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Fishing, fast growth and climate variability increase the risk of collapse

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Species around the world have suffered collapses, and a key question is why some populations are more vulnerable than others. Traditional conservation biology and evidence from terrestrial species suggest that slow-growing populations are most at risk, but interactions between climate variability and harvest dynamics may alter or even reverse this pattern. Here, we test this hypothesis globally. We use boosted regression trees to analyse the influences of harvesting, species traits and climate variability on the risk of collapse (decline below a fixed threshold) across 154 marine fish populations around the world. The most important factor explaining collapses was the magnitude of overfishing, while the duration of overfishing best explained long-term depletion. However, fast growth was the next most important risk factor. Fast-growing populations and those in variable environments were especially sensitive to overfishing, and the risk of collapse was more than tripled for fast-growing when compared with slow-growing species that experienced overfishing. We found little evidence that, in the absence of overfishing, climate variability or fast growth rates alone drove population collapse over the last six decades. Expanding efforts to rapidly adjust harvest pressure to account for climate-driven lows in productivity could help to avoid future collapses, particularly among fast-growing species.

1. Introduction

Dramatic declines across many species remain an important issue in ecology and conservation, particularly given the consequences of these declines for entire communities and the future resilience of these systems [1]. Evidence from terrestrial species suggests that a large body size or feeding high in the food chain can increase vulnerability [2,3], patterns that are consistent with theory and increased extinction risk in species with slow population growth rates [4]. These patterns, however, may not hold in the ocean. Instead, marine species with fast life histories are as likely, if not more likely, to decline below low thresholds compared to species with slower growth rates [5]. Why these patterns may be substantially different in the ocean remains unclear.

One possible explanation is that short-lived species display larger population fluctuations in response to climate variability than long-lived species, making them more likely to decline below any fixed threshold [6–9]. The influences of climate on marine population dynamics appear widespread: environmental regimes are detectable in nearly seven out of every 10 stocks and temperature effects on population dynamics are common [10,11]. Fast-growing species may be especially sensitive to such climate variability because populations grow and decline quickly [9,12,13]. Sardines in southern California, for example, have fluctuated by more than an order of magnitude for at least the past couple of millennia, often on a 50–60 year period, with no influence from fishing [14]. An open question is whether high sensitivity to climate alone can explain the high vulnerability to collapse of otherwise fast-growing species over the past half-century. If this were a strong effect, one would expect that the probability of collapse would increase with growth rate even among populations that do not experience overfishing.

The interactions between fishing and climate variability may also be important. Fishing effects include both immediate impacts on abundance as well as longer term consequences for population dynamics through the truncation of age-distributions, selection for particular life-history strategies (e.g. early maturation), reduction of intraspecific diversity, alteration of species interactions and destruction of habitat [15,16]. A growing body of evidence suggests that these changes create populations that are more sensitive to climate variability for reasons that include the loss of long-lived individuals, strengthened cohort resonance, reduced density-dependent effects, enhanced nonlinear dynamics, or a lower intraspecific diversity of climate responses [8,16–19]. These changes can increase the magnitude of population fluctuations driven by environmental variability [8,15–18], and may increase the probability or duration of a large population decline [12,13,19].

In addition, fishing could interact with climate variability through coupled social–ecological dynamics, rather than through ecological changes alone. When the environment causes a decline in population productivity, fisheries management risks driving the population to collapse if harvest is not rapidly reduced [13,20]. Delays in management responses, as are common in complex social systems, increase the probability of a collapse [20]. In this context, fast-growing species are especially difficult to manage, because they respond especially rapidly to environmental change [13,20,21]. If interactions between fishing and climate variability (rather than climate alone) are important in driving population collapse, we would expect fewer collapses among unfished populations, even in regions with highly variable climates.

Despite strong interest in fishing, climate and the life histories of populations that decline, most analyses to date examine only a few populations or a few species [9,11–13,18,22]. Whether there are general phenomena affecting most marine fishes across a diversity of ecosystems remains unclear, and there have been calls for expanded analyses [13]. In addition, it remains unclear whether the sensitivity of fast-growing species to climate variability can explain their high vulnerability to collapse in recent decades across a wide range of species [5]. Here, we used boosted regression trees (BRTs) [23] to identify which aspects of fishing, climate, species traits and their interactions best explain collapses and relative population levels for marine fish populations around the world. BRTs provide a quantitative approach that can account for nonlinear relationships and interactions between different variables, therefore making this method particularly appropriate. In particular, we address four questions: (i) do the interactions of fishing with rapid growth rates contribute to population collapses? (ii) are fishery collapses more likely in regions with more variable climates? (iii) do the interactions of climate and fishing contribute to collapses? and (iv) what are the relative influences of fishing, life history and climate on population collapses? Across more than 150 populations, we found that overfishing played a strong role in collapse, but interactions suggested that fast-growing species in variable climates were especially sensitive to overfishing.

2. Material and methods

(a) Fish and fisheries data

We examined population collapses within the RAM Legacy Stock Assessment Database version 1.0, which has compiled time-series of population biomass and fishing pressure from 1950 to 2008 [24]. We defined a stock as collapsed if its minimum annual biomass (B_{min}) fell to less than 20% of the biomass necessary to support maximum sustainable yield (B_{MSY}) [5]. B_{MSY} values were either from stock assessments or from Schaefer surplus-production models fit to catch and biomass [5,24]. This definition of collapse used a fixed threshold, and declines below this level could be driven by fishing, climate, natural variability or other factors. Temporal variation in B_{MSY} has been recognized in many populations, though we do not consider it here [13]. In addition, we examined mean depletion to measure the relative population level of each stock (average B/B_{MSY} for a stock).

