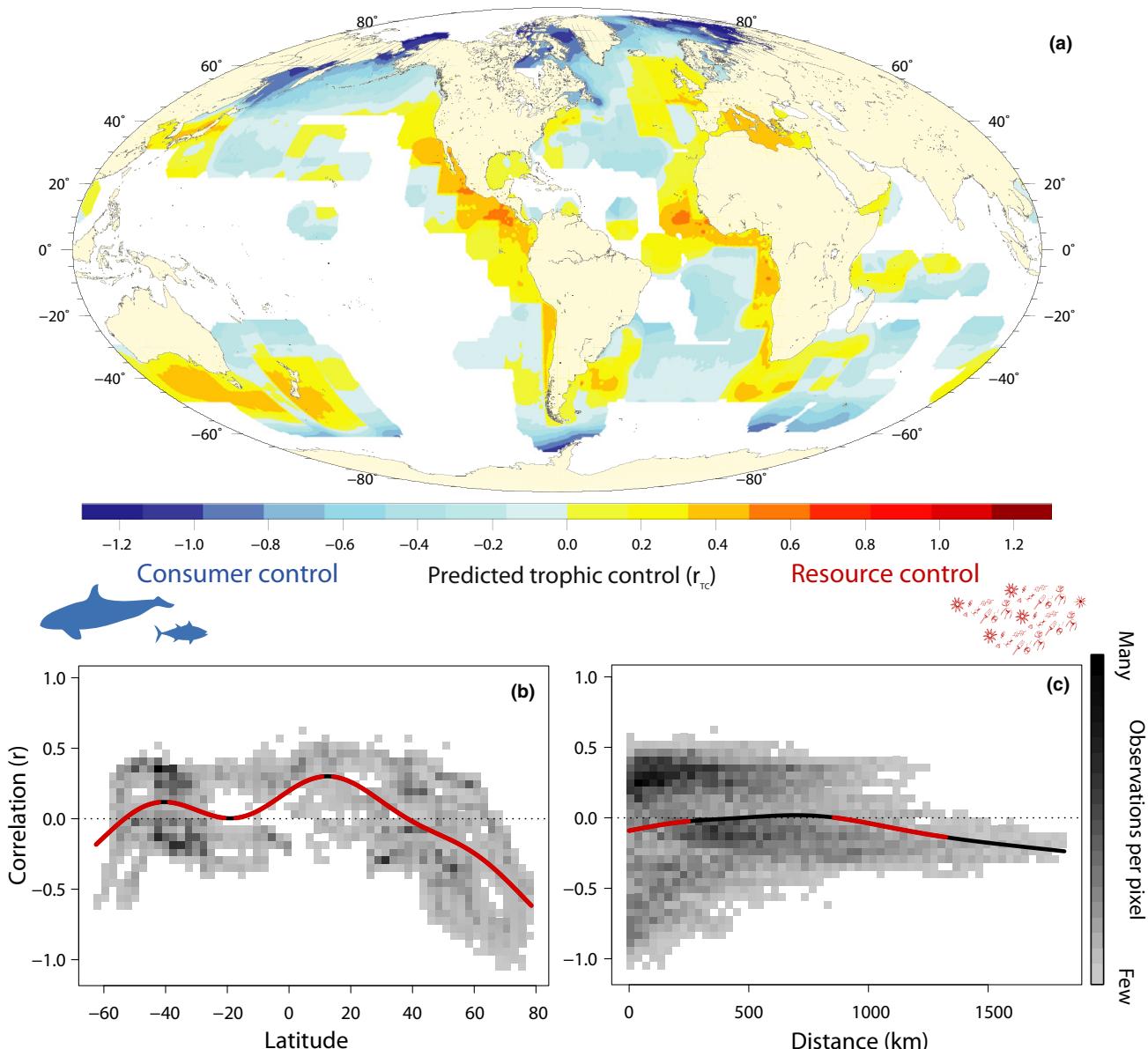


Figure 4 Predicted global patterns of trophic control. (a) Predicted \hat{r}_{TC} values were made using the multivariate model ($r^2 = 47$; $P < 0.0001$), and spatially interpolated to areas within 500 km from the nearest individual prediction. White denotes areas where no predictions were made. (b–c) Estimated variation in \hat{r}_{TC} as a function of (b) latitude and (c) distance from the nearest coastline. Gray shading depicts the number of observations per pixel. Trend lines were estimated from GAMs and weighted on the inverse of the standard error of the predictions; red line segments denote areas of significant change. The dashed horizontal lines denote a correlation of 0.

