

Why fishing magnifies fluctuations in fish abundance

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It is now clear that fished populations can fluctuate more than unharvested stocks. However, it is not clear why. Here we distinguish among three major competing mechanisms for this phenomenon, by using the 50-year California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval fish record. First, variable fishing pressure directly increases variability in exploited populations. Second, commercial fishing can decrease the average body size and age of a stock, causing the truncated population to track environmental fluctuations directly. Third, age-truncated or juvenescent populations have increasingly unstable population dynamics because of changing demographic parameters such as intrinsic growth rates. We find no evidence for the first hypothesis, limited evidence for the second and strong evidence for the third. Therefore, in California Current fisheries, increased temporal variability in the population does not arise from variable exploitation, nor does it reflect direct environmental tracking. More fundamentally, it arises from increased instability in dynamics. This finding has implications for resource management as an empirical example of how selective harvesting can alter the basic dynamics of exploited populations, and lead to unstable booms and busts that can precede systematic declines in stock levels.

Ecologists have long suspected that harvesting a species has the unintended consequence of destabilizing the abundance of that species^{1,2}. This would be undesirable, because boom-and-bust cycles can increase the likelihood of local extinctions³ and can harm the economic market for the species. However, this connection has been remarkably difficult to prove. A historic example is the collapse of the California sardine fishery in the late 1940s, which some argued was caused primarily by fishing^{4,5}, but which others attributed to cooling sea surface temperatures or to shifting wind patterns^{6–8}. Because landings records contain no information about unexploited species, there is no control group to disentangle environmental effects from fishing effects. Partly to address this conundrum, CalCOFI was initiated to collect data both on fished and unfished species living in the same environment. CalCOFI overcame the reliance on landings data by sampling the ichthyoplankton assemblage, a well-known proxy for current adult (spawning) biomass^{9–11}. Fifty years into the study, Hsieh *et al.*⁹ used the CalCOFI ichthyoplankton database¹² to separate the effects of fishing from other variables, and demonstrated that fishing significantly increases temporal variability of populations in the southern sector of the California Current ecosystem (Fig. 1). Increased variability is thought to be related to the truncated age/size structure^{3,4,9,13–17} of commercially fished species, a phenomenon caused by selective removals of larger, older individuals that previously provided stability to the population.

Here we examine three competing hypotheses for the link between fishing and stock variability^{1,2,9,16,18}. First, fishing itself can vary year to year and this can translate directly into increased population variability¹⁹. Second, fished populations that become dominated by relatively small-bodied and young individuals are less able to smooth out environmental fluctuations, and are thus more likely than unfished stocks to track directly those fluctuations^{4,9,13}. Finally,

fished populations that become dominated by small-bodied and young individuals are more prone to exhibit unstable dynamics due to changing demographic parameters^{20,21}. These are not mutually

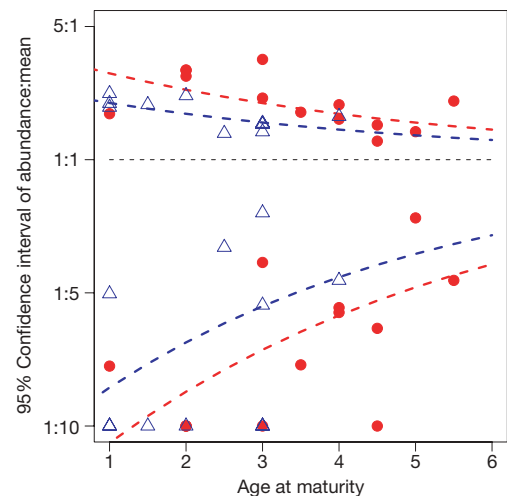


Figure 1 | In addition to an increased coefficient of variation⁹, exploited species (red dots) exhibit larger booms and busts than unexploited species (blue triangles) of a similar age. The 95th and the 5th percentiles of abundance are shown for each species, with exponential fits (dashed lines) for the exploited and unexploited species. Note that for all species, the busts (lower range) are more pronounced than the booms ($P < 0.0001$). Populations less than one-tenth mean size probably fell below detection levels and were conservatively fixed at one-tenth mean size; thus, the effect may be more pronounced than depicted here.