We also examined alternative metrics of population status to test the sensitivity of our results. Collapses may be more likely in longer time-series, and so we also used metrics of collapse and depletion that only examined the last 20 years. Similarly, we examined a metric of collapse that required stocks to stay below 20% of B_{MSY} for at least 4 years, so that a single year of low biomass would not appear as a collapse. We also examined collapses after filtering out small pelagics (families *Clupeidae* and *Engraulidae*), since these species are known to fluctuate strongly [9,14]. Finally, it is possible that our definition of collapse highlights stocks that are highly variable, rather than primarily those that fall to low levels. We therefore also examined those species that had grown to at least twice the level of B_{MSY}.

We developed two metrics of overfishing from the RAM Legacy dataset. Maximum fishing was defined as the maximum fishing mortality (F_{max}) relative to the mortality consistent with maximum sustainable yield (F_{MSY}). Duration of overfishing was the proportion of years in which overfishing ($F/F_{MSY} > 1$) occurred. We note that F_{MSY} varies across species (e.g. typically higher for species with higher productivity), and so our metrics of overfishing are partially corrected for these differences to aid comparisons. We also examined mean relative fishing pressure (mean F/F_{MSY}), but found it to be closely correlated to maximum fishing (F_{max}/F_{MSY}) ($r^2 = 85\%$).

We compiled data on maximum length, individual growth rate (von Bertalanffy K), trophic level, average egg diameter and fecundity from Fishbase [25] in April 2015, supplemented by a literature search where values were missing [5]. We also classified each stock by its management organization to help account for regional differences in management. Organizations were defined at the national level, with the exception of 'Europe' and 'multinational' (non-European).

(b) Climate data

We calculated climate variability for each large marine ecosystem (LME). There are 63 coastal LMEs, and to this, we added seven open ocean 'LMEs' (West Pacific, East Pacific, Indian Ocean, North Atlantic, South Atlantic, Subantarctic and Arctic) to help match measures of climate variability to each fish stock (figure 1).

We calculated climatic variability from sea surface temperatures (SSTs) in the 1870–2014 HadISST dataset [26]. We spatially averaged the monthly SSTs within each LME and de-trended each time-series by subtracting a linear regression from the values. We measured short-term climate variability as the standard deviation of the de-trended SSTs, which is dominated by the seasonal cycle. We also measured long-term climate variability by low-pass filtering the de-trended monthly SSTs with a 10-year running mean before calculating the standard deviation. These latter time-series were significantly correlated to the Pacific Decadal Oscillation, the North Atlantic Oscillation or the Atlantic Multidecadal Oscillation for all LMEs ($p < 0.05$), except the Chukchi Sea. We also examined other running mean window sizes (2–119 months), but climate variability at annual or lower frequencies were well correlated to decadal variability ($r^2 > 0.8$), while climate variability at frequencies higher than annual
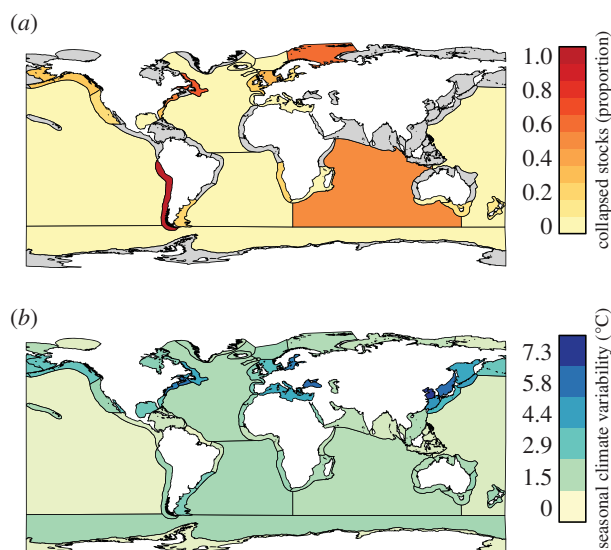
Figure 1. Maps of large marine ecosystems (LMEs) showing global variation in (*a*) proportion of stocks that have ever collapsed, and (*b*) seasonal climatic variability (standard deviation of detrended monthly SSTs, °C). Grey regions in (*a*) indicate LMEs without stock status information. (Online version in colour.)

were well correlated to monthly variability ($r^2 > 0.9$; electronic supplementary material, figure S1). Finally, we also calculated the 'colour of noise' in the SSTs. Colour in this context measures the relative importance of high versus low frequency oscillations, and it is calculated as the exponent of a $1/f^\beta$ model fit against the power spectrum in log-coordinates [27]. We note that temperature is only one of many possible factors that drive marine dynamics; others include transport and the magnitude and type of production [28].

(c) Statistical modelling

We used BRTs to determine which explanatory variables (electronic supplementary material, table S1) and interactions were most closely related to fishery declines. Regression trees provide a statistical learning technique that is well suited to detecting nonlinear relationships and interactions among factors [23]. Each tree is formed by sequentially dividing the data into homogeneous regions defined by a predictor variable. BRTs increase predictive performance by combining many, relatively simple regression tree models together by sequentially fitting each to the residuals from previous trees [29]. The final model is formed as an average across the full set of trees [23].

Here, we fitted separate BRT models for collapse and depletion. Models were fitted to the 154 stocks across 72 species and 25 LMEs that had information on fishing pressure and life-history traits (electronic supplementary material, figure S8). We used a Bernoulli error distribution for collapse and a Gaussian distribution for depletion after log-transforming mean B/B_{MSY}. A Shapiro–Wilks test did not reject normality of the residuals for the depletion model ($p = 0.27$). We measured relative interaction strength using the Elith metric, which measures the residual variation between pairwise model predictions with and without interactions [23]. Values near zero indicate negligible interactions.

For tree-building, we used a learning rate of 0.001, a tree complexity of 10 and a bag fraction of 75%. Slower learning rates and higher tree complexities provided negligible increases in predictive power. Tree complexity controls how many levels of interactions are fitted, while learning rate determines the contribution of each new tree. We used 500 bootstrap replicates to calculate 95% confidence intervals (CIs) [29].