turnover (Fig. 3a; Polovina *et al.* 2008; O'Connor *et al.* 2009; Tittensor *et al.* 2010; Polovina & Woodworth 2012). This temperature effect was general, and not driven by observations from any single study, ocean basin, or trophic level (Fig. 3b,c).

Our finding that temperature is a strong determinant of the spatial variability in trophic control across marine ecosystems is consistent with the findings of Frank *et al.* (2007). However, whereas Frank *et al.* (2007) explored trophic control within continental shelf ecosystems across the temperate north Atlantic (0–13 °C), our study includes both shelf and oceanic ecosystems in the Atlantic, Pacific and Arctic Oceans (0–22 °C). Additionally, while Frank *et al.* (2007) investigated the effects of two factors (temperature and species diversity)

on trophic control using correlation analysis, we quantitatively examined the influence of 45 biophysical variables using a more comprehensive combination of statistical approaches. In addition to increasing the scale and rigour of the analysis, the inclusion of additional variables in the analysis facilitated an exploration of the pathways by which temperature might be influencing trophic control. For instance, we found that temperature co-varied with several important predictors of trophic control, such as species diversity, phytoplankton cell size and turnover, exploitation rate and omnivory (Figs S10 and S11).

Temperature also co-varies with other variables, not included in our analysis, which may influence trophic control,

such as metabolic (O'Connor *et al.* 2009) or demographic (Petrie *et al.* 2009) rates, or organism size (Shackell *et al.* 2010; DeLong *et al.* 2015). Given the strong co-variation between temperature and many other factors, and the multiple pathways by which temperature effects may operate, we hypothesize that temperature exerts a dominant effect on trophic control by integrating over multiple correlated individual effects. This would explain why temperature emerged as a stronger predictor of trophic control than any other single factor. It is also noteworthy that the observed effect of temperature on trophic control we report within and across marine pelagic ecosystems differs from what has been reported in some terrestrial (Post & Pedersen 2008; Barton *et al.* 2009; Hoekman 2010), freshwater (Kratina *et al.* 2012), or marine intertidal (Harley 2011) ecosystems. The unimodal scaling of trophic control with temperature we observed is, however, similar to those reported in the global meta-analysis of terrestrial experiments of Rodríguez-Castañeda (2013) in which strong consumer control prevailed at locations where mean annual temperature was at the low and high extremes ($> 25^{\circ}\text{C}$) of the global temperature range. The authors hypothesized that this unimodal effect of temperature across terrestrial ecosystems was driven by the removal of specialist interactions occurring at temperature extremes, which may facilitate greater consumer control (Rodríguez-Castañeda 2013). Unimodal temperature effects on trophic control have also been observed in other marine studies (Boudreau *et al.* 2014), and have been hypothesized to arise from the ‘abundant centre hypothesis’ which argues that populations at the extreme of their geographic range are more variable and prone to extinction, resulting in stronger consumer control there (Holt & Keitt 2000). We observed a similar unimodal temperature effect: consumer control prevailed where temperatures were $< 5^{\circ}\text{C}$, and where temperatures were $> 20^{\circ}\text{C}$. This relationship is suggestive of a temperature-driven metabolic effect on trophic control (i.e. Frank *et al.* 2006; O'Connor *et al.* 2009), as metabolism also scales unimodally with temperature (Cossins & Bowler 1987). However, since our data set contained no studies in which average temperatures exceeded 22°C , we were unable to evaluate trophic control over the full temperature range observed throughout the global ocean (-2 to 32°C).

