LETTERS

Fishing elevates variability in the abundance of exploited species

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The separation of the effects of environmental variability from the impacts of fishing has been elusive, but is essential for sound fisheries management[1–7]. We distinguish environmental effects from fishing effects by comparing the temporal variability of exploited versus unexploited fish stocks living in the same environments. Using the unique suite of 50-year-long larval fish surveys from the California Cooperative Oceanic Fisheries Investigations[4] we analyse fishing as a treatment effect in a long-term ecological experiment. Here we present evidence from the marine environment that exploited species exhibit higher temporal variability in abundance than unexploited species. This remains true after accounting for life-history effects, abundance, ecological traits and phylogeny. The increased variability of exploited populations is probably caused by fishery-induced truncation of the age structure, which reduces the capacity of populations to buffer environmental events[1,5,8,9]. Therefore, to avoid collapse, fisheries must be managed not only to sustain the total viable biomass but also to prevent the significant truncation of age structure[1,5,8,9]. The double jeopardy of fishing to potentially deplete stock sizes and, more immediately, to amplify the peaks and valleys of population variability[7], calls for a precautionary management approach[10,11].

One of the most difficult issues in the management of fisheries is to evaluate the effects of fishing in the context of a changing environment[2,3,6]. Statistics from the Food and Agriculture Organization of the United Nations[12] and recent studies[5,6,13,14] indicate that many commercially important fish populations have been declining in the past several decades. However, the extent to which such declines are due to fishing, to environmental change, or to some combination of these effects remains a matter of debate[15–17].

Understanding how fishing and environmental variability interact to produce an effect on exploited populations (commercially targeted species) is an unsolved problem in fisheries science[7,18]. For example, it is not known how fishing and environmental variability can either magnify or diminish management risk by affecting the variability (resilience) of exploited populations[7,18]. Lack of understanding of the sources of temporal variability in fish abundance affects biological reference points, decision making and risk assessment in precautionary fisheries management[19], and determination of extinction risk for populations[20]; it is largely responsible for the uncertainty and indecision that have led to past failures in managing fisheries[21]. In many historical cases, fisheries management has failed to recognize possible fishing effects until population collapse[2,5,21].

We show that fishing effects may appear even in the absence of significant declining trends in populations. We find that fishing increases population variability (fluctuations of populations through time) and that this is an indication that fishing is having a negative impact on populations that is not yet reflected in declining abundance. We evaluate fishing effects by comparing temporal variability in the larval abundance of exploited species to that of unexploited species living in the same ecosystem. Larval abundance is an established proxy for adult biomass (see Methods and Supplementary Data). Although no environmental variables are directly examined, environmental effects are implicit in our measurements of the temporal variability of fish populations[11].

Whether fishing will increase or decrease the population variability of exploited species is a long-standing debate[7,18]. The discussion (the origins of which trace back at least to the 1970s) remained theoretical because no data existed to resolve the controversy. These data are now available from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval fish time series (1951–2002) for the California Current System. We use the coefficient of variation of annual larval abundance to represent temporal variability for the adults of 29 coastal or neritic species (13 exploited and 16 unexploited species) that were abundant and consistently enumerated within CalCOFI[4] (Supplementary Data Table S2).

Fishing is a selective process, thus the exploited and unexploited groups may not be random with respect to other potential explanatory variables that could relate to the coefficient of variation. In addition to fishing there could be systematic differences with respect to other factors such as life-history traits that could influence the coefficient of variation. Therefore, to isolate the effect of fishing as an explanatory variable, we use multiple regression analysis to factor out variables that could produce biases associated with fishing. These variables include life-history effects, abundance, ecological traits and phylogeny (see Methods). We consider life-history traits that are known to influence population responses to fishing and the environment[22]. In theory[20,22–24], the coefficient of variation of annual larval abundance is negatively related to maximum length, length at maturation, age at maturation, spawning duration and trophic level, and positively related to fecundity. Abundance is included in the regression model because higher variability could be statistically associated with higher abundance[20]. Finally, ecological traits (geographic region, habitat and spawning mode) and phylogenetic constraints are examined (see Methods and Supplementary Data).

