

LETTER

Predator decline leads to decreased stability in a coastal fish community

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Abstract

Fisheries exploitation has caused widespread declines in marine predators. Theory predicts that predator depletion will destabilise lower trophic levels, making natural communities more vulnerable to environmental perturbations. However, empirical evidence has been limited. Using a community matrix model, we empirically assessed trends in the stability of a multispecies coastal fish community over the course of predator depletion. Three indices of community stability (resistance, resilience and reactivity) revealed significantly decreasing stability concurrent with declining predator abundance. The trophically downgraded community exhibited weaker top-down control, leading to predator-release processes in lower trophic levels and increased susceptibility to perturbation. At the community level, our results suggest that high predator abundance acts as a stabilising force to the naturally stochastic and highly autocorrelated dynamics in low trophic species. These findings have important implications for the conservation and management of predators in marine ecosystems and provide empirical support for the theory of predatory control.

Keywords

Autoregressive model, community matrix, community stability, ecological role of predators, stability analysis, top-down control, trophic dynamics.

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INTRODUCTION

‘Trophic downgrading’ (*sensu* Estes *et al.* 2011) occurs when high trophic level predators are removed from ecosystems, leaving greater proportions of low trophic level species. Over the past decades, a growing body of work has aimed to document and quantify the ecological consequences of trophic downgrading. Some consequences, such as predator release (Rayner *et al.* 2007; Prugh *et al.* 2009; Ferretti *et al.* 2010) and trophic cascades (Frank *et al.* 2005; Carpenter *et al.* 2008; Baum & Worm 2009) are now well studied, along with landscape level effects (e.g. on kelp forests; Estes & Duggins 1995) and water quality impacts (Carpenter *et al.* 2001). However, the consequences for the temporal dynamics and stability of communities are less understood. While these impacts have been discussed based on theory and observations (Kondoh 2003; Rooney *et al.* 2006; Ferretti *et al.* 2010), empirical evidence for shifts in the stability of natural communities is limited. Here, we evaluated the evidence for changes in community stability in a natural fish community over a period of strong, long-term predator decline.

Definitions of community stability are diverse (Grimm & Wissel 1997) and have been placed into two general categories (McCann 2000): (1) dynamic stability, meaning the stability of temporal variation in abundance and (2) structural stability or the ability to resist compositional change such as species extinctions. While predators have been suggested to control

stability in both cases (Kondoh 2003 and Rooney *et al.* 2006 respectively) we focus here on dynamic stability and investigate the role of predators in controlling the characteristic fluctuations in their prey.

We adopt a general representation of dynamic community stability that comes from a matrix parameterisation of the community interactions, termed the *community matrix* (May 1973; Ives *et al.* 2003). This matrix describes the characteristic time-variability of the community in the form of a linear dynamical system. Patterns of community interactions are embodied in the coefficients of the matrix and imbue the community with characteristic dynamics and response to perturbation. As originally described by May (1973), the community matrix exhibits mathematical properties, such as the magnitude of its eigenvalues which characterise the theoretical community dynamics.

Regarding predators, ecological theory has suggested ways predatory interactions may act to control dynamic community stability. For example, McCann *et al.* (1998) showed that communities with a few strong and many weak interactions have greater relative stability, while Rooney *et al.* (2006) showed the importance of top-down interactions in stabilising multiple prey populations which have naturally asynchronous dynamics. Rooney *et al.* (2006) also showed that an erosion in the strength of top-down control acts to destabilise the community dynamics. Other factors including species diversity (Doak *et al.* 1998; McCann 2000), temperature (Chust *et al.*

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2014), and fishing effort (Anderson *et al.* 2008; Shelton & Mangel 2011) have also been shown to influence stability. Importantly, these factors do not act in isolation, whereby less diverse systems may be less stable in response to warming or fishing (McCann 2000; Worm *et al.* 2006). A similar mechanism may also be at play with trophic downgrading (Estes *et al.* 2011) in that predator-depleted systems may be more prone to exogenous human and environmental pressures (Bascompte *et al.* 2005).

Testing theories of dynamic community stability is empirically difficult, partly due to the observational hurdles in monitoring and analysing the high-frequency dynamics of entire communities. In systems with fewer species, empirical studies have shown measures such as the coefficient of variation (CV) to increase in prey species when predators are experimentally removed (Fussmann *et al.* 2000); yet, the CV does not incorporate temporal dynamics into the calculation and thus does not describe dynamic stability *per se*. Other empirical work in predator–prey systems suggests that top-down predation may actually induce chaotic prey dynamics (Hanski *et al.* 1993). At the community level, the question of whether predators tend to amplify or dampen the oscillations of entire community assemblages of low trophic species has far-reaching ecological implications. Yet, much of our current understanding of predatory control of dynamic community stability is limited to theory and/or relatively simple systems, while the consequences of ongoing trophic downgrading of natural communities remain more uncertain.