We evaluated models against subsets of the data withheld during model fitting using 10-fold cross-validation. We used area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS) to evaluate the collapse model, and the correlation between predictions and observations for the depletion model [30]. Generally, AUC values greater than 0.75 are considered useful [31]. We also used bootstrap resampling to test the null hypothesis of no interaction among explanatory variables. For each of 100 bootstraps, we resampled the collapse and depletion values before re-fitting a BRT model, and then recorded the size of the interactions to generate a distribution under the null hypothesis.

In addition, we fit generalized linear models (GLMs) with a binomial error term for collapse and ordinary least squares (OLS) regression models for log-transformed mean depletion after standardizing the explanatory variables to mean zero and variance one. We fitted models with all possible combinations of terms and then used Akaike's information criterion corrected (AICc) for small sample size to identify a minimal adequate model. We also calculated relative variable importance (RVI) as the sum of AICc weights from all models that included a particular variable. Statistical modelling was done in R v. 3.0.2 using the *gbm* package v. 2.1 [32], published BRT code [23] and the *MuMIn* package v. 1.13.4 [33].

3. Results

(a) Summary patterns

Overall, a quarter of the populations (25%) included in our dataset experienced a collapse. Twelve LMEs contained at least one collapsed stock and 13 LMEs contained no collapsed stocks (figure 1*a*). The LMEs with the greatest seasonal climatic variability were enclosed or coastal areas and those at intermediate latitudes (figure 1*b*; electronic supplementary material, figure S2). Before accounting for multiple factors through statistical models, the raw data suggested that collapsed stocks experienced more overfishing and had faster growth and lower trophic levels (figure 2). More depleted populations appeared to have greater overfishing durations, faster growth and more seasonal variability (figure 2).

(b) Single factor effects

Overall, BRT models were relatively effective at explaining variation among stocks in the probability of collapse and degree of depletion. Collapse models had an AUC score of 0.84 ± 0.04, and a TSS of 0.79 ± 0.04 when tested against out-of-sample, cross-validation data. As expected, these values were lower than from the training data where over-fitting was more likely (AUC of 0.99 and TSS of 0.97). Predictions from the mean depletion model had a cross-validation r^2 of $69 \pm 3\%$ (92% for training data).

Both BRT models ranked similar terms as important and emphasized the role of overfishing in population collapse and depletion (table 1 and figure 3*a,g*). For both models, overfishing metrics (F/F_{MSY}) contributed 40–53% of the explanatory power (table 1). Life-history traits provided 27–41% of the models' explanatory power, particularly individual growth rate (K). Seasonal variability was the most important climatic factor and the third or fourth most important variable in both models (table 1). A higher probability of collapse and lower population levels were correlated with more overfishing (figure 3*a,g*), higher growth rates (figure 3*b,h*), greater seasonal variability (figure 3*c,j*), and high or low fecundities (figure 3*d*).
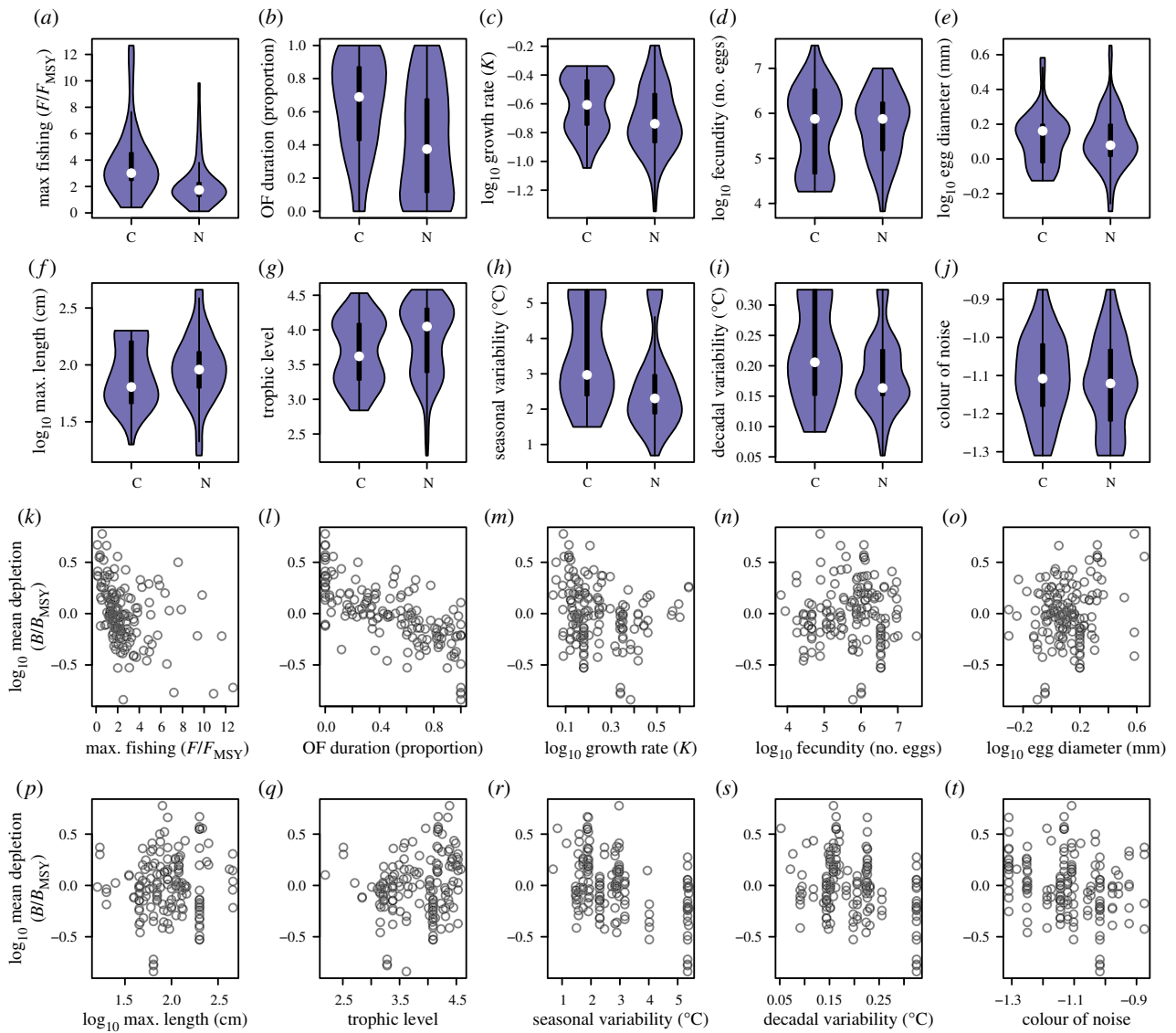
Figure 2. Plots of population characteristics against metrics of collapse and depletion. Violin plots $(a-j)$ are for populations that ever collapsed (C) or did not (N). Scatter plots $(k-t)$ are for the mean depletion (B/B_{MSY}) of each population. (Online version in colour.)