When data from exploited and unexploited species are grouped together, two of the six life-history traits fail to show the expected relationships with the coefficients of variation of annual larval abundance (Fig. 2 of Supplementary Data). The coefficients of variation are positively correlated with maximum length and length at maturation whereas theory predicts negative correlations[20,22–24]. However, when the analyses are performed separately on exploited and unexploited groups, the relationships between the coefficients of variation and life-history traits follow the theoretical predictions (Fig. 3 of Supplementary Data). Except for fecundity (for which data for unexploited species are too sparse to be conclusive, $n = 4$), the predicted relationship between life-history traits and coefficients of

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variation is stronger for the unexploited species data set. The relationship between life-history traits and coefficients of variation is weaker for the exploited species data set, perhaps because fishing pressure varies among species and this in itself might obscure the predicted relationships (see Supplementary Data).

The most important result is that, after accounting for life-history effects, abundance, ecological traits and phylogeny, the coefficients of variation of annual larval abundance for exploited species are significantly higher than those for unexploited species. When accounting for all effects, the overall significance of the multiple regression is $P < 0.001$. Notably, age at maturation (Fig. 1) and geographic region (Fig. 2a) emerge as the only two significant factors in the full model ($P = 0.015$ and $P < 0.001$, respectively). Age at maturation is probably the best proxy for generation time, which should be important in determining population variability. The remaining life-history traits and abundance are highly correlated with age at maturation, so it is not surprising to find them redundant (and eliminated) in the regression model. Warm-water species exhibit higher coefficients of variation than cool-water and widely distributed species (Fig. 2). Phylogeny is not a significant variable affecting the coefficients of variation (see Fig. 5 of Supplementary Data).

Could the higher variability in larval abundance of the exploited species be caused by a long-term declining trend in their abundance due to exploitation? Contrary to this speculation, we found no systematic differences between the exploited and unexploited groups in the prevalence of declining trends in the 50-yr interval (Table 1). Out of 13 exploited species, only 2 had significant declines, which is similar to the fraction (2 out of 16) of unexploited species that showed significant declines. However, for safe measure, we recalculated coefficients of variation after removing low-frequency trends in the abundance time series, and found that the exploited species still exhibit higher variability after accounting for our ancillary variables (see Table 5 of Supplementary Data). All these results indicate that the exploited (fished) species are more variable in terms of abundance than the unexploited species.

How might fisheries cause an increase in variability in the abundance of exploited populations? As suggested nearly 30 yr ago[7], in many fish populations the main source of variability lies in recruitment: the transition from the larval stage to the adult stage. This can be shown in a simple population model:

$$N_{t+1} = N_t e^{(-M-F)} + R_t$$

where N_t is the adult abundance and R_t is the recruitment at time t, and M and F are natural and fishing mortality, respectively. Clearly, as the level of fishing mortality increases, the population dynamics are increasingly dominated by recruitment, and at the limit the population variability is equal to the variability of recruitment. Thus, one would expect fishing to increase population variability.

However, beyond this effect, recruitment variability itself should be further amplified through the effect that fisheries have on truncating the size–age structure of a population[1,5,8,9]. It is believed that fisheries operate by selectively removing large and old individuals through size–age selective fishing mortality[1,5,25]. This is supported by our analysis, in which declining trends in average age or length through time are seen for all exploited species (Fig. 3 in Supplementary Data). Reducing the average age and length of individuals within a population can increase recruitment variability by diminishing the capacity to weather short-term unfavourable environmental conditions. Many fish species use bet-hedging strategies to increase the survival rate of larvae under harsh and variable environmental conditions. Such hedging strategies are associated with

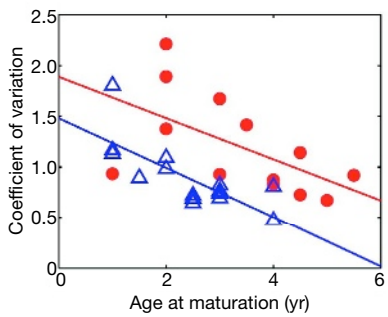

Figure 1 | Relationships between coefficients of variation of annual larval abundance and age at maturation for exploited and unexploited species. The correlations between coefficients of variation and age at maturation were significant for both exploited (red, filled circles) and unexploited (blue, open triangles) groups ($P < 0.05$). The coefficients of variation for the exploited group were higher than those for the unexploited group, even after accounting for the effect of age at maturation ($P = 0.002$). For graphical presentation, missing data on age at maturation for five species were imputed using the expectation maximization algorithm[30] (for species names, see Fig. 4 of Supplementary Data).