An important advancement in the empirical analysis of community stability was developed by Ives *et al.* (2003), who showed how the community matrix may be couched into a linear statistical framework using first-order multivariate autoregressive models (MAR(1)) and fit to observed time series of species abundance. With respect to the role of predators, the methodology enables us to construct empirical community matrices (ECMs) across various levels of predator abundance to determine potential patterns of quantitative interactions and measure their stability. The goal in this work is to adapt the ECM methodology to evaluate the role of predation in controlling the fluctuations and stability of lower trophic levels within a complex natural fish community off the coast of Italy. We utilise a uniquely time-resolved multispecies data set spanning 25 years over which predators were serially depleted.

MATERIALS AND METHODS

Data

The data represent 25-year series of species-level catch data from a large floating, stationary fish trap anchored to the seabed 200 m from the Camogli coast of the Ligurian Sea (Fig. 1, and see Balestra *et al.* 1976; Boero & Carli 1979; Boero 1996). The data span 1950–1974 where each year contained *c.* 6 months of fishing, separated by an off season with no recorded catch. The trap was emptied *c.* 3 times per day (before sunrise, after sunrise and before sunset), and fish were identified to species level and weighed (kg). To reduce zeroes and focus the analysis on trophic dynamics, we aggregated the data into three trophic groups according to data in Fish-

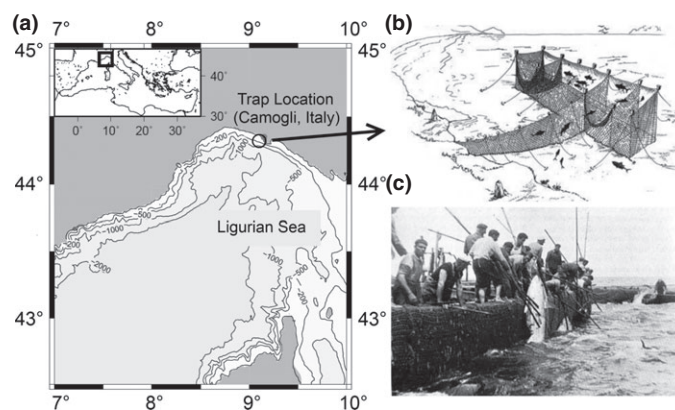


Figure 1 Geographic location and structure of the trap. (a) Geographic depiction of the trap located off the coast of Camogli, Italy, within the Ligurian Sea; insert shows the larger Mediterranean Sea for reference with black box showing the Camogli coast. Panel (b) gives an artist's rendering of the trap structure (credit Raul Cristoforetti). Panel (c) gives a historical picture of fishermen emptying the catch (credit Annamaria Mariotti).

Base (Froese & Pauly 2011) representing: (1) high-predatory (HP) piscivorous species without higher predators in their adult stage (e.g. large sharks, large tunas), (2) meso-predatory (MP) piscivorous species with higher predators in their adult stage (e.g. smaller tunas, garfish, small sharks) and (3) low-trophic (LT) level herbivorous or planktivorous species [e.g. Salema porgy (*Sarpa salpa*), European anchovy (*Engraulis encrasicolus*); Appendix Table S1]. The trap caught adults and juveniles but these could not be differentiated in the data set because individuals were generally not weighed separately; therefore, each classification contains a proportion of juveniles which may not entirely fit the trophic position. We also collected generation time and fecundity estimates for these species from FishBase (Table S1) to evaluate the distribution of key life-history traits in the community and potential asynchronies with respect to individual species' population dynamics (Fig. S1).

Each fishing season lasted on average from mid-April to mid-September, producing 250–350 catch records per year. Our analysis required constant sampling intervals; therefore, we corrected for variable haul times by splitting the daily catch into 12-h intervals, divided by midday. If no hauls were recorded over one or more 12-h periods, the next recorded catch was averaged over all preceding unrecorded intervals. The stationary trap remained completely unaltered over the 25 years; therefore, catch-per-unit-time was directly interpreted as catch-per-unit-effort (CPUE) due to constant catchability. The CPUE index was log-transformed for the stability analysis. Several intervals contained zeroes in at least one trophic group; therefore a small value of 0.1 was added to every record to facilitate log-transformation. In order to satisfy the stationarity requirements for the analysis, each annual time series had the mean and trend removed by estimating and subtracting the simple linear regression line from each trophic level. As an example of both the raw and fitted data, we plotted HP, MP and LT catch and log-transformed CPUE in Fig. S2.

Empirical community matrix

We applied the ECM methodology (Ives *et al.* 2003) to the multivariate ($p = 3$) time series of HP, MP and LT CPUE. The ECM analysis can be applied to any length series; however, we structured the analysis *sequentially* using sliding subsets (or time windows) of the data which allowed us to investigate non-stationary trends in stability over time (outlined below). We first outline the methods for an arbitrary time window and then explain our sliding window approach.

