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FROM THE COVER

# Meta-analysis reveals lower genetic diversity in overfished populations

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## Abstract

**While population declines can drive the loss of genetic diversity under some circumstances, it has been unclear whether this loss is a general consequence of overharvest in highly abundant marine fishes. We compiled data from 11 049 loci across 140 species and found that allelic richness was lower in overfished populations within 9 of 12 genera and families. A multiple linear regression showed that allelic richness was on average 12% lower ($P < 0.0001$) in overharvested populations after accounting for the effects of body size, latitude and other factors. Heterozygosity was on average 2% lower ($P = 0.030$). Simulations confirmed that these patterns are consistent with a recent bottleneck in abundant species and also showed that our analysis likely underestimates the loss of rare alleles by a factor of two or three. This evidence suggests that overharvest drives the decay of genetic diversity across a wide range of marine fishes. Such reductions of genetic diversity in some of the world's most abundant species may lead to a long-term impact of fishing on their evolutionary potential, particularly if abundance remains low and diversity continues to decay.**

*Keywords*: conservation genetics, fish, fisheries management, population dynamics

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## Introduction

Overexploitation can cause the loss of genetic variation and a consequent reduction in evolutionary potential and adaptive ability (Ryman *et al.* 1995; Allendorf *et al.* 2008), but the genetic drift driving this decline is predicted to be weak in wide-ranging and abundant species (Frankham *et al.* 2002). Nearly all marine fishes have large population sizes with millions of individuals or more, and so initial expectations were that genetic bottlenecks would be rare (Hauser *et al.* 2002). However, the strength of drift is determined by effective population size, and this can be much lower than census abundance in marine species (Hauser *et al.* 2002; Hare *et al.* 2011). Empirical evidence for genetic bottlenecks in marine fishes is mixed: some case studies found that neutral genetic diversity decayed or inbreeding increased as populations declined (Smith *et al.* 1991; Hauser *et al.* 2002; Hutchinson *et al.* 2003; Hoarau *et al.* 2005), while other studies found no change (Ruzzante *et al.* 2001; Poulsen *et al.* 2006; Therkildsen *et al.* 2010; Jakobsdóttir *et al.* 2011). However, genetic samples are only available before and after declines for a relatively small number of species, and it therefore remains unclear whether genetic loss is a common consequence of overfishing or a rare anomaly. With hundreds or thousands of overfished populations around the world, this remains an important question.

If genetic impacts are indeed rare, genetic diversity in overfished species should be similar to that in species that have not declined. Within a meta-analytical framework, we therefore compiled data on genetic diversity across a wide range of marine fishes and asked whether overfished species had lower diversity than closely related species. While this approach did not allow us to

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observe reductions in genetic diversity directly, it did allow us to study a much wider range of species than those few previously examined with historical samples. Genetic diversity is both theoretically expected and empirically documented to be similar within closely related species (José *et al.* 2008; Flight 2010), and so close relatives that have not declined provide a proxy for historical genetic diversity. The phylogenetic approach minimizes life history differences within our comparisons, including differences in genetic population structure, and hence reduces potentially confounding factors (Dunham & Miles 1985; Duminil *et al.* 2007; Sethi *et al.* 2010; Pinsky *et al.* 2011).

## Methods

### *Literature selection*

We built a database from measurements of genetic diversity in overfished fishes and in control species closely related to these overfished species. We focused on microsatellites because of their widespread use, large number of available loci, presumed neutrality and high variability. Microsatellites may also be more closely associated with contemporary population size than other types of loci (McCusker & Bentzen 2010).

We used the RAM Legacy stock assessment database (Ricard *et al.* 2012) to identify 131 populations across 72 species of fish that had been overfished in the last 50 years (biomass <50% of that predicted to sustain maximum sustainable yield, or approximately a 75% decline from unfished biomass) (Pinsky *et al.* 2011). We then conducted searches in ISI Web of Science and Google Scholar with species name and 'microsatellite' as keywords to identify population genetic studies. We also searched species synonyms as listed in Fishbase (Froese & Pauly 2012).