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exclusive hypotheses; all three could act together to increase variability. Here we analyse the relative importance of each hypothesis as a cause of the increase in population variability of fished stocks observed in the southern California Current ecosystem.

Hypothesis 1 (variable fishing)

According to hypothesis 1, a fish stock is expected to vary more if exploited heavily some years and lightly in others. Jonzén *et al.*²² discovered a positive correlation between the variance in fishing mortality and the variance in the standing stock biomass of Baltic cod populations. We use their method on the CalCOFI database, to test this hypothesis for the seven exploited species whose fishing mortality is available from National Marine Fisheries Service stock assessment reports (Supplementary Table 1) and find no evidence that variability in fishing mortality is associated with variability in either larval density (Fig. 2) or estimated spawning biomass (Supplementary Fig. 2). Therefore, although it is reasonable to expect the variability of these populations to be somewhat influenced by year-to-year differences in fishing effort, hypothesis 1 alone does not explain the observed increase in variability of these data.

Hypotheses 2 and 3 (age-truncation effects)

The other two hypotheses are closely related. Because fishing typically targets the larger individuals of a species, the average size—and thus age—of target populations is often found to decrease^{14–16,18,23}. Age truncation leading to increased population variability has been documented in several populations⁹, and is here referred to as the ‘age truncation effect’ (ATE)¹³. Such juvenescence can affect population variance in two separable ways.

Hypothesis 2 suggests that when new recruits compose most of the stock, the juvenescence population is more likely to track variable environmental processes directly^{4,5}. Although younger and smaller fish are more susceptible to changes in the environment, older and larger fish tend to integrate over environmental fluctuations and survive hard times better through ‘bet-hedging’ strategies^{18,24–27} including fat storage, the ability to migrate and avoid poor areas, having flexibility in spawning times and locations, and production of high-quality offspring that survive in a broader suite of environmental conditions¹⁸. Bet-hedging strategies are well documented in

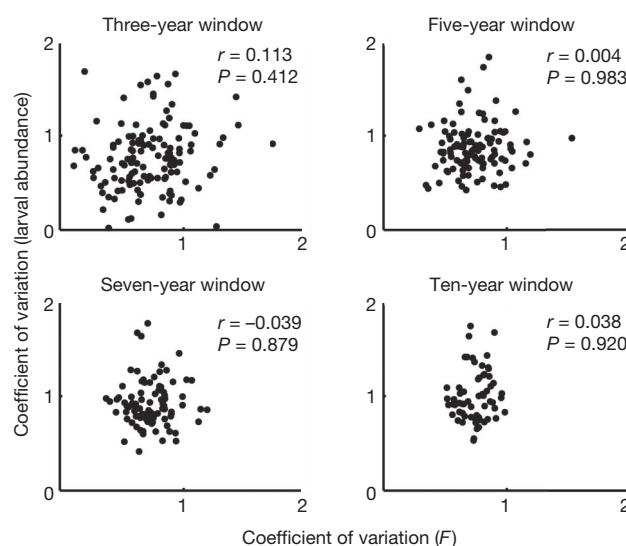


Figure 2 | Hypothesis 1: does variable fishing cause variability in fish stocks? There is no positive relation between the variability in the coefficient of variation of fishing mortality (F) and population variability coefficient of variation (larval abundance) using a three-, five-, seven-, and ten-year moving window. Thus variability in fishing mortality (removing more fish some years than others) does not account for variability in fished stocks in the CalCOFI domain.

association with long-tailed age distributions^{18,24–27}. Loss of hedging capacity through age truncation should produce a time-series signal that more closely exhibits the linear (statistically noisy) characteristics found in physical oceanographic data for that region²¹.

By contrast, under hypothesis 3, the increased variability of exploited fish stocks comes from changes in demographic parameters that amplify nonlinear behaviour^{20,21}. There are many ways that the ATE can change demographic parameters, for example by increasing intrinsic population growth rates or by increasing nonlinear coupling of demographic parameters to environmental noise^{20,28}. The resulting population dynamics will produce a more variable time series with more nonlinear behaviour than seen in unexploited fish stocks.