The ECM is based on fitting a first-order multivariate autoregressive (MAR(1)) time series model (Ives *et al.* 2003) to the multivariate CPUE data of the form

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{e}_t = \begin{bmatrix} b_{1,1} & b_{1,2} & b_{1,3} \\ b_{2,1} & b_{2,2} & b_{2,3} \\ b_{3,1} & b_{3,2} & b_{3,3} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}_{t-1} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}_t, \quad (1)$$

where \mathbf{x}_t and \mathbf{x}_{t-1} contain the three CPUE indices for HP (x_1), MP (x_2) and LT (x_3) species at time t and $t-1$ respectively. Here, \mathbf{B} is the community matrix (i.e. the coefficients of the linear dynamical system) which describes the relationships between HP, MP and LT CPUE, and \mathbf{e}_t is a vector of multivariate-normal distributed process errors with zero mean and covariance Σ that can be interpreted as environmental forcing (Ives *et al.* 2003). In our three trophic level case, matrix \mathbf{B} contains nine elements which describe the CPUE dynamics. The diagonal coefficients of the ECM represent the persistence (autocorrelation) within a trophic level and the off-diagonal coefficients represent the intertrophic relationships. For example, HP species (x_1) would follow the linear relationship

$$x_{1(t)} = b_{1,1}x_{1(t-1)} + b_{1,2}x_{2(t-1)} + b_{1,3}x_{3(t-1)} + e_{1(t)}, \quad (2)$$

where the $b_{1,1}x_{1(t-1)}$ term gives the persistence of HP, $b_{1,2}x_{2(t-1)}$ measures the effect of MP CPUE and $b_{1,3}x_{3(t-1)}$ is the effect of LT CPUE on that of HP respectively, and $e_{1(t)}$ gives the environmental forcing experienced by HP. Mathematically, \mathbf{B} is a stochastic analogue to the Jacobian matrix, formed by first-order partial derivatives evaluated at the equilibrium of a general deterministic community dynamics model. Following the deterministic stability analysis of May (1973), Ives *et al.* (2003) also derive analogous stochastic stability metrics for MAR(1) models.

Parameter estimation

If T is the length of the time series, the parameters of the \mathbf{B} matrix in the MAR(1) model are estimated using ordinary least squares regression using lagged time coordinates, i.e.

$$\hat{\mathbf{B}} = (\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'\mathbf{Y}. \quad (3)$$

Here, $\mathbf{X} = [x_1, x_2, x_3]_{[1:(T-1)]}'$ contains rows 1 to $T-1$ of the CPUE matrix and $\mathbf{Y} = [x_1, x_2, x_3]_{[2:T]}'$ is the CPUE matrix with the first row removed (note that T ranged between 250 and 350 for any particular year). Also note that the 'hat' notation $\hat{\cdot}$ represents an empirical estimate. The MAR(1) model is then a multivariate (lagged) regression between times t and $t-1$. The environmental perturbation matrix Σ is estimated by

$$\hat{\Sigma} = \frac{1}{T-p-1} (\mathbf{Y} - \hat{\mathbf{B}}\mathbf{X})' (\mathbf{Y} - \hat{\mathbf{B}}\mathbf{X}), \quad (4)$$

where p is the number of trophic levels (here $p = 3$). In order to validate the statistical assumptions of the MAR(1) model, which include independence and normality of the errors, the quantile–quantile (QQ) plot of model residuals along with their multivariate sample autocorrelation function were evaluated and are given in Figs S3–S4.

Stability properties of MAR(1) models

Ives *et al.* (2003) derive three measures of stability from MAR(1) models that characterise the community in terms of its resilience, reactivity and resistance to the environmental forcing contained in Σ . These stability properties of the MAR(1) model are determined from the \mathbf{B} matrix and defined below; full derivations of the stability metrics are given in Ives *et al.* (2003).

Resilience is a measure of return time of the community from an ecological disturbance, or displacement from equilibrium. The return rate to equilibrium (i.e. the resilience) is governed by the leading eigenvalue of \mathbf{B} , therefore,

$$\text{Resilience} = -\max(\lambda_{\mathbf{B}}), \quad (5)$$

where $\lambda_{\mathbf{B}}$ is the leading eigenvalue of \mathbf{B} . For small eigenvalues, the trophic abundances are resilient to perturbations from the environment and community equilibrium is quickly regained following displacement. With larger values approaching one, disturbances decay more slowly.

Reactivity measures the average size of displacement for a system when an environmental disturbance occurs. The average reaction to disturbance is quantified as the ratio between the summed environmental matrix eigenvalue, and the summed eigenvalues of the total covariance matrix \mathbf{V}_{∞} , i.e.

$$\text{Reactivity} = -\frac{\text{tr}[\Sigma]}{\text{tr}[\mathbf{V}_{\infty}]}, \quad (6)$$

where the operator $\text{tr}[\cdot]$ is the matrix trace, equal to the sum of the eigenvalues and $\mathbf{V}_{\infty} = \mathbf{B}\mathbf{V}_{\infty}\mathbf{B}' + \Sigma$ (see Formula S1 for an expression for \mathbf{V}_{∞}). In a reactive system, disturbances cause a large initial displacement, whereas a stable community is displaced less.

Resistance is a measure of overall variability in community interactions. The CPUE data have covariance matrix \mathbf{V}_{∞} which includes environmental effects (Σ) and the trophic interactions. The amount of total CPUE variance explained by community interactions (as opposed to environmental effects) is calculated as the determinant of the difference between these matrices ($\mathbf{V}_{\infty} - \Sigma$). Standardised by the total variance, the index is

$$\text{Resistance} = \frac{-\det(\mathbf{V}_{\infty} - \Sigma)}{\det(\mathbf{V}_{\infty})}. \quad (7)$$

Note that, as given, the resilience (5) and resistance (7) metrics are of the opposite sign compared to those given in Ives *et al.* (2003); the rationale is that these measures decrease as com-

munity stability decreases, making the interpretation of temporal trends more intuitive.