For comparison against these overfished populations, we compiled studies from other populations in the same species and from congeners not recorded as overfished in the RAM Legacy database. We used confamilials when more than one congener was not available. For simplicity in this paper, we refer to the overfished and control species as being from the same taxon, whether defined at the genus or family level. We only compared marine species to other marine species, and only anadromous species to other anadromous species. We also excluded endangered or critically endangered species from the control species (as defined by the IUCN Redlist, http://www.iucnredlist.org) because these species have suffered declines similar to overfished species and so were not appropriate as controls in our study. Studies were collected until 1 May 2011.

From each study, we recorded allelic richness ($A$), expected heterozygosity ($H_e$), number of individuals, whether the study was a primer note, whether the loci were originally developed in other species (cross-species use of microsatellites) and the collection location. Because observed allelic richness is dependent on sample size, we used Ewen's sampling formula to correct all estimate of richness to a standard sample size of 50 individuals ($A_{50}$), the median in our data set (Ewens 1972). We also explored an alternative correction, namely to analyse observed allelic richness ($A$) directly but to include sample size as an explanatory term (following McCusker & Bentzen 2010). We only included data from wild populations with a sample size >10, excluded loci that were linked to expressed sequence tags, and excluded monomorphic loci and those expressly chosen for low diversity (e.g. some used for forensic analysis). For overfished populations, we only included samples taken after the population became overfished (as defined by the RAM Legacy database).

In some cases, studies only reported average diversity across multiple loci. We listed each locus from such an average separately, but added a small amount of normally distributed error to each entry. The error had a standard deviation equal to that reported by each study. For heterozygosity, the average standard deviation was 0.16 and did not vary with the magnitude of heterozygosity ($P = 0.56$). We used this average standard deviation if a study did not report a standard error for their mean. For allelic richness, the standard deviation for loci within averages was proportional to allelic richness (slope of 0.64, $P = 0.007$), and we used this relationship to add error where a study failed to report it.

### *Statistical analysis*

Many factors can influence genetic diversity in marine fishes in addition to fishing. For example, genetic diversity is generally higher in fishes with smaller body sizes and larger fisheries catch, presumably because body size and catch are related to abundance (McCusker & Bentzen 2010). Genetic diversity also tends to decline towards the poles, reflecting postglacial colonization events (Hewitt 2000; Hasselman *et al.* 2013). Study design, location and methodological factors may also be important. For example, authors of population genetic studies often select particular microsatellites for their research, while primer notes generally report all polymorphic loci discovered. In addition, cross-species loci may tend to have lower diversity (Rico *et al.* 1996; Barbará *et al.* 2007).

Given these influences, we analysed the effects of overfishing in a multiple regression framework that

allowed us to simultaneously account for other factors. We fit mixed-effects models in which the response variable was the corrected allelic richness ($A_{50}$), the expected heterozygosity ($H_e$) or the observed allelic richness ($A$) of each locus. Allelic richness was log-transformed and heterozygosity was arc-sin transformed to improve normality. The explanatory factors (fixed effects) included overfished status, latitude, major fishing area, body size, fisheries catch, whether or not the study was a primer note and whether or not it was a cross-species locus. Sample size was also included in models for observed allelic richness ($A$). Latitude was included as a quadratic term to allow hump-shaped responses. Overfished status was defined for each population using the RAM Legacy stock assessment database (Ricard *et al.* 2012), and populations without known status were assumed not to be overfished. Where this assumption was incorrect, it would tend to reduce our statistical power and hence was a conservative choice. Fishing areas were those defined by the Food and Agriculture Organization (http://www.fao.org/fishery/cwp/handbook/H/en). Data on maximum body size were from Fishbase (Froese & Pauly 2012) and were log-transformed. Fisheries catch was defined as the log-transformed, average, annual, global fisheries landings reported to the Food and Agriculture Organization (FAO) from 1950 to 2006 (http://www.fao.org/fishery/figis) (following McCusker & Bentzen 2010). Species not listed by the FAO were assumed to have a global catch of zero. We accounted for the correlated error structure of these data (e.g. multiple loci from the same species and multiple species from the same taxon) by including random effects for species nested within random effects for taxon (Zuur *et al.* 2009).