Separating environment and demography

Because hypothesis 2 implies increased tracking of linear environmental variation, whereas hypothesis 3 describes an enhanced nonlinear response, we can distinguish these subtle alternatives by comparing the nonlinearity in the time series of exploited species relative to unexploited species. Here, nonlinearity is quantified using S-maps²⁹, a model validation criterion that uses out-of-sample predictions from equivalent linear versus nonlinear models to identify the dynamics behind time-series observations. The model either weights all data equally ($\theta = 0$) to make linear forecasts, or gives more weight to data points with similar recent histories ($\theta > 0$), a hallmark of nonlinear behaviour^{29,30}. The nonlinearity of a time series is determined by how much the correlation (ρ) between forecasts and observations increases as models are tuned towards nonlinear solutions; that is, how much forecast skill increases ($\Delta\rho$) when $\theta > 0$ ($\Delta\rho = \rho_{\theta > 0} - \rho_{\theta = 0}$; see Methods).

When CalCOFI ichthyoplankton time series are modelled using linear autoregression (S-maps with $\theta = 0$), fished species are slightly more predictable than unfished species ($\rho = 0.514$ and 0.504 , respectively; Fisher’s test $P = 0.64$; Supplementary Fig. 3). However, this possible evidence for hypothesis 2 is marginal (Supplementary Table 2). Indeed, nonlinear models describe the CalCOFI ichthyoplankton time series better ($\theta = 0.3$ for both), and more importantly, fished species exhibit significantly more nonlinearity than the unfished group (Fig. 3a; unfished $\Delta\rho = 0.037$, $P = 0.25$; fished $\Delta\rho = 0.083$, $P < 0.01$; Fisher’s test, $P < 0.003$). If the increase in variance is due to vulnerable, young fish simply tracking the linear environment more closely, then the nonlinearity ($\Delta\rho$) of fished species should decrease. This prediction is contradicted by the data.

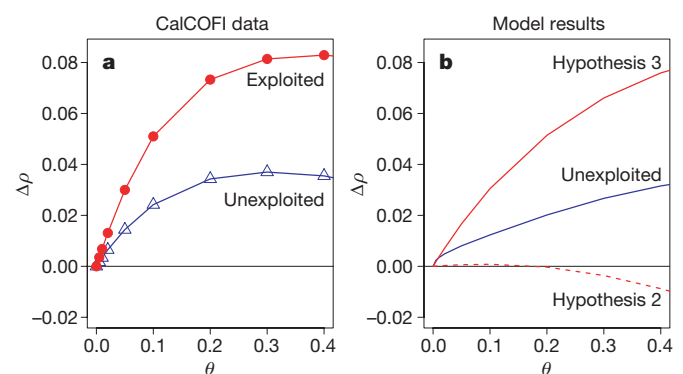


Figure 3 | Discriminating between hypotheses 2 and 3. A larger $\Delta\rho$ as θ is tuned from linear ($\theta = 0$) towards nonlinear solutions ($\theta > 0$) indicates a stronger nonlinear signal ($\Delta\rho = \rho_{\theta > 0} - \rho_{\theta = 0}$). **a**, S-map analysis shows that fished populations (red) are significantly more nonlinear than unexploited populations (blue) ($P = 0.0027$), supporting hypothesis 3 (demographic change), not hypothesis 2 (tracking), as the agent behind amplified variability with fishing. **b**, Corroborative model results. Equation (1) was fitted to data for unexploited species (blue line). Increased environmental sensitivity makes time series appear more linear (dashed red line). However, increasing growth rate r produces an enhanced nonlinear signature (solid red line) as observed for exploited species in **a**.

Rather, fishing pressure has enhanced the nonlinear behaviour of the fished populations. Therefore, the data suggest that altered dynamics resulting from a truncated age structure overwhelm the propensity of young fish to track the environment passively and that dynamic instability is the agent behind the observed increase in variance. Increased nonlinearity has explained higher variance in other contexts^{29,31}.