To compare the empirical stability analysis with more traditional metrics, we calculated the coefficient of variation (CV) within each year for HP, MP, LT and the total CPUE and then estimated trends over time. To evaluate the uncertainty in the stability estimates, we generated a bootstrap distribution ($n = 500$) of the community matrix coefficients and stability metrics as described in Ives *et al.* (2003).

Trends and drivers of stability

To investigate non-stationary trends in community stability, we applied the MAR(1) stability analysis sequentially by estimating the parameters using sliding subsets of CPUE data. Our first window comprised a single year, meaning the stability analysis was applied to each individual year time series, generating a 25-year time series of MAR(1) parameters and stability metrics. To investigate lower frequency change in the community dynamics and test the sensitivity of our results, we also performed the analysis using overlapping five and 10-year windows. This was done by forming the lagged rows of **X** and **Y** within each individual year, then stacking **X** and **Y** matrices into five- and 10-year blocks and performing the regression on those. For example, the 5-year sliding window would first stack years 1–5, then years 2–6, and so on. The five- and 10-year analysis then yielded time series of stability with length 21 and 16 years respectively. All trends (including CPUE and estimated stability indices) were calculated using generalised least squares regression. For simplicity, we assumed a first-order autoregressive structure to account for correlations in the regression model residuals. Note that statistical significance of trends was assessed using the single-year window only to avoid inflating the significance and underestimating the *P*-value of the trends by using the data multiple times.

As another sensitivity analysis and to further test the top-down control hypothesis, we repeated the stability analysis three additional times, each time leaving out one trophic level time series (i.e. HP, MP or LT) from the CPUE data. We then correlated (using the absolute value of Pearson's correlation) the estimated bivariate community stability time series against the excluded trophic level CPUE time series, thereby testing the relationship between a trophic level and the stability in the remainder of the community. This 'leave-one-out' sensitivity analysis was a way to objectively correlate individual trophic level CPUE with the stability of the rest of community. A further sensitivity analysis was performed with respect to the trophic classifications of species. Based on size and predator/prey data available in FishBase (Froese & Pauly 2011), some trophic classifications were uncertain (e.g. *Microsistius poutassou* (Blue whiting) is similar in size to forage species, but is primarily piscivorous in diet). Therefore, we changed the category of these borderline species to assess the impact on the results. In total there were 10 species that could be reasonably placed in at least two categories (symbol * in Table S1).

To investigate potential drivers of community stability, we used multiple regression and model selection based on the Akaike Information Criterion (AIC) (Zuur *et al.* 2009) to

compare estimated trends in stability with community species richness (*R*) and diversity (*H*) as well as regional fishing effort (*E*) and sea surface temperature (SST). Species richness was calculated as the total number of species caught in a particular year. Diversity was estimated by the Shannon Index $H = -\sum_{i=1}^R p_i \ln p_i$, where p_i is the proportion of species *i* in *R*, which is a measure of how evenly the CPUE was distributed among the total number of species. Regional fishing effort was compiled by splicing two historical records: the number of boats registered (1950–1964) and the total horsepower (1964–1972) of fishing vessels in the local region of the Ligurian Sea (ISTAT 1972). This was calculated as a relative index between zero and one to account for the different units of the two records. Finally, regional SST was downloaded from the Simple Ocean Data Assimilation (SODA; University of Maryland 2014) database available from <http://www.atmos.umd.edu/~ocean/>. These data are shown in Fig. S5. All statistical analyses were performed in R and the scripts necessary to estimate the **B** matrix, stability metrics, and perform bootstrapping for uncertainty are provided in Table S2.

RESULTS

Based on the biological parameters extracted from FishBase, we found that generation times were highly variable at any particular trophic level, suggesting highly asynchronous dynamics in HP, MP and LT. Species from all three trophic levels exhibited generation times and absolute fecundity estimates varying several-fold (Table S1, Fig. S1).

Across the study period 1950–1975, total CPUE remained relatively stable (Fig. 2a) but experienced a strong trophic reorganisation. Both HP and MP CPUE declined by *c.* 80%

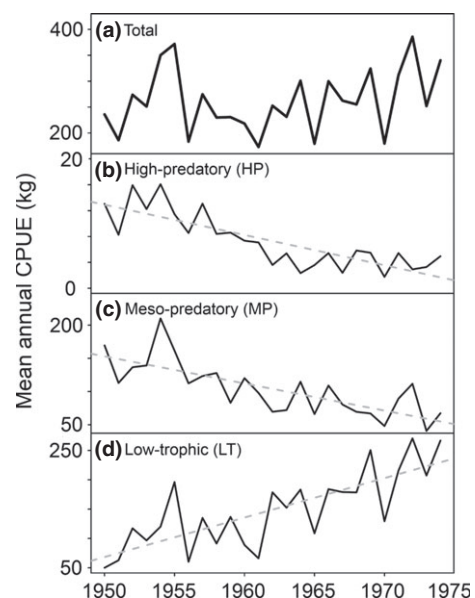


Figure 2 Trophic reorganisation. Mean annual CPUE (kg day^{-1}) for (a) all species caught in the trap (Total); (b) High-predatory (HP) species; (c) Meso-predatory (MP) species; and (d) Low-trophic (LT) herbivorous/planktivorous species. Trends lines are also shown. See Table S1 for a list of species in each trophic level.