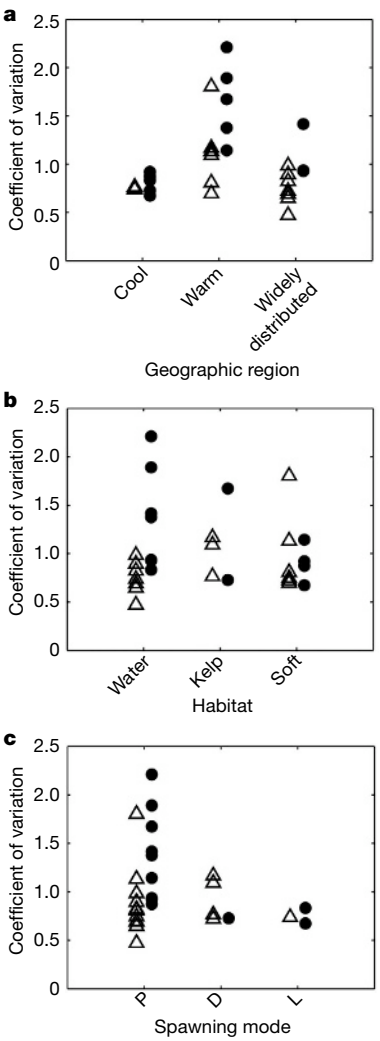

Figure 2 | Coefficients of variation of annual larval abundance of exploited and unexploited species associated with geographic regions, habitats and spawning modes. a–c, Filled circles indicate exploited species whereas open triangles indicate unexploited species associated with geographic regions (**a**), habitats (**b**) and spawning modes (**c**). P, pelagic spawners; D, demersal spawners; L, live-bearers. No significant association between coefficients of variation and habitats or spawning modes are found. For geographic regions (**a**), coefficients of variation for warm-water species are higher than those for cool-water species and widely distributed species. However, after accounting for the effect of regions, the coefficients of variation for the exploited species are still higher than those for the unexploited species (multiple regression, $P = 0.005$).

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Table 1 | Results of the correlation analysis between fish abundance and time

	Species	Correlation coefficient	*P*-value
Exploited	*Engraulis mordax*	−0.126	0.439
Exploited	*Merluccius productus*	0.072	0.659
Exploited	*Sardinops sagax*	0.583	<0.001
Exploited	*Scomber japonicus*	0.159	0.327
Exploited	*Trachurus symmetricus*	−0.451	0.004*
Exploited	*Microstomus pacificus*	0.105	0.521
Exploited	*Paralabrax clathratus*	0.179	0.270
Exploited	*Paralichthys californicus*	−0.010	0.950
Exploited	*Parophrys vetulus*	−0.050	0.758
Exploited	*Scorpaenichthys marmoratus*	−0.097	0.550
Exploited	*Sebastes aurora*	−0.243	0.131
Exploited	*Sebastes paucispinis*	−0.505	0.001*
Exploited	*Sphyraena argentea*	0.230	0.154
Unexploited	*Cololabis saira*	0.037	0.822
Unexploited	*Icichthys lockingtoni*	−0.569	<0.001*
Unexploited	*Leuroglossus stilbius*	−0.359	0.023*
Unexploited	*Tetragonurus cuvieri*	0.100	0.539
Unexploited	*Trachipterus altivelis*	0.040	0.809
Unexploited	*Chromis punctipinnis*	−0.099	0.544
Unexploited	*Lyopsetta exilis*	0.172	0.289
Unexploited	*Hippoglossina stomata*	−0.097	0.554
Unexploited	*Pleuronichthys verticalis*	0.069	0.673
Unexploited	*Sebastes jordani*	−0.206	0.203
Unexploited	*Symphurus atricaudus*	−0.123	0.448
Unexploited	*Zaniolepis frenata*	0.541	<0.001
Unexploited	*Argentina sialis*	0.437	0.005
Unexploited	*Hypsoblennius jenkinsi*	0.042	0.799
Unexploited	*Ophidion scrippsae*	−0.167	0.303
Unexploited	*Oxylebius pictus*	0.189	0.244