Identifying sources of nonlinearity

We illustrate the distinction between hypotheses 2 and 3 with a population growth model having the familiar Ricker-form^{29,32}

$$N_{t+1} = N_t \exp[r(1 - N_t)] + c\varepsilon \tag{1}$$

where N is population size (in units of number or biomass), r is the intrinsic population growth rate, ε is environmental variability with unit standard deviation, and c is environmental susceptibility (see Methods, Supplementary Fig. 4 and Supplementary Discussion). Hypothesis 2 corresponds to an increase in environmental susceptibility c ; hypothesis 3 corresponds to alteration of a demographic parameter: for this example we increase r . Forecast skill does not improve with nonlinear tuning ($\theta > 0$) as environmental noise ($c\varepsilon$) is increased, but declines with θ , as would be expected if the time series were dominated by linear statistical effects (Fig. 3b, dashed line; see Methods). We find this result is maintained whether ε is ‘white’ noise, autocorrelated ‘red’ noise, $1/f$ ‘pink’ noise or the actual values of the Pacific Decadal Oscillation^{33–35}. However, under hypothesis 3 (Fig. 3b, solid red line), exploited model populations present an enhanced nonlinear signature as r is increased.

At first glance, it seems counterintuitive that age truncation would increase intrinsic population growth rates (because fishing removes the largest individuals that produce the most and best quality eggs^{18,24–27}); yet this trend is observed empirically in the California Current ecosystem. Because individual body size decreased and total biomass remained statistically constant (26 of 29 stocks⁹), the number of young fish has increased. A larger population of shorter-lived fish requires a higher intrinsic rate of growth (r); the population must produce more surviving offspring per capita per year to compensate for the shortened life span. The ultimate mechanism behind this ATE-induced increase could be competitive release and/or decreased cannibalism or possibly evolution^{23,36,37}, leading to increased somatic growth or increased per-capita fecundity. Although other factors are probably operating, the evidence from CalCOFI points to increased growth rates as a dominant factor supporting the increase in nonlinearity observed in Fig. 3a.

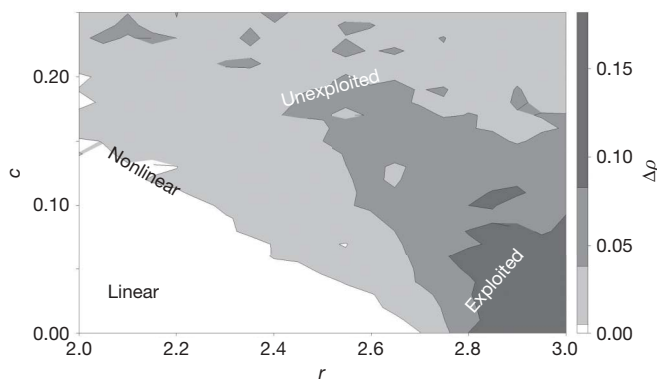


Figure 4 | Nonlinear behaviour can emerge at modest growth rates (r) with process noise ($\varepsilon_{\text{process}}$). Models that are underspecified (missing important components) are said to contain process noise. In this example, we evaluate the nonlinearity of $Z_{t+1} = G(Z_t + \varepsilon_{\text{process}})$, where G is equation (1) and $\varepsilon_{\text{process}}$ is normally distributed with mean 0 and standard deviation c . Process noise can amplify a nonlinear signature in the simple model for values of r that would be linear alone.

Although it is well known that increasing growth rates in simple discrete growth models can lead to unstable dynamics³⁸, values of r required to evoke such behaviour in single species models are often unrealistically high. However, models with multiple species³⁹, multiple stable states²⁸ or models having demographic parameters that vary in complex ways with the environment^{20,21} produce nonlinear behaviour even at modest growth rates. More generally, process noise (error from incompletely specified models) can induce instability in otherwise stable models when the error multiplies in specific ways; that is, when an essential detail is added that has a nonlinear effect. Using the commonly studied²⁹ form of process noise $Z_{t+1} = G(Z_t + \varepsilon_{\text{process}})$ where equation (1) is an example of G , Fig. 4 shows that generic process noise evokes nonlinear behaviour at lower growth rates. This toy representation portrays nonlinear or biologically amplified process errors.