(Fig. 2b and c), whereas LT CPUE increased four-fold (Fig. 2d). Species richness (# of species caught per year) showed no statistical trend for all species combined ($P > 0.1$; Fig. S5C) or individual trophic levels ($P > 0.1$; Fig. S6A). Total richness had an annual mean of 49 and a maximum of 51 species, meaning that nearly every species was caught at least once per year; however, many species were caught infrequently (e.g. *Coryphaena hippurus* only late in the season) while others were caught almost daily (e.g. *Auxis rochei rochei*). Shannon's diversity showed some interannual variation with no significant trend over time for total CPUE ($P > 0.1$; Fig. S5D) or individual trophic levels ($P > 0.1$; Fig. S6B). Some LT species (e.g. *Sarpa salpa*, *Torarodes sagittatus*, *Oblada melanura*, *Loligo vulgaris*) increased 10-fold and exhibited strong oscillations over the 25 years, while others, including large predatory sharks, decreased and were almost completely absent from the catch by 1974 (Fig. S7).

The estimated ECM coefficients indicated that top-down relationships were stronger than bottom-up over the course of the 25 years (Fig. 3a). Examining the frequency distribution of individual matrix coefficients, the negative effect of HP on MP and of MP on LT (coefficients $b_{2,1}$ and $b_{3,2}$ respectively) was consistently further from zero (in a negative direction) than the positive effect of prey on the CPUE of their predators (i.e. $b_{2,1}$ and $b_{3,2}$ differ by *c.* 10% absolute difference relative to $b_{1,2}$ and $b_{3,2}$ respectively). However, temporal trends in autoregressive coefficients (Fig. 3b) indicated that these top-down relationships generally weakened over time as negative top-down coefficients (e.g. $b_{1,2}$ and $b_{3,2}$) trended upwards towards zero ($P < 0.01$). Bottom-up coefficients (e.g. $b_{1,2}$, $b_{3,2}$) did not change significantly over time ($P > 0.1$) except for the positive effect of LT CPUE on HP ($b_{1,3}$), which had a strong positive slope with coefficients ranging from slight negative to

slight positive values ($P < 0.001$). The persistence terms (i.e. diagonal matrix coefficients) showed no trend in HP ($b_{1,1}$) and MP groups ($b_{2,2}$) while the LT group ($b_{3,3}$) showed a strong increasing trend ($P < 0.01$), which resulted in more highly autocorrelated dynamics with longer characteristic excursions from the mean LT CPUE.

All three derived stability indices showed significant trends over time, with decreasing resistance and resilience and increasing reactivity ($P < 0.001$; Fig. 4) as estimated from changes in the ECM. Stability trends from all three time windows showed similar patterns. The general tendency was for the longer windows to give smoothed versions of the shorter. In general, all three stability metrics appeared to follow a linear trend which closely tracked the declines in HP and MP, and increases in LT.

The leave-one-out analysis (Fig. S8) indicated that predators more strongly controlled the stability of prey than prey controlled the stability of predators. The strongest correlation occurred as a positive relation between HP CPUE and the stability of the MP and LT community ($\bar{r} = 0.753$, where \bar{r} is the average magnitude of the correlation across the three stability metrics), indicating that highest stability was found when CPUE of HP was high. MP CPUE showed a similar positive correlation with the stability of the HP and LT community ($\bar{r} = 0.748$) while the effect of LT CPUE on the stability of HP and MP was weaker ($\bar{r} = -0.520$) and in an opposite direction. Additionally, the results of our reclassification sensitivity analysis confirmed that the observed results were robust to species classification. No single-species reclassification changed any of the direction or statistical significance of the trends in the coefficients and stability metrics. When all 10 uncertain classifications were reclassified, results still remained similar (all trends had the same sign) but the