In addition to evaluating $P$-values on the full model, we fit all 192 possible combinations of explanatory factors and compared models using Akaike's Information Criterion (Burnham & Anderson 2002). The model with the lowest AIC was considered the minimal model, one that fit the data well while using few parameters. We assessed the relative importance of each variable by summing AIC weights across all models that included that variable (Burnham & Anderson 2002). Analyses were conducted in R 2.15.3 with the nlme package (Pinheiro *et al.* 2011).

### *Simulations*

To examine expected loss of genetic diversity following a bottleneck, we used the BOTTLESIM program (Kuo & Janzen 2003) to simulate the process of genetic drift in populations with either discrete or entirely overlapping generations that declined by either 50% or 90%. Genetic diversity generally declines faster in species with overlapping generations (Kuo & Janzen 2003). We used a lifespan of 36 years and a 4-year age of maturity, the average values for the fishes in our data set. We conducted 1000 simulations in BOTTLESIM at each prebottleneck population size of $N_e = 10^x$, where $x$ = [2, 2.5, 3, 3.5, 4]. We sampled populations for 30 generations after the bottleneck. We modified BOTTLESIM slightly to report the allelic richness from a sample of 50 individuals (as we used in our meta-analysis) as well as from the entire population and to handle population sizes greater than 1000. The simulations were initialized with average allele frequency distributions for a microsatellite-like locus in a stable population with $2N_e$ alleles generated by fastsimcoal (Excoffier & Foll 2011). We used a mutation rate of $5 \times 10^{-4}$ per generation, an average value for microsatellites (Selkoe & Toonen 2006; Yue *et al.* 2007), but also conducted sensitivity analyses with $1 \times 10^{-4}$ and $1 \times 10^{-3}$.

The above simulations assume closed populations, which may not be appropriate for species with high gene flow. We therefore wrote a forward Wright–Fisher genetic simulation for five populations connected in a circle by stepping-stone migration. The model sampled $2N_b$ alleles for each population in each generation with replacement, where $N_b$ was the effective size after the bottleneck. Some of these alleles (a quantity *Poisson* ($mN_b$) for immigration rates $m$ = [0.001, 0.01, 0.1]) were from the population to the left, while others (again *Poisson*($mN_b$)) were from the right. The populations were arranged in a circle to avoid edge effects. We ran 500 simulations for each parameter set and imposed the bottleneck either on all populations or only on a focal population. We calculated allelic richness and heterozygosity from a random sample of 100 alleles (i.e., 50 individuals) from one focal population. The simulations were initialized with allele frequency distributions from fastsimcoal as before, but for five populations connected by migration in a circle. Neither of our bottleneck simulation methods considered mutation, which was reasonable given the short time frame that we examined.

Finally, we calculated the statistical power to detect declines in genetic diversity with temporal (before-after) sampling around a bottleneck. To do so, we sampled loci from 50 individuals before and after the bottleneck in our simulations, calculated allelic richness ($A_{50}$) and heterozygosity ($H_e$) for each locus and used a t-test to determine whether diversity after the bottleneck was significantly different than diversity before the bottleneck. We used three sets of simulation parameters that produced results consistent with our meta-analysis results: initial effective sizes of $10^3$, $10^{3.5}$ and $10^4$ with respective sampling times after the bottleneck of 3, 5 and 15 generations. All three parameter sets were simulated with overlapping generations and a 90% decline,

as described above. We examined 1000 simulations for each parameter set and calculated the proportion of times that a statistically significant ($P < 0.05$) decline in diversity was detected.

## Results

### *Data*

We compiled data on 11 049 microsatellite loci from 202 studies of 140 species (Table S1, Supporting information). Of these species, 32 had data from overfished populations and 108 were included as controls not known to be overfished. The species were organized into 12 taxa with both overfished and control species (Table 1). About a third of the studies (32%) were primer notes, and about a third of the loci (38%) were cross-species amplifications.