Thus, increasing either process noise or growth rates can amplify nonlinearity. And fishing may affect both. For example, incorporating variable fishing F_t into equation (1) so that variability in F is an expression of process noise,

$$N_{t+1} = N_t \exp[r_i(1 - N_t/K_t - F_t)] \tag{2}$$

leads to amplified nonlinearity (Fig. 5). (However, the lack of a relation in Fig. 2 eliminates this as a cause for increased variability in these data.) Similarly, modelling process errors more explicitly by adding variability directly to the demographic parameters r or K in equation (2) will provoke a nonlinear signature, regardless of the particular form of the noise (see Methods and Supplementary Fig. 5). It is reasonable to speculate that the baseline nonlinearity seen in the unexploited state is an expression of nonlinear process errors related to variable demographic parameters, such as those tied to ecosystem shifts and climate events for example^{8,9,20}. So, although neither variability in fishing nor in the environment correlates with variability in abundance, these two sources of process error may be implicated in complex ways with the instability that accompanies fishing. Notwithstanding their potential destabilizing effects, by themselves these processes have little direct effect on the overall stock variability we observed in CalCOFI (Fig. 2, Supplementary Fig. 2, and Supplementary Tables 2 and 3).

Life-history traits and nonlinearity

Are there characteristics that make some fish stocks more susceptible to the nonlinear effects of fishing than others? To answer this question we compared the nonlinearity of exploited and unexploited stocks for various life-history traits (Table 1 and Supplementary Table 4). Table 1 identifies a qualitative tendency for the following characteristics to be associated with vulnerability to fishing: larger size at sexual maturity (≥ 25 cm), greater age at sexual maturity (≥ 3 years), longer spawning duration (> 7 months), higher fecundity ($\geq 200,000$ eggs per female per year), lower trophic level and

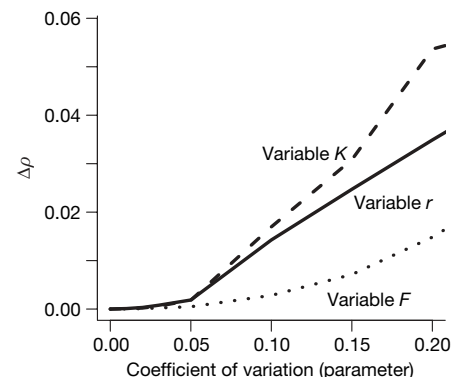


Figure 5 | Variable fishing F (dotted line), growth r (solid line), or carrying capacity K (dashed line), can induce nonlinearity.

Table 1 | Vulnerability of species with different life histories to destabilization by fishing

Life-history trait	Cut-off value	Below cut-off			Above cut-off			Difference in fishing effect
		Unfished $\Delta\rho$ (n)	Fished $\Delta\rho$ (n)	Fishing effect	Unfished $\Delta\rho$ (n)	Fished $\Delta\rho$ (n)	Fishing effect	
Maximum size (cm)	50	0.062 (14)	0.171 (3)	0.109 ($P = 0.06$)	0.067 (2)	0.113 (10)	0.047 ($P < 0.01$)	-0.062 ($P = 0.19$)
Size at maturity (cm)	25	0.071 (13)	0.078 (4)	0.007 ($P = 0.04$)	0.040 (3)	0.143 (9)	0.103 ($P < 0.01$)	0.096 ($P < 0.01$)
Age at maturity (years)	3	0.065 (9)	0.055 (4)	-0.010 ($P = 0.92$)	0.055 (7)	0.064 (9)	0.009 ($P = 0.03$)	0.019 ($P = 0.11$)
Fecundity (eggs per female per year)	200,000	0.071 (13)	0.082 (5)	0.011 ($P = 0.03$)	0.040 (3)	0.072 (8)	0.032 ($P = 0.03$)	0.021 ($P = 0.21$)
Spawning duration (months per year)	7	0.023 (6)	0.093 (7)	0.070 ($P < 0.01$)	0.091 (10)	0.205 (6)	0.114 ($P < 0.01$)	0.044 ($P = 0.03$)
Trophic level	3.5	0.066 (11)	0.092 (6)	0.026 ($P < 0.01$)	0.063 (5)	0.056 (7)	-0.006 ($P = 0.84$)	-0.032 ($P = 0.04$)
Coefficient of variation	0.9	0.055 (11)	0.081 (4)	0.026 ($P = 0.02$)	0.054 (5)	0.100 (9)	0.047 ($P < 0.01$)	0.020 ($P = 0.11$)