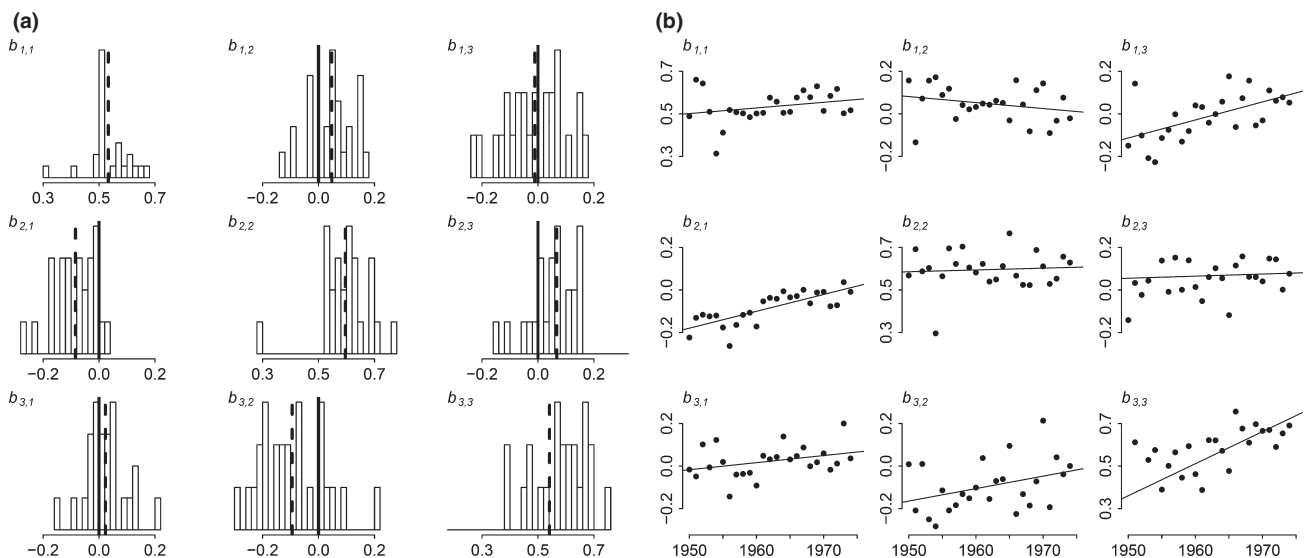


Figure 3 Community dynamics. (a) Frequency distributions of the elements of the estimated autoregressive coefficient matrix \hat{B} . The matrix is organised as in Equation 1 where the top row gives the coefficients for the effects on high-predators (HP), the second row for the meso-predators (MP) and third row for the low-trophic (LT) group. The dashed line gives the mean coefficient across 25 years, the dark line gives the zero line representing no effect, and note that the diagonal and off-diagonal elements are shown with different axis values. (b) Trends in the autoregressive coefficients over time along with the generalised least squares regression line. Note that each subfigure in (a) and (b) is created using only the single-year window of CPUE data (see text).

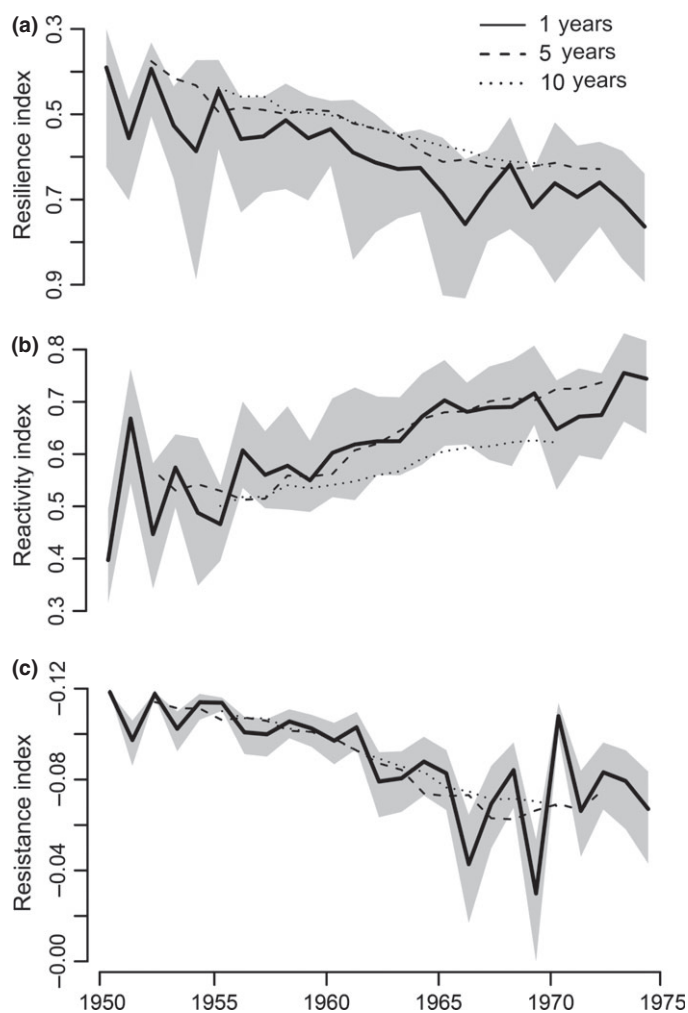


Figure 4 Trends in stability. Trends in empirically estimated indices of community stability: (a) ‘Resilience’, (b) ‘Reactivity’, (c) ‘Resistance’ – see text for definitions. Each plot gives three sets of time series based on the three analysis time windows (one, five and 10 years). Trends for each individual time window are significant ($P < 0.001$) based on generalised least squares regression. The gray area represents the 95% bootstrapped confidence intervals.

trend in the resistance metric was no longer statistically significant.