Table 1. Results from the boosted regression tree (BRT) and linear (GLM or OLS) models for collapse probability and mean depletion. (The contributions of each variable to the BRT models (in per cent) are shown, and the six most important variables are highlighted in italics. The coefficients for the variables retained by AICc in the minimal adequate linear models are shown, along with the relative variable importance (RVI) from model averaging. Variables with $p < 0.05$ in the linear models are highlighted in italics.)

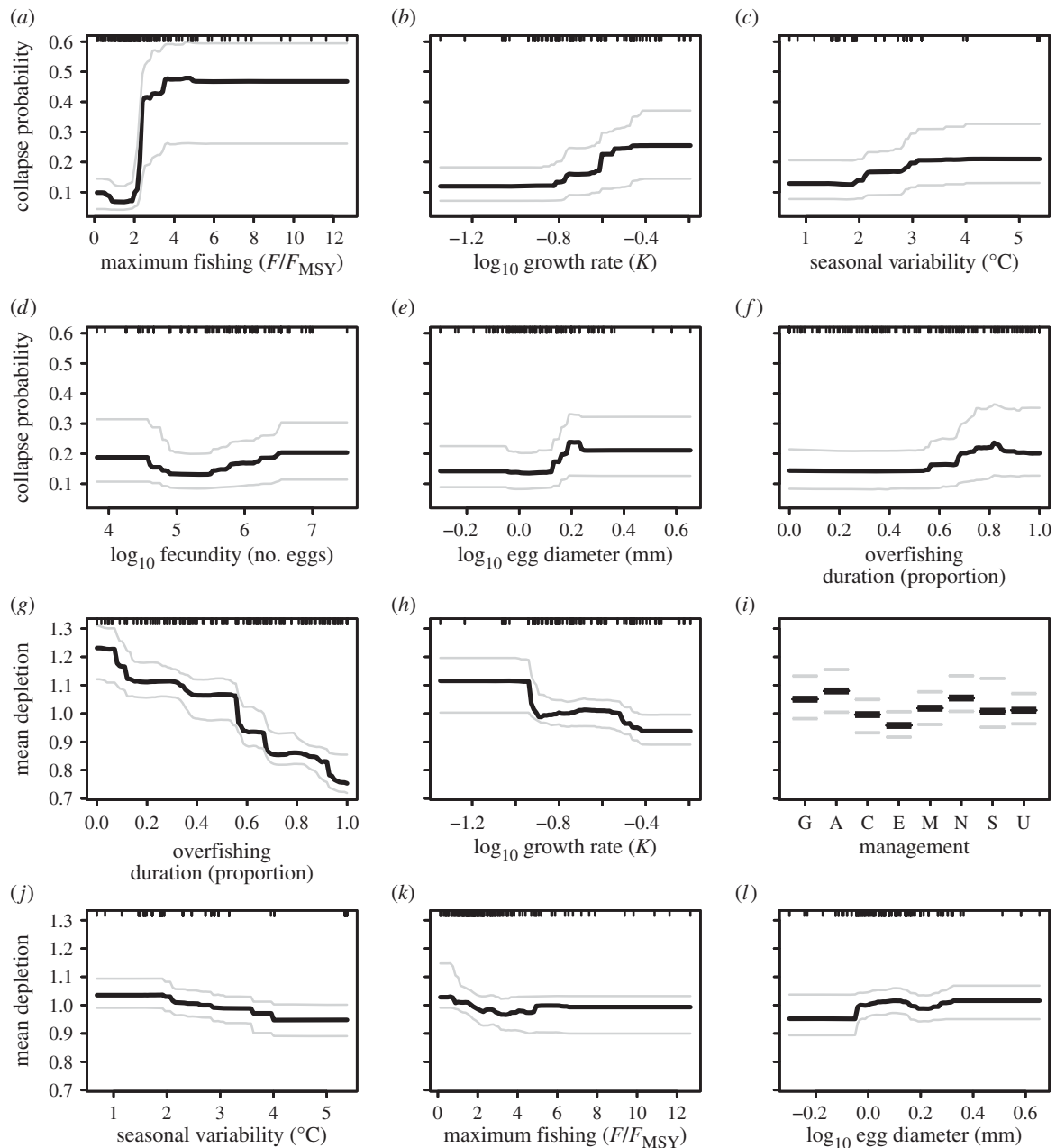|	collapse			mean depletion		
variable	**BRT (%)**	**GLM coefficients**	**GLM RVI**	**BRT (%)**	**OLS coefficients**	**OLS RVI**
maximum fishing pressure (F_{max}/F_{MSY})	*33.5*	*2.0*	*1.0*	*5.8*		*0.51*
$\log_{10}$ growth rate (K)	*18.6*	*1.6*	*1.0*	*11.2*	*−0.28*	*1.0*
seasonal variability (°C)	*8.0*	*0.44*	*0.63*	*6.2*	*−0.23*	*0.99*
$\log_{10}$ fecundity (eggs)	*7.7*	*0.47*	*0.5*	*3.4*		*0.36*
$\log_{10}$ egg diameter (mm)	*7.3*	*1.4*	*1.0*	*5.2*		*0.28*
overfishing duration (proportion)	*7.1*		*0.5*	*47.5*	*−0.65*	*1.0*
management	6.0		0.13	9.6		0.19
trophic level	4.0		0.28	5.1		0.51
colour of noise	3.3		0.37	1.8		0.34
$\log_{10}$ length (cm)	3.3		0.32	1.9		0.34
decadal variability (°C)	1.2		0.32	2.3		0.37