Biodiversity is broadly hypothesized to reduce consumer control, by increasing food chain connectivity and complementarity (McCann 2000). We observed consistently positive effects of cumulative and taxa-specific biodiversity gradients and r_{TC} , yet shark diversity was the single strongest predictor. In highly diverse ecosystems, the removal of one or more consumer species may be compensated for by corresponding increases in the abundance of species that perform a similar ecological role (McCann 2000). In continental shelf communities such compensatory increases of sharks (specifically dogfish *Squalus acanthus*) have been observed following overexploitation of cod (*Gadus morhua*) and other large-bodied fish species (Shackell & Frank 2007). The influence of biodiversity on trophic control through compensation is also contingent on the presence of species able to fill specific ecological niches. The presence or absence of such species may explain some of the residual variability about the diversity-trophic control

relationship (Fig. 2e). Shark diversity which, following temperature, was the single most important regulator of trophic control may also influence r_{TC} through behavioural risk effects (Heithaus *et al.* 2008). Here, the presence of sharks or other predators may modify the behaviour of other consumers in the ecosystem, thus requiring them to invest more energy in predator avoidance and less energy in pursuing their prey, resulting in reduced consumer control.

The effect of trophic level on r_{TC} has been observed previously (McQueen *et al.* 1986; Micheli 1999; Shurin *et al.* 2002), and is consistent with the hypothesis that direct and indirect effects of overexploitation of predator species act like exclusion experiments that reveal strong consumer control (Strong 1992; Worm & Myers 2003; Frank *et al.* 2005, 2006; Myers *et al.* 2007).

Exploitation rate alone was a significant predictor of trophic control (Fig. 2i), and this effect was strongest at high trophic levels and dissipated downward. This finding is consistent with reports of damped cascading effects in situations where high trophic level consumers have collapsed due to excessive exploitation (Frank *et al.* 2005, 2011; Myers *et al.* 2007). However, this exploitation effect was non-significant after accounting for the influence of temperature (Fig. 3a). We calculated exploitation pressure from stock assessment time-series for a subset of commercially harvested species rather than the entire ecological community. It is possible that the temporal and taxonomic incompleteness of available stock assessments, or illegal and unreported fishing activities may have obscured the detection of the effects of exploitation on trophic control. In addition to the rate of exploitation, it is also possible that the manner in which exploitation is apportioned across species or trophic levels, as well as the duration of exploitation may influence the type of trophic control. The remaining six perturbation indices (Table S2) were non-significant predictors of trophic control, further supporting the hypothesis that the type of perturbation may be more important than the level of perturbation.

Mathematical food web models predict omnivory to be a destabilizing force (i.e. Pimm 1993), while empirical syntheses suggest a stabilizing effect on trophic structure (Strong 1992; Polis & Strong 1996; Siuda & Dam 2010). Our results are consistent with the latter hypothesis: the observed effect of ecosystem omnivory on r_{TC} was consistent with the theory that high omnivory leads to stronger resource control. The additive effect of omnivory and shark diversity on r_{TC} we observed (Fig. S12b) may also be due to the increased connectivity associated with these factors, which may operate to diffuse consumer or resource effects. Generally, increased complexity and connectivity within food webs is believed to weaken consumer control (Strong 1992; Polis & Strong 1996).

Phytoplankton cell diameter was also a significant predictor of r_{TC} . Due to the constraints of size-based-predation, small cells ($0.1\text{--}2 \mu\text{m}$) may be inedible by larger zooplankton ($> 300 \mu\text{m}$), whereas larger cells may be directly grazed by these large zooplankton (Stibor *et al.* 2004; Polovina & Woodworth 2012; Boyce *et al.* 2015). Thus, the energy contained in larger cells is more likely to rapidly transfer to higher trophic levels, possibly leading to increased consumer control. For instance, mesocosm experiments have demonstrated contrasting patterns

of trophic control that are highly dependent on the size structure of the phytoplankton community (Stibor *et al.* 2004). The observed effects of primary producer turnover rate on \hat{r}_{TC} are possibly a consequence of reduced grazer metabolic rates, as indicated by mathematical models (Shurin & Seabloom 2005).