The multiple regression analysis and AIC model selection showed that fishing pressure was the most important predictor of declining community stability (Fig. S9). Across all three stability metrics, fishing effort was the only variable retained and exhibited a highly significant slope coefficient ($P < 0.001$). Finally, calculated trends in the coefficient of variation (CV) showed no significant trend over time in total CPUE ($P > 0.1$) or individual trophic levels ($P > 0.1$; Fig. S10).

DISCUSSION

Reduced dynamic stability due to trophic downgrading has important implications for conservation and management, yet has been difficult to empirically demonstrate in natural systems. Applying an empirical stability analysis to a long-term,

high-resolution, community-wide multispecies data set from the Ligurian Sea, we were able to demonstrate the destabilisation of community stability over a period of strong predator depletion. The trophically downgraded community exhibited a rise in the level of autocorrelation of prey, leading to higher sensitivity to stochastic forcing (lower resistance), larger mean displacements from forcing (higher reactivity) and longer characteristic return times (lower resilience). Trends in stability could be best explained by regional increases in fishing effort, and not by temperature, species diversity, nor richness (according to AIC model selection).

In ecological terms, the erosion of stability is a consequence of trophic downgrading when high trophic biomass is replaced with low trophic species of more variable life history. Although the total CPUE of the system remained relatively stable over time, the trophic distribution of CPUE changed significantly (Fig. 2; also see Boero 1996). In the Ligurian system and in general, LT species are characterised by faster life histories including shorter generation times and higher fecundities (Table S1, Fig. S1), relative to HP and MP. We observed the replacement of HP and MP with LT which naturally gave rise to more variable community dynamics, thus decreasing community stability. This predator-release process of asynchronous dynamics is in line with the theory that generalist predators act as community-wide integrators of multiple asynchronous natural cycles (Rooney *et al.* 2006). Early in the time series, the Ligurian community was characterised by several predators with a highly generalist diet (e.g. *Thunnus thynnus*, *Isurus oxyrinchus*; see www.fishbase.org for dietary studies), which likely predated upon multiple species of various life histories at any one trophic level (Table S1). A food-web model of the nearby Catalan Sea (Coll *et al.* 2006) showed a similar ecosystem structure where predators interact with a diverse assemblage at each level of the trophic web. A similar type of structure was likely present in the Ligurian system, leading to predator release of asynchronous population dynamics in lower trophic levels as predators declined.

In our study system, and in any complex ecological setting, there are likely a suite of factors influencing community dynamics. Diversity–stability relationships (Doak *et al.* 1998; McCann 2000), along with potentially destabilising effects of increased temperature (Chust *et al.* 2014) and fishing (Anderson *et al.* 2008; Shelton & Mangel 2011) do not act independently. Although data were not available at the daily time scales to include these factors as covariates in our analysis, we used annual data series and found that decreases in stability were best explained by increased fishing effort (based on AIC variable selection). One explanation is that fishing caused the decline of predators and lead to the rise of LT species and the destabilisation of the resulting community. Alternatively, the variance of fishing effort (opposed to the mean) may have also caused unstable oscillations in the community; however, previous single-species work in California found no relationship between the variance of fishing pressure and the stability of individual populations (Anderson *et al.* 2008). In the Ligurian system, it is difficult to determine the role of variable fishing effort without high-resolution fishing effort data for the regional fleet. However, we note that data

for the broader Mediterranean ecosystem indicate that landings of all trophic levels increased consistently over the study period (see Fig. S11). In terms of other variables, the lack of relationship between stability and species diversity, richness or temperature is largely due to a lack of any trends in these quantities over the study period (Fig. S5). Unfortunately, we were unable to test potential bottom-up effects on stability from primary productivity due to a lack of available data. Furthermore, some potentially confounding effects of measurement error are introduced by using CPUE as an index of abundance (e.g. Harley *et al.* 2001). Such error may include spatial effects, such as range shifts, which may partly explain the overall changes in CPUE (Fig. 2). However, the primary result of the paper is that stability declined concurrent with a trophic shift in the local assemblage (defined as the region surrounding the trap). The precise cause of this trophic shift is likely explained by a complex suite of factors, including fishing, spatial effects and range shifts.

The ECM derivation of Ives *et al.* (2003) provides a powerful tool to connect community dynamic theory with observed time series. Beyond our specific focus on predator decline, the methodology can be used to study a range of community interactions thought to affect stability. A major advantage of the ECM methodology is its link to the large body of pre-existing theory related to the community matrix representation (May 2001). In our study, the ECM was extended in a straightforward way to investigate non-stationary cases where stability was hypothesised to change over time. The ECM methodology, including non-stationary cases, could also be integrated with more sophisticated statistical tools, such as autoregressive state space models (Holmes *et al.* 2012) that are specifically designed for data with complex error structures.

Definitions of stability vary in their interpretation (Grimm & Wissel 1997; McCann 2000). Here, we focused on dynamic stability as defined by the community matrix; however, other definitions of stability focusing on different aspects may show alternative relationships with predator abundance. Compared to the coefficient of variation (CV), ECM stability showed declines while the CV was relatively flat (Fig. S10). While the CV provides a summary measure of variation, the ECM is specifically defined with respect to time, and therefore directly quantifies dynamic stability. Additional definitions of dynamic stability focus on single-species dynamics; for example, Anderson *et al.* (2008) and Shelton & Mangel (2011) focus on nonlinearity and environmental variation in single stock dynamics and do not directly deal with the dynamics of full communities. It is, therefore, critical that hypotheses are clear with respect to the definition of stability, in order to properly test mechanisms and avoid conflicting results (see Grimm & Wissel 1997).