As one example, overfished populations of the sea bream *Pagrus auratus* had 10.0 ± 1.3 (±1 SE) alleles per locus ($A_{50}$), while other populations in the *Pagrus* genus had, on average, 15.7 ± 0.7 alleles. Expected heterozygosity ($H_e$) was also slightly lower (0.75 ± 0.04 vs. 0.76 ± 0.01). Overfished yelloweye rockfish (*Sebastes ruberrimus*) populations also had lower allelic richness ($A_{50}$ = 6.9 ± 2.8) compared to rockfishes that were not known to be overfished ($A_{50}$ = 13.4 ± 0.2).

When we looked across all taxa, overfished populations had slightly fewer alleles per locus and slightly lower heterozygosity ($A_{50}$ = 11.9 ± 1.2; $H_e$ = 0.70 ± 0.03) than in control populations ($A_{50}$ = 12.7 ± 1.0; $H_e$ = 0.73 ± 0.02) (Table 1). Within nine of the twelve taxa for which we had data, the number of alleles per locus ($A_{50}$) was lower in overfished populations than in control populations. We found similar patterns for heterozygosity, with lower heterozygosity in overfished populations for nine of twelve taxa. We caution that any single comparison is based on relatively few species and does not account for other differences among species that could affect genetic diversity, such as body size, global catch, latitude of sampling or the prevalence of cross-species loci or primer notes (Table 1). For example, *Lutjanus* appeared to have higher genetic diversity in overfished populations, but the control populations also had a higher prevalence of cross-species loci with potentially low diversity (Table 1). Trimming out cross-species loci from all *Lutjanus* species suggested that genetic diversity was lower in overfished populations ($A_{50}$ = 8.9 ± 0.3; $H_e$ = 0.61 ± 0.01) as compared with control populations ($A_{50}$ = 12.6 ± 0.8; $H_e$ = 0.76 ± 0.02), though cross-species loci did not explain higher diversity in overfished Osmeridae and *Trachurus* populations (Table S2, Supporting information). Given these caveats about single comparisons and

**Table 1** Summary of sample size (in total number of species and in number of overfished species), allelic richness ($A$), expected heterozygosity ($H$), the proportion of microsatellites that were cross-species amplifications ($X$), the proportion of studies that were primer notes ($P$), the average global catch ($C$), the average length ($L$) and the average latitude of sampling ($T$). Data are reported separately for overfished populations ($A_{OF}$, $H_{OF}$, $X_{OF}$, $P_{OF}$, $C_{OF}$, $L_{OF}$ and $T_{OF}$) and for those that were not overfished ($A_{NO}$, $H_{NO}$, $X_{NO}$, $P_{NO}$, $C_{NO}$, $L_{NO}$ and $T_{NO}$)