Exploited species are defined as fisheries-targeted species[4]. Asterisks indicate a significant negative correlation between fish abundance and time. Only four among the 29 species show significant declining trends. No systematic differences exist between the exploited and unexploited groups in the prevalence of declining trends.

long-tailed age structures (a long tail of old individuals in the age distribution), and include: age-related differences in spawning locations and time[26,27], and increased quantity and quality of eggs produced by older (experienced) or larger fish[28]. A long-tailed age structure can dampen environmental stochasticity and thus stabilize fish populations. In contrast, when fishing truncates age structure, fish populations become more variable because bet-hedging strategies are undermined and the populations more closely track short-term environmental variability. This well-documented mechanism[26–28] suggests how fishing can make populations more susceptible to extrinsic environmental forcing. We call this phenomenon the age truncation effect (the ATE phenomenon), and show it is an effect that can operate independently of significant declining trends in abundances.

To our knowledge, our results provide the first empirical evidence to show that fishing increases variability in the abundance of exploited populations (even after accounting for life-history effects, ecological traits, phylogeny and a changing environment). The elevated variability of exploited populations is probably the result of the increased importance of recruitment and the elevated variability of recruitment caused by fishery-induced truncation of age structure[1,5,8,9] (the ATE phenomenon). Indeed, as has been speculated[29], it is quite plausible that at low stock sizes the only regulatory process operating is a stochastic one. The most immediate implication for the management of fisheries is that, beyond the potential for causing a decline in abundance, fishing can provoke greater variability in exploited populations (and therefore reduced resilience) and thereby increase the risk of collapse of a fishery from stochastic environmental events[11]. Obviously, this risk increases if fishing results in both higher variability and declining populations. That these two undesirable consequences of fishing can occur together represents a double jeopardy and should be of concern to fisheries managers.