Global patterns of trophic control

Our predictions of the patterns of trophic control in areas outside the spatial domain of our analysis suggest that strong resource control (large \hat{r}_{TC}) may be characteristic of the eastern boundary current and of upwelling zones of the equatorial Atlantic and Pacific Oceans (Fig. 4a). This pattern is likely related to the effect of phytoplankton turnover rate, which is higher at these locations (Fig. S19). The variability in \hat{r}_{TC} (indicated by the magnitude of the standard error) also exhibited a spatial pattern, and was highest at oceanic and low-latitude locations and lowest at temperate locations ($\sim 35^\circ\text{--}65^\circ \text{N or S}$; Fig. S20). Finally, it is important to note that \hat{r}_{TC} predictions based on temperature alone (Fig. S21) differed from those based on the MVM (Fig. S20), emphasizing the multifarious nature of the factors explaining these global patterns.

CONCLUSIONS

Notwithstanding the uncertainty associated with data and statistical inference (see Caveats section of SI), our analyses strongly suggest that changes in temperature influence the type and strength of trophic control in marine ecosystems: the effects were clearly visible both within and across studies, oceans and trophic levels. This finding adds an important dimension to recent reports that ocean warming has already contributed to a restructuring of marine ecosystems (Polovina *et al.* 2008; O'Connor *et al.* 2009; Boyce *et al.* 2010, 2014; Polovina & Woodworth 2012; Shurin *et al.* 2012). This warming trend is also expected to result in increases in both primary producer turnover rates (O'Connor *et al.* 2009) and biodiversity (Tittensor *et al.* 2010), and reductions in average phytoplankton concentration (Boyce *et al.* 2010) and cell sizes (Polovina & Woodworth 2012) over the next century, thereby creating context-dependent changes in trophic control. These synergistic effects create the potential for nonlinear effects of temperature on trophic control, which have also been experimentally demonstrated (Shurin *et al.* 2012). Rigorously evaluating the effects of ocean warming on trophic control would require analyses of trophic control in the time domain. However, based on an Ergodic assumption (Rosenzweig 1998), our analyses suggests that continued ocean warming may lead primarily to increased resource control in ecosystems located in cold ($< 5^\circ \text{C}$) high latitude seas, and to greater consumer control in those located in warmer regions ($> 10^\circ \text{C}$). Such increased consumer control is widely interpreted to be characteristic of ecosystems at disequilibrium (Strong 1992; Frank *et al.* 2005; Myers *et al.* 2007; Di Lorenzo *et al.* 2013).

We anticipate that this improved knowledge of how particular ecosystems are structured and how this structure is influenced by different factors will be useful to contemporary marine management and conservation initiatives. Our results suggest that biodiverse ecosystems in warmer waters tend to be more

commonly constrained by resource availability. From a fishery management perspective such resource-controlled ecosystems may be more resistant to the effects of exploitation (Petrie *et al.* 2009), because the production at higher trophic levels is constrained by variability at the base of the food chain rather than by consumers. Removing consumer species from such ecosystems may have a weaker effect on ecosystem structure, because they have little effect on the abundance of lower trophic level species. Alternately, cold-water ecosystems tend to be under strong consumer control and as such are predicted to be more sensitive to harvesting of top consumers. In such ecosystems, apex consumers constrain the abundance of other consumers, and the effects of their removal can cascade downward through the food chain. In some cases, this has been shown to lead to the formation of alternate states, altered food chain structure (Frank *et al.* 2005; Myers *et al.* 2007), changes in biogeochemical cycles (Atwood *et al.* 2013) and failures to respond to conventional management measures (Frank *et al.* 2011).

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AUTHOR CONTRIBUTIONS

D.G.B and K.T.F initiated the study and compiled the data; D.G.B conducted the analyses and drafted the manuscript. All authors discussed the results and contributed to the writing of the manuscript.

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