| Taxon | # (OF) | $A_{OF}$ | $A_{NO}$ | $H_{OF}$ | $H_{NO}$ | $X_{OF}$ | $X_{NO}$ | $P_{OF}$ | $P_{NO}$ | $C_{OF}$ | $C_{NO}$ | $L_{OF}$ | $L_{NO}$ | $T_{OF}$ | $T_{NO}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clupeidae | 9 (6) | 13.0 ± 0.3 | 15.7 ± 0.3 | 0.83 ± 0.00 | 0.83 ± 0.01 | 0.22 | 0.22 | 0.03 | 0.06 | $1.4 \pm 0.033 \times 10^5$ | $9.4 \pm 0.13 \times 10^4$ | 47 ± 0.18 | 46 ± 0.26 | 51.4 ± 0.2 | 49.6 ± 0.3 |
| *Cynoscion* | 5 (1) | 3.6 ± 0.4 | 6.2 ± 0.3 | 0.46 ± 0.06 | 0.57 ± 0.02 | 1 | 0.91 | 0 | 0.3 | $4.7 \pm 0 \times 10^3$ | $2.7 \pm 0.047 \times 10^3$ | 98 ± 0 | 98 ± 0.63 | 36.9 ± 0.8 | 26.5 ± 0.3 |
| Gadidae | 10 (6) | 16.2 ± 0.5 | 17.5 ± 0.4 | 0.81 ± 0.01 | 0.81 ± 0.01 | 0.24 | 0.16 | 0.11 | 0.04 | $1.4 \pm 0.15 \times 10^5$ | $2.3 \pm 0.11 \times 10^5$ | 100 ± 3 | 140 ± 1.8 | 52.9 ± 0.3 | 49.7 ± 0.5 |
| *Lutjanus* | 10 (2) | 9.0 ± 0.3 | 8.8 ± 0.4 | 0.61 ± 0.01 | 0.68 ± 0.01 | 0.04 | 0.69 | 0.06 | 0.39 | $4.7 \pm 0.1 \times 10^3$ | $1.7 \pm 0.11 \times 10^3$ | 99 ± 0.11 | 71 ± 1.7 | 28.1 ± 0.1 | 21.6 ± 0.6 |
| Osmeridae | 4 (1) | 15.5 ± 0.9 | 10.4 ± 0.3 | 0.78 ± 0.02 | 0.69 ± 0.01 | 0 | 0.11 | 0.19 | 0.12 | $1.6 \pm 0 \times 10^4$ | $2.4 \pm 0.21 \times 10^3$ | 25 ± 0 | 35 ± 0.19 | 71.3 ± 0.2 | 48.9 ± 0.2 |
| *Pagrus* | 4 (2) | 12.1 ± 1.6 | 15.7 ± 0.7 | 0.70 ± 0.03 | 0.76 ± 0.01 | 0.93 | 0.51 | 0 | 0.13 | $3.7 \pm 0.51 \times 10^3$ | $4.7 \pm 0.43 \times 10^3$ | 96 ± 1.8 | 110 ± 1.3 | 22.9 ± 3.2 | 6.5 ± 2.6 |
| Pleuronectidae | 10 (2) | 9.4 ± 0.5 | 12.5 ± 0.4 | 0.57 ± 0.01 | 0.73 ± 0.01 | 0.02 | 0.17 | 0.04 | 0.39 | 810 ± 120 | 280 ± 67 | 110 ± 1.4 | 77 ± 1 | 51.9 ± 0.3 | 52.1 ± 0.3 |
| Scombridae | 6 (1) | 10.5 ± 0.7 | 14.0 ± 0.5 | 0.71 ± 0.02 | 0.74 ± 0.01 | 0.24 | 0.43 | 0 | 0.25 | $4.7 \pm 0 \times 10^3$ | $5.1 \pm 0.16 \times 10^4$ | 460 ± 0 | 260 ± 2.9 | 39.6 ± 0.3 | 12.8 ± 1.2 |
| Scophthalmidae | 4 (1) | 8.3 ± 1.7 | 9.3 ± 0.3 | 0.64 ± 0.06 | 0.67 ± 0.01 | 0 | 0.21 | 0 | 0.03 | 300 ± 0 | 610 ± 22 | 60 ± 0 | 100 ± 1.9 | 41.5 ± 0.8 | 50.8 ± 0.4 |
| *Sebastes* | 45 (8) | 12.9 ± 0.6 | 13.4 ± 0.2 | 0.73 ± 0.01 | 0.75 ± 0.00 | 0.96 | 0.6 | 0 | 0.05 | 170 ± 20 | $1.2 \pm 0.039 \times 10^3$ | 69 ± 0.62 | 65 ± 0.51 | 41.7 ± 0.2 | 51.3 ± 0.2 |
| Serranidae | 30 (1) | 12.1 ± 0.9 | 12.4 ± 0.3 | 0.78 ± 0.02 | 0.71 ± 0.01 | 0.5 | 0.32 | 0 | 0.32 | 11 ± 0 | 390 ± 63 | 140 ± 0 | 73 ± 1.6 | 27.5 ± 0.2 | 23.2 ± 0.4 |
| *Trachurus* | 3 (1) | 20.3 ± 2.7 | 16.0 ± 2.2 | 0.83 ± 0.03 | 0.81 ± 0.02 | 0.6 | 0.07 | 0.4 | 0.17 | $2.9 \pm 0 \times 10^5$ | $4.7 \pm 1 \times 10^4$ | 70 ± 0 | 67 ± 1 | −33.5 ± 1.5 | 34.7 ± 2.8 |

multiple influences, we now turn to statistical models to examine patterns across the full data set while accounting for a wider range of potential explanatory factors.