Figure 3. Partial dependence plots from the BRT models for the effects of the six most influential variables on stock collapse (*a–f*) and mean depletion (*g–l*). Black line shows the mean effect of each focal variable while controlling for the average effect of all other variables. The 95% CIs are in grey. Variables are shown in decreasing order of importance for collapse (*a–f*) and depletion (*g–l*). Management organizations in (*i*) correspond to Argentina (G), Australia (A), Canada (C), Europe (E), Multinational (M), New Zealand (N), South Africa (S) and the United States (U).

Stocks were more depleted in Europe and Canada and less depleted in Australia and New Zealand (figure 3*i*).

The minimal adequate linear models supported the importance of the same set of factors. For both collapse and mean depletion models, AICc retained overfishing, growth rate and seasonal climate variability (table 1). Collapse was more likely and population levels were more depleted for stocks that experienced more overfishing, faster growth rates and more seasonal variability, as in the BRT models.

Models for alternative metrics of collapse (collapsed in most recent 20 years, collapse length of at least 4 years or collapses excluding small pelagics) or depletion (over last 20 years) also highlighted similar factors as important (electronic supplementary material, table S2). Overfishing remained the most important risk factor and rapid growth rate remained the most important species trait (electronic supplementary material, table S2 and figures S3–S6). By contrast, rapid

growth rate was not strongly correlated to populations that reached high abundance ($B/B_{MSY} > 2$) (2% contribution to model; electronic supplementary material, table S2 and figure S7). Instead, short overfishing duration and management were the best predictors of high abundance.

(c) Interaction effects

A benefit of BRTs is their ability to reveal nonlinear interactions among explanatory factors. Interactions were important in the collapse model, particularly between maximum overfishing (F_{max}/F_{MSY}) and growth rates or climate (table 2 and figure 4). Interactions of this strength were not likely under the null hypothesis of no relationship between collapse and explanatory variables ($p < 0.01$). In both cases, models suggested that species with rapid growth rates or in highly variable ecosystems were not vulnerable to collapse
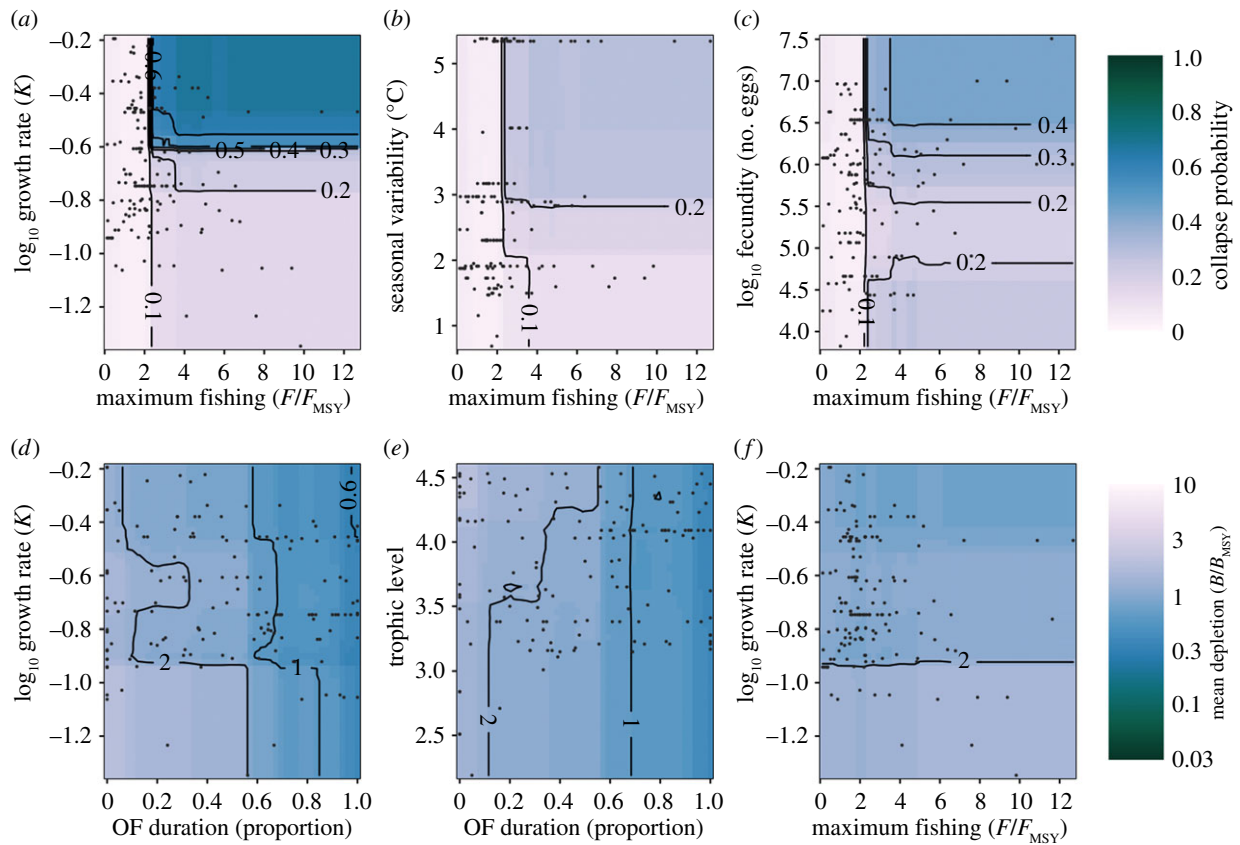
Figure 4. Interactions in BRT models explaining probability of collapse ($a-c$) or mean depletion ($d-f$), including (a) growth rate and maximum fishing, (b) seasonal variability and maximum fishing, (c) fecundity and maximum fishing, (d) overfishing (OF) duration and growth rate, (e) overfishing duration and trophic level and (f) maximum fishing and growth rate. Small dots show the location of data points. Interactions involving management (a categorical variable) are not plotted. (Online version in colour.)