In summary, our results provide empirical support for the hypothesis that the depletion of predatory species can cause declines in the dynamic stability of natural communities. These findings have important implications in the context of widespread predator declines in exploited systems (Veit *et al.* 1997; Ward & Myers 2005; Ferretti *et al.* 2008, 2010). Through targeted fishing and bycatch, many fisheries have depleted high trophic level species such as large sharks and

tunas and our results suggest these trophically downgraded communities may be destabilised as a result. Understanding the role of predators in community dynamics is crucial to determine and manage the consequences of trophic downgrading (Estes *et al.* 2011) which is occurring throughout the world's oceans and ecosystems.

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AUTHORSHIP

GLB, MD, CM, FF, HKL designed the research; GLB, CM analysed the data; FF, FB contributed data; GLB, MD, CM, FF, FB, HKL wrote the paper.

REFERENCES

- Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J. *et al.* (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, 452, 835–839.
- Balestra, V., Boero, F. & Carli, A. (1976). Andamento del pescato della tonnarella di camogli dal 1950 al 1974. *Boll. Pesca Piscic. Idrobiol.*, 31, 105–115.
- Bascompte, J., Melian, C.J. & Sala, E. (2005). Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl Acad. Sci.*, 102, 5443–5447.
- Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.*, 78, 699–714.
- Boero, F. (1996). Episodic events: their relevance to ecology and evolution. *Mar. Ecol.*, 14, 237–250.
- Boero, F. & Carli, A. (1979). Catture di Elasmobranchi nella tonarella di Camogli. *Boll. Mus. Ist. Biol. Univ. Genova*, 47, 28–34.
- Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D. *et al.* (2001). Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol. Monogr.*, 71, 163–186.
- Carpenter, S.R., Brock, W.A., Cole, J.J., Kitchell, J.F. & Pace, M.L. (2008). Leading indicators of trophic cascades. *Ecol. Lett.*, 11, 128–138.
- Chust, G., Allen, J.I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K. *et al.* (2014). Biomass changes and trophic amplification of plankton in a warmer ocean. *Glob. Chang. Biol.*, 2010, 2124–2139.
- Coll, M., Palomera, I., Tudela, S. & Sardà, F. (2006). Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *J. Mar. Syst.*, 59, 63–96.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.
- Estes, J.A. & Duggins, D.O. (1995). Sea otters and kelp forest in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.*, 65, 75–100.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet earth. *Science*, 333, 301–306.
- Ferretti, F., Myers, R.A., Serena, F. & Lotze, H.K. (2008). Loss of large predatory sharks from the Mediterranean Sea. *Conserv. Biol.*, 22, 952–964.

- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecol. Lett.*, 13, 1055–1071.
- Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.
- Froese, R. & Pauly, D. (2011). FishBase [WWW Document]. FishBase. Available at: www.fishbase.org. Last accessed 1 May, 2014.
- Fussmann, G.F., Ellner, S.P., Shertzer, K.W. & Hairston, N.G. Jr (2000). Crossing the Hopf bifurcation in a live predator-prey system. *Science*, 290, 1358–1360.
- Grimm, V. & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109, 323–334.
- Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, 364, 232–235.
- Harley, S.J., Myers, R.A. & Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Can. J. Fish. Aquat. Sci.*, 58, 1760–1772.
- Holmes, E.E., Ward, E.J. & Willis, K. (2012). MARSS: multivariate autoregressive state space models for analyzing time series data. *R J.*, 4, 11–19.
- ISTAT (1972). *Istituto Nazionale di Statistica. Annu. Stat. Della Pesca E Della Caccia*. Istituto Centrale Di Statistica, Rome.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73, 301–330.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299, 1388–1391.
- May, R. (1973). *Stability and Complexity in Model Ecosystems*, 1st edn. Princeton University Press, Princeton.
- May, R. (2001). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.
- McCann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. *et al.* (2009). The rise of the mesopredator. *Bioscience*, 59, 779–791.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. (2007). Spatial heterogeneity of mesopredator release within an oceanic island system. *Proc. Natl Acad. Sci.*, 104, 20862–20865.
- Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, 442, 265–269.
- Shelton, A.O. & Mangel, M. (2011). Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl Acad. Sci.*, 108, 7075–7080.
- University of Maryland. (2014). Simple Ocean Data Assimilation [WWW Document]. Available at: <http://www.atmos.umd.edu/~ocean/>. Last accessed 1 May, 2014.
- Veit, R., McGowen, J., Ainsley, D., Wahl, T. & Pyle, P. (1997). Apex marine predator declines ninety percent in association with changing oceanic climate. *Glob. Chang. Biol.*, 3, 23–28.
- Ward, P. & Myers, R.A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, 86, 835–847.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. *et al.* (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, 787–790.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

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