### *Statistical analysis*

The full models for both corrected allelic richness ($A_{50}$) and heterozygosity ($H_e$) included statistically significant terms for overfished status and cross-species loci (Table 2). The full model for richness also included significant terms for fisheries catch, primer notes and FAO area. As selected by AIC, the minimal models for richness and heterozygosity included the same terms that were significant in their respective full models, though the minimal heterozygosity model also included terms for fisheries catch and latitude.

The models suggested that allelic richness in overfished populations was 11.7% lower. Interpreting the overfished term for arc-sin transformed heterozygosity was less intuitive, but equalled a 1.7% loss (full model) or 1.6% loss (minimal model) for an average microsatellite in our data set (heterozygosity of 0.75). Richness and heterozygosity both increased with catch and were lower in cross-species amplifications of microsatellites, as expected. Richness and heterozygosity showed weak down-curved relationships with latitude in the full models (lower at both poles), but only an increasing term with latitude was retained in the minimal heterozygosity model. AIC weights suggested that whether or not a locus was a cross-species amplification and whether or not a population was overfished were the two most important terms for allelic richness, while latitude was also important for heterozygosity (Table 2).

As an alternative approach, we also analysed observed allelic richness ($A$, not corrected for sample size) and included sample size as an explanatory term. This model suggested similar results: overfished populations had 9.6% (full model) or 9.5% (minimal model) fewer alleles ($P = 0.0002$). In addition, richness increased with sample size ($P < 0.0001$), increased with fisheries catch ($P = 0.001$), was lower in cross-species loci ($P < 0.0001$) and varied with FAO area ($P < 0.0001$).

Finally, we tested whether our results were sensitive to fishes from any one family. Removing each family in turn revealed approximately 10% fewer alleles and slightly lower heterozygosity in overfished species (7.7–15% fewer alleles, $P = 0.005$ to <0.0001; +0.4% higher to 4.6% lower heterozygosity, $P = 0.7$ to 0.0002). The heterozygosity difference was negative in all cases, except when removing Pleuronectids (+0.4%, $P = 0.7$), consistent with a small or possibly negligible decline in heterozygosity.

### *Simulations*

We next simulated population bottlenecks to determine whether a ~10% loss of allelic richness ($A_{50}$) and a 0–2% loss of heterozygosity ($H_e$) were reasonable. Our analysis suggested that we should expect these or greater losses in species with discrete generations that had an initial effective size <3000 and that declined by 90%

**Table 2** Models to explain variation in log-transformed allelic richness ($A_{50}$) and arc-sin transformed expected heterozygosity ($H_e$) across marine fishes

| | $A_{50}$ models | | | $H_e$ models | | |
|---|---|---|---|---|---|---|
| Term | Full | Minimal | RVI | Full | Minimal | RVI |
| Overfished? | −0.12 ± 0.027 (<**0.0001**) | −0.12 ± 0.027 (<**0.0001**) | 1.0 | −0.015 ± 0.0073 (**0.042**) | −0.014 ± 0.0071 (0.051) | 0.69 |
| Latitude | 2.5 ± 3.1 × $10^{-3}$ (0.43) | | 0.49 | 5.4 ± 9.7 × $10^{-4}$ (0.58) | 6.0 ± 3.2 × $10^{-4}$ (0.057) | 0.76 |
| Latitude$^2$ | −9.8 ± 34 × $10^{-6}$ (0.77) | | 0.14 | −2.0 ± 10.7 × $10^{-6}$ (0.85) | | 0.28 |
| FAO Area | (**0.011**) | (**0.0073**) | 0.69 | (0.36) | | 0.0056 |
| log(Length) | −0.034 ± 0.069 (0.62) | | 0.29 | −0.022 ± 0.023 (0.33) | | 0.34 |
| log(Catch) | 0.031 ± 0.0097 (**0.0019**) | 0.030 ± 0.0094 (**0.0021**) | 0.98 | 5.6 ± 3.3 × $10^{-3}$ (0.087) | 5.4 ± 3.1 × $10^{-3}$ (0.082) | 0.57 |
| Primer note? | 0.12 ± 0.033 (**0.0005**) | 0.12 ± 0.033 (**0.0005**) | 0.99 | −8.8 ± 11 × $10^{-3}$ (0.42) | | 0.43 |
| Cross-species? | −0.15 ± 0.027 (<**0.0001**) | −0.15 ± 0.026 (<**0.0001**) | 1.0 | −0.051 ± 0.0084 (<**0.0001**) | −0.049 ± 0.0083 (<**0.0001**) | 1.00 |
| ΔAIC | 4.7 | 0 | | 15.5 | 0 | |