Table 2. The relative strength of the four strongest interactions in models for collapse probability or mean depletion. (Values near zero indicate negligible interactions. Values are comparable within a model but not between models because response variables are on different scales (binomial versus log).)

model	variable 1	variable 2	interaction size
collapse	maximum fishing	growth rate	160
	maximum fishing	seasonal variability	22.5
	maximum fishing	fecundity	16.8
	maximum fishing	management	12.6
mean depletion	overfishing duration	growth rate	0.32
	overfishing duration	management	0.29
	overfishing duration	trophic level	0.18
	maximum fishing	growth rate	0.18

in the absence of overfishing. However, for populations that experienced overfishing, the risk of collapse was more than tripled for fast-growing when compared with slow-growing species. We caution, however, that we lacked data for very fast-growing species at the highest levels of overfishing (figure 4a). Similarly, populations experiencing overfishing in the most variable ecosystems were about twice as likely to collapse as those in more stable ecosystems (figure 4b).

The interactions in the model for mean depletion were weaker but also involved overfishing (figure 4$d-f$).

4. Discussion

By examining patterns of collapse across more than 150 populations around the world, we found evidence that fishery collapses are best explained by a combination of overfishing, life-history traits and climatic variability. Acutely high overfishing was correlated to acute declines in abundance, while chronic overfishing explained long-term depletion. However, our results also expand upon theory and regional results to highlight the particularly high sensitivity of fast-growing species in climatically variable environments to overfishing.

Despite a large and growing body of evidence for the role of climate and other environmental factors in the dynamics of marine species [10,11,27], including dramatic fluctuations of small pelagic species over millennial timescales [9,14], our results suggest that collapses over the last half-century were most strongly driven by overfishing. Overfishing was the dominant factor in both models, constituting two of the six most important predictors and appearing in every strong interaction. Efforts to avoid overfishing continue to appear as an important step to prevent fishery collapses. Our models also revealed important distinctions between chronic overfishing and acutely high levels of overfishing, with the former correlated to depletion and the latter correlated to collapses. Going forward, time-series of fishing pressure may be useful for distinguishing acute declines from long-term depletion.

However, our findings expand on this result by showing that life-history characteristics and climate variability predispose certain fished populations to collapse and depletion. For example, species with a more rapid growth rate were at greater risk of collapse and had lower relative population levels. Individual growth rate is correlated to intrinsic rates of population increase [34], and so our results suggest that species with 'fast' life histories were more likely to collapse than would be predicted from simple models of extinction risk [4]. We note that the high sensitivity to overfishing ($F > F_{MSY}$) that we find is different from asking which species can withstand the highest absolute rates of fishing (absolute F, not scaled to F_{MSY}), and in fact, these latter species tend to have fast growth rates [35]. However, fisheries science also recommends more intensive fishing (higher F) on these species, which in practice may counter-balance their ability to withstand higher fishing mortalities. While other studies have found that these patterns may not apply as strongly in the North Atlantic or for bycatch species [36,37], our results match well to evidence that many populations of fast-growing species have fallen to low levels, including winter flounder (*Pseudopleuronectes americanus*), mackerel (*Scomber* spp.) and sardine (*Sardinops* spp.) [5,12,38].

An important and relatively underappreciated mechanism for this sensitivity may relate to the dynamics of coupled social–ecological systems. Fast-growing species have short generation times and respond quickly to environmental changes [21]. In addition, delays in reducing harvest rates after population growth declines can increase the risk of population collapse. Such delays are pervasive for a variety of reasons, including social resistance, lags between data collection and analysis, and scientific uncertainty [20]. However, species with short generation times can only tolerate a short delay, while longer generation species can tolerate longer delays, which makes management of fast-growing species more difficult [20,21]. This mechanism may explain our finding that fast-growing species and those in climatically variable regions were especially sensitive to overfishing. While fast-growing species fluctuate strongly even in the absence of fishing [14], the strong interaction we found between fishing and growth rate suggested that collapses among fast-growing species over the last half-century were primarily caused by overfishing.

The collapse of the fast-growing California Current sardine (*Sardinops sagax*) provides a well-studied example of these interacting factors. The stock famously declined in the 1950s during a period of cooling temperatures that were tied to poor recruitment and a much-delayed response from management to reduce harvest quotas [12]. Simulations show that both fishing and climate probably contributed to this collapse: fishing induced high-frequency oscillations in sardine abundance and made a collapse nearly five times more likely [12]. Our results suggest that similar mechanisms may operate in a wide range of population collapses, not just small pelagic species.

Synergistic interactions between fishing and life history or climate have also been identified through models, case studies and regional analyses of population variability [6,8,12,15,22], providing a base of support for our findings. For example, models show that cohort resonance causes short-lived species to be particularly sensitive to environmental variability and that the effects are amplified by age-truncation from fishing [6]. Fishing also tends to reduce intraspecific diversity, including genetic, geographical, age and phenotypic diversity. Lower diversity reduces the ability of populations to buffer environmental

stochasticity by limiting bet-hedging and the portfolio effect [19]. Our results were consistent with this increased sensitivity of heavily harvested populations to climatic variability and suggest that these mechanisms are widespread.