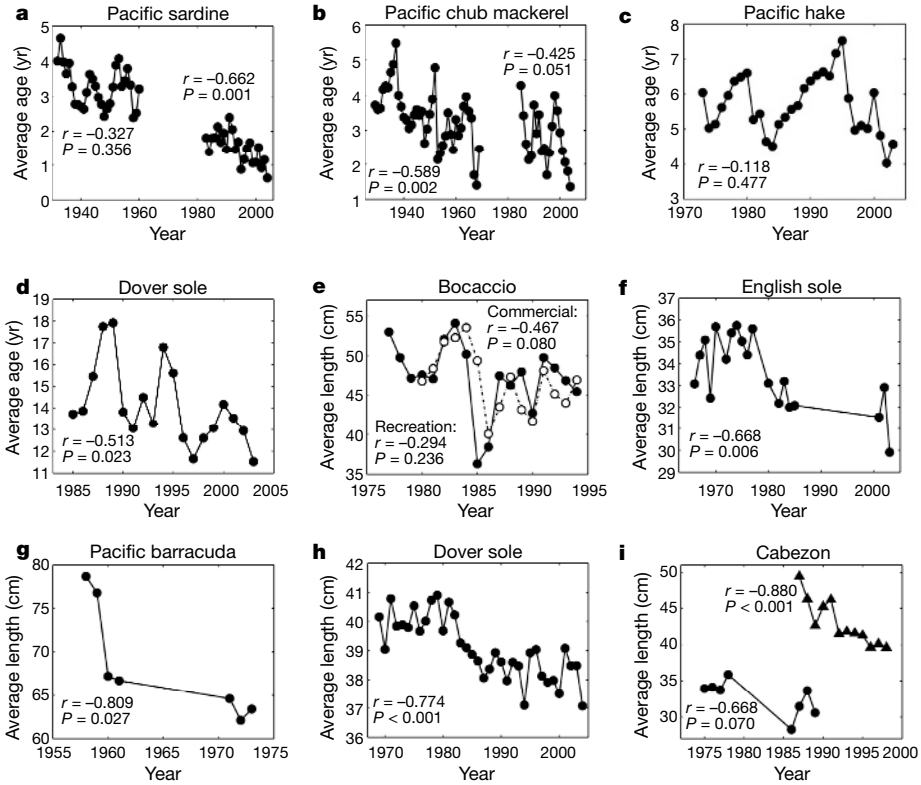

Figure 3 | Long-term declining trends in the average age and length of exploited species. a–i, Data are from fisheries catch records (see Supplementary Data). In **a** and **b**, analysis is carried out separately in the period before and after a moratorium on fishing. In **e**, filled and open circles represent data from recreational and commercial fisheries, respectively. In **i**, circles and triangles represent data from southern and northern California, respectively. The *P*-values are corrected for serial dependence in the time series. Although only 7 out of 13 time series show a significant trend at $P < 0.05$, all exhibit a declining trend, which is highly significant as an ensemble result (binomial test, $P < 0.005$).

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METHODS

The larval fish data used here were collected in the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The CalCOFI programme is one of the most comprehensive observational oceanography programmes in the world with at least four cruises per year (except for tri-annual cruises between 1966 and 1984) and 66 stations per cruise, from 1949 (ref. 4). This data set provides fishery-independent data that are free from confounding effects (changes in fishing gear or areas) commonly associated with fishery catch data in estimating fish abundances. Because the CalCOFI programme spans more than 50 yr, the data reflect how fish populations respond at various time scales (from annual to decadal) of environmental forcing, as well as how they react to fishing. Because the fish populations live in the same area, they experience much the same large-scale environmental forcing. Importantly, both exploited and unexploited species were consistently sampled. These properties allow us to separate fishing effects from environmental effects on fish dynamics. We can use unexploited species as an objective reference and regard fishing as a treatment in a long-term experiment.

In this study, we used the well-documented assumption that larval fish abundances are proportional to the standing stock of the adults that produced them[4]. Evidence for this comes from studies that demonstrate correlations between larval counts and estimates of adult biomass (obtained independently from other surveys and fisheries assessment models)[4]. In addition to responding to changes in adult biomass, in our study counts of larvae may potentially vary due to changes in the reproductive effort of adults, mortality rates of eggs and early larvae, and large-scale movements of reproducing adults in and out of the CalCOFI survey grid. Despite these potential sources of added variability, the larval data for most species in our study were shown to track faithfully long-term variation in adult biomass (see Supplementary Data and Supplementary Table 1).

We used coefficients of variation of the annual abundance of larval fish as the measure of temporal variability for fish species. The coefficient of variation is a useful measurement of temporal variability because it is unitless (and therefore is suitable for cross-species comparison[20]) and because each time series contains the same sample size[20]. Our aim was to test whether the coefficients of variation of the exploited group were higher than those of the unexploited group, after factoring out the effects of ancillary variables (life-history traits, larval abundance, ecological traits and phylogeny). Stepwise multiple linear regression analysis was used to test the effect of fishing (dummy variable) and the ancillary variables on the coefficients of variation as well as the interactions between fishing and the ancillary variables on the coefficients of variation. Because of limited sample sizes we implemented forward stepwise regression to select sequentially significant variables to incorporate in the regression model. We used an F-test at each step to identify the variable with the most significant P-value for inclusion in the next step. We assumed that there are no systematic differences between exploited and unexploited populations with regard to interspecific interactions. By-catch effects on unexploited species were assumed to be minimal[4].

Missing data on life-history traits in the multiple regression were accounted for using the multiple imputation method[30] (1,000 imputations). Because life-history traits are correlated[22], we used their correlation structure to impute the missing data, assuming a multivariate normal distribution[30]. The statistical inferences were generated by combining the results of the 1,000 analyses[30].

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

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Author Contributions C.H. and G.S. conceived the original study. C.H. is responsible for the statistical analyses and uncovering the main result. All co-authors contributed to refining the analysis, framing and interpreting the result, and to its final exposition.

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