The full model included all terms, while the minimal model was selected by AIC. $P$-values are in parentheses (bold for $P < 0.05$). Relative variable importance (RVI) values are also listed. The fitted values for the FAO Area term are not listed because it had 14 levels.

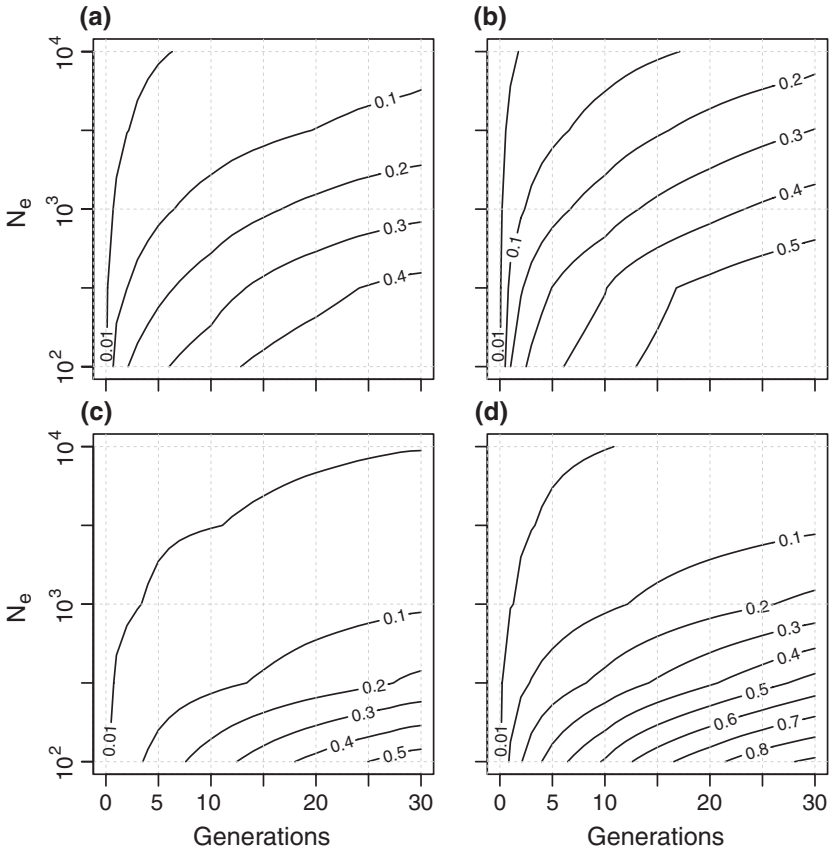


**Fig. 1** Simulated bottlenecks of 90% in a species with discrete generations (a, c) or with overlapping generations (b, d). Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b) or proportion of heterozygosity lost (c, d). Initial effective population size ($N_e$) is indicated along the *y*-axis, and generations postbottleneck are indicated along the *x*-axis.

more than ten to fifteen generations ago (Fig. 1a, c). The loss of richness occurred faster for smaller initial effective sizes (e.g. a 10% loss after only seven generations for initial effective sizes of 1000). Weaker bottlenecks (50% decline) could also produce these patterns in populations with smaller effective sizes or bottlenecks further in the past (Fig. S1a, c, Supporting information).

Marine fishes generally have overlapping generations