Our models also suggested that trophic level provided little explanatory power for collapse or depletion. The result appears to contradict the suggestion that fishing first depletes top predators [39]. However, more recent analyses have revealed that fishery development patterns are more often driven by a transition from low-cost/high-value to high-cost/low-value species, rather than down the food web [40]. In addition, our dataset does not include fishery collapses before 1950, and so may not capture early declines of top predators. Finally, our dataset is composed of stock assessments, and so is restricted to species that are fished. Fished species tend to have a larger body size and a higher trophic level than unfished species [5].

While our model suggested that both high fecundity and large egg size may be risk factors for stock collapse, this appears contradictory because species with high fecundity tend to have small eggs [7]. However, fecundity also increases strongly with body size, and our dataset includes a number of relatively large-bodied fishes with high fecundity and relatively large eggs that have collapsed to low abundance (e.g. American plaice (*Hippoglossoides platessoides*) and Atlantic cod (*Gadus morhua*)).

We were surprised that seasonal climate variability was more closely correlated to population collapses and depletion than longer term climate variability, in part because most literature on marine population dynamics focuses on inter-annual or lower frequency climate variation [27,28]. However, fish recruitment is more variable in highly seasonal environments because spawning seasons are short [41], and this stochasticity may make fisheries management more difficult. This problem will be particularly acute for short-lived species that rely on a small number of recruitment events. We note that highly seasonal environments (as measured by SST) are found in small ocean basins and at intermediate latitudes (electronic supplementary material, figure S2), away from the consistently warm temperatures of the tropics and the consistently cold temperatures of the poles.

Despite the breadth of the datasets in our analysis, there remain important limitations. Because our indicators of population status were derived from stock assessments, they were concentrated in developed countries [24] and included few tropical climates (with particularly limited seasonality and climate variability). Including a broader range of climatic conditions might detect a stronger climate effect or overturn the climate effect that we detect. We note, however, that we did include high latitude ecosystems with low climatic variability (electronic supplementary material, figure S2). It is also possible that other indicators of climate would be more appropriate than variability in SSTs, such as variation in primary productivity, upwelling or climate regime shifts. Environmental variability may also help explain the magnitude of population variability.

Overall, our results suggest that information on overfishing, life history and climate variability can improve our ability to understand global patterns of fisheries declines. While overfishing is a dominant risk factor, fast-growing species in variable environments appear especially sensitive to overfishing. Even though short-lived species may recover more quickly from collapse than other fishes, collapses in these species can last from years to decades [42,43]. These durations are long enough to

have substantial impacts on food webs [13]. Intensive fishing during climate-driven lows in productivity are likely to be particularly problematic, and dynamic management that can rapidly reduce harvest appears important for avoiding collapses among fast-growing species [13,21]. Such advice has become common for small pelagic species [9,13,44] but is less often applied more broadly. Most standard fisheries assessments at the moment assume a constant environment [45]. Efforts to relax this assumption and to build an appreciation for multiple and interacting drivers of population decline appear important for preventing future collapses.

References

1. Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014 The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 987. (doi:10.1126/science.1246752)

2. Fisher DO, Owens IPF. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398. (doi:10.1016/j.tree.2004.05.004)

3. Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005 Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241. (doi:10.1126/science.1116030)

4. Lande R. 1993 Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**, 911–927. (doi:10.1086/285580)

5. Pinsky M, Jensen OP, Ricard D, Palumbi SR. 2011 Unexpected patterns of fisheries collapse in the world's oceans. *Proc. Natl Acad. Sci. USA* **108**, 8317–8322. (doi:10.1073/pnas.1015313108)

6. Botsford LW, Holland MD, Field JC, Hastings A. 2014 Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES J. Mar. Sci.* **71**, 2158–2170. (doi:10.1093/icesjms/fsu063)

7. Winemiller KO. 2005 Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* **62**, 872–885. (doi:10.1139/f05-040)

8. Hsieh C-H, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G. 2006 Fishing elevates variability in the abundance of exploited species. *Nature* **443**, 859–862. (doi:10.1038/nature05232)

9. Schwartzlose RA *et al.* 1999 Worldwide large-scale fluctuations of sardine and anchovy populations. *South African J. Mar. Sci.* **21**, 289–347. (doi:10.2989/025776199784125962)

10. Vert-pre KA, Amoroso RO, Jensen OP, Hilborn RW. 2013 Frequency and intensity of productivity regime shifts in marine fish stocks. *Proc. Natl Acad. Sci. USA* **110**, 1779–1784. (doi:10.1073/pnas.1214879110)

11. Rouyer T, Fromentin J-M, Hidalgo M, Stenseth NC. 2014 Combined effects of exploitation and temperature on fish stocks in the Northeast Atlantic. *ICES J. Mar. Sci.* **71**, 1554–1562. (doi:10.1093/icesjms/fsu042)

12. Lindegren M, Checkley DM, Rouyer T, Maccall AD, Stenseth NC. 2013 Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Natl Acad. Sci. USA* **110**, 13 672–13 677. (doi:10.1073/pnas.1305733110)

13. Checkley DM, Alheit J, Oozeki Y, Roy C. 2009 *Climate change and small pelagic fish*. Cambridge, UK: Cambridge University Press.

14. Baumgartner TR, Soutar A, Ferreira-Bartrina V. 1992 Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millenia from sediments of the Santa Barbara basin, California. *CalCOFI Rep.* **33**, 24–40.