Species are separated into groups on the basis of having life-history traits above or below a cut-off value, and the nonlinearity ($\Delta\rho$) of exploited and unexploited species within these groups is compared. Significance is calculated by jack-knifing the data set, S-mapping and then comparing $\Delta\rho$ distributions of the fished and unfished data (one-tailed P values). Fishing significantly increased the nonlinearity of 12 of the 14 groups investigated. To evaluate which life-history traits are most impacted by fishing, the differences in $\Delta\rho$ values were compared (two-tailed P values in the right-hand column). Qualitatively, susceptibility to fishing is greater in late-maturing, fecund, low-trophic-level species with year-round spawning and high variability.

more variability in abundance (coefficient of variation ≥ 0.9). Thus, acknowledging the uncertainty arising from the small number of species involved in some groups, one may speculate that to a first approximation, large-maturing lower-trophic-level species that are also fecund, may be most susceptible to further destabilization by fishing, and regardless of life history the evidence suggests that increasing growth rates are driving this effect.

Management implications

In summary, fishing for big individuals without consideration of the impact on the age distribution can lead to unstable nonlinear population dynamics, and this enhanced nonlinearity helps to explain much of the volatility seen in fish stocks today (Fig. 1). Our study shows that when unconstrained, an observed demographic consequence of the ATE, that is, the effective increase of r , makes dramatic population change more likely—and paradoxically, in this case, can make those changes slightly more predictable in the short run. Thus target species are in double jeopardy from both fishing removals and the ATE, as stocks with higher mortality also suffer increasing fluctuations. Reduced size and age distributions have been documented in many common fisheries species, for example in Pacific salmon⁴⁰, Pacific rockfish⁴¹, and North Sea ground fish^{42,43}, suggesting the potential relevance of the ATE for many commercially important species. In terms of stock recovery, it can be premature therefore to resume fishing activities solely on the basis of recovery of biomass but before restoration of historical age distributions, even though short-term industry pressures may make this difficult to realize (for example, Atlantic swordfish⁴⁴).

It is encouraging, however, that some managers are adopting precautionary harvest policies that protect against stock depletion and the ATE^{45,46}. For example, in Alaska, where fishing is managed through a complex system of harvest controls, there has been relatively minor impact on the mean age of the population^{47,48}. Nonetheless, in other areas, current policies and industry pressures that encourage lifting bans on fishing when biomass is rehabilitated, but where maximum age is not, contain risk^{18,44,49}. Unless fishing is conducted with informed harvest controls and with market mechanisms to align incentives and manage financial risks associated with volatile supplies, we can expect a future of instability in fish populations and suboptimal performance of the industries built on them.

METHODS SUMMARY

Hypothesis 1 was tested by examining the relation between the coefficient of variation in fishing mortality and the coefficient of variation of spawning biomass (larval indicators and fishery-based estimates) for Southern Region California Current fisheries (Fig. 2 and Supplementary Fig. 2). Variability was calculated for windows 3–10 years long.

Hypotheses 2 and 3 were tested with S-maps on composite CalCOFI ichthyoplankton time series, using methods described in detail elsewhere^{21,50}. Briefly, larval time series were composited end-to-end, and nonlinearity of fished versus unfished species was assessed by computing $\Delta\rho$ with an embedding dimension $E = 3$ (Supplementary Materials).

Hypotheses 2 and 3 are illustrated with a simple model (equation (1)) whose behaviour is generic to a large class of fisheries models (Supplementary Discussion). First, a baseline is established by fitting parameters to the observed variance (Supplementary Fig. 6) and nonlinearity of unexploited CalCOFI populations (Fig. 3b, blue line). Next, to model hypothesis 2, environmental susceptibility (c) is increased to simulate direct environmental tracking with the ATE (Fig. 3b, dashed line). Alternative types of environmental noise were simulated for hypothesis 2 (red, $1/f$; white, low-pass filtered and the actual Pacific Decadal Oscillation values^{33–35}), and did not affect the qualitative outcome. Finally, hypothesis 3 is here simulated by increasing species-specific growth rates (r) (Fig. 3b, solid red line). Various forms of process noise were also simulated. All standard statistical analyses were performed with R software version 2.3.0.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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