15. Rouyer T, Ottersen G, Durant JM, Hidalgo M, Hjermann DØ, Persson J, Stige LC, Stenseth NC. 2011 Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biol.* **17**, 3046–3057. (doi:10.1111/j.1365-2486.2011.02443.x)

16. Planque B, Fromentin J-M, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S. 2010 How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* **79**, 403–417. (doi:10.1016/j.jmarsys.2008.12.018)

17. Shelton AO, Mangel M. 2011 Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl Acad. Sci. USA* **108**, 7075–7080. (doi:10.1073/pnas.1100334108)

18. Hidalgo M, Rouyer T, Molinero J, Massutí E, Moranta J, Guijarro B, Stenseth NC. 2011 Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Mar. Ecol. Prog. Ser.* **426**, 1–12. (doi:10.3354/meps09077)

19. Schindler DE, Hilborn RW, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS. 2010 Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612. (doi:10.1038/nature09060)

20. Brown CJ, Fulton EA, Possingham HP, Richardson AJ. 2012 How long can fisheries management delay action in response to ecosystem and climate change? *Ecol. Appl.* **22**, 298–310. (doi:10.1890/11-0419.1)

21. King JR, McFarlane GA. 2006 A framework for incorporating climate regime shifts into the management of marine resources. *Fish. Manage. Ecol.* **13**, 93–102. (doi:10.1111/j.1365-2400.2006.00480.x)

22. Rouyer T, Sadykov A, Ohlberger J, Stenseth NC. 2012 Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecol. Lett.* **15**, 658–665. (doi:10.1111/j.1461-0248.2012.01781.x)

23. Elith J, Leathwick JR, Hastie T. 2008 A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813. (doi:10.1111/j.1365-2656.2008.01390.x)

24. Ricard D, Minto C, Jensen OP, Baum JK. 2012 Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish.* **13**, 380–398. (doi:10.1111/j.1467-2979.2011.00435.x)

25. Froese R, Pauly D. FishBase version 02/2015 2015 April 2015. See http://www.fishbase.org.

26. Met Office. HadISST 1.1 - Global sea-ice coverage and SST (1870-Present). UK Meteorological Office Hadley Centre, Natural Environmental Research Council's Natioanl Centre for Atmospheric Science (NCAS), British Atmospheric Data Centre; 2010 cited 27 June, 2012. See http://badc.nerc.ac.uk/.

27. Rouyer T, Fromentin J-M, Stenseth NC. 2010 Environmental noise affects the fluctuations of Atlantic large pelagics. *Prog. Oceanogr.* **86**, 267–275. (doi:10.1016/j.pocean.2010.04.025)

28. Lehodey P *et al.* 2006 Climate variability, fish, and fisheries. *J. Clim.* **19**, 5009–5030. (doi:10.1175/JCLI3898.1)

29. Buston PM, Elith J. 2011 Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. *J. Anim. Ecol.* **80**, 528–538. (doi:10.1111/j.1365-2656.2011.01803.x)

30. Liu C, White M, Newell G. 2011 Measuring and comparing the accuracy of species distribution models with presence absence data. *Ecography* **34**, 232–243. (doi:10.1111/j.1600-0587.2010.06354.x)

31. Elith J *et al.* 2006 Novel methods improve prediction of species' distributions from occurrence data.

8

rspb.royalsocietypublishing.org Proc. R. Soc. B 282: 20151053

Ecography **29**, 129 – 151. (doi:10.1111/j.2006.0906-7590.04596.x)

32. Ridgeway G. 2013 gbm: generalized boosted regression models. R package version 2.1 2013. See http://cran.r-project.org/package=gbm.

33. Bartoń K. 2015 MuMIn: multi-model inference. R package version 1.13.4 2015. See http://CRAN.R-project.org/package=MuMIn.

34. Denney NH, Jennings S, Reynolds JD. 2002 Life-history correlates of maximum population growth rates in marine fishes. *Proc. R. Soc. Lond. B* **269**, 2229 – 2237. (doi:10.1098/rspb.2002.2138)

35. Jennings S, Reynolds JD, Mills SC. 1998 Life history correlates of responses to fisheries exploitation. *Proc. R. Soc. Lond. B* **265**, 333 – 339. (doi:10.1098/rspb.1998.0300)

36. Dulvy NK, Reynolds JD. 2002 Predicting extinction vulnerability in skates. *Conserv. Biol.* **16**, 440 – 450. (doi:10.1046/j.1523-1739.2002.00416.x)

37. Jennings S, Greenstreet SPR, Reynolds JD. 1999 Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**, 617 – 627. (doi:10.1046/j.1365-2656.1999.00312.x)

38. Juan-Jordá MJ, Mosqueira I, Cooper AB, Freire J, Dulvy NK. 2011 Global population trajectories of tunas and their relatives. *Proc. Natl Acad. Sci. USA* **108**, 20 650 – 20 655. (doi:10.1073/pnas.1107743108)

39. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres FJr. 1998 Fishing down marine food webs. *Science* **279**, 860 – 863. (doi:10.1126/science.279.5352.860)

40. Sethi SA, Branch TA, Watson R. 2010 Global fishery development patterns are driven by profit but not trophic level. *Proc. Natl Acad. Sci. USA* **107**, 12 163 – 12 167. (doi:10.1073/pnas.1003236107)

41. Longhurst A. 2002 Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fish. Res.* **56**, 125 – 131. (doi:10.1016/s0165-7836(01)00351-4)

42. Neubauer P, Jensen OP, Hutchings JA, Baum JK. 2013 Resilience and recovery of overexploited marine populations. *Science* **340**, 347 – 349. (doi:10.1126/science.1230441)

43. Beverton RJH. 1990 Small marine pelagic fish and the threat of fishing: are they endangered? *J. Fish Biol.* **37**, 5 – 16. (doi:10.1111/j.1095-8649.1990.tb05015.x)

44. Cochrane KL, Butterworth DS, De Oliveira JAA, Roel BA. 1998 Management procedures in a fishery based on highly variable stocks and with conflicting objectives: experiences in the South African pelagic fishery. *Rev. Fish Biol. Fish.* **8**, 177 – 214. (doi:10.1023/A:1008894011847)

45. Link JS. 2010 *Ecosystem-based fisheries management: confronting tradeoffs*. Cambridge, UK: Cambridge University Press.

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rspb.royalsocietypublishing.org *Proc. R. Soc. B* **282**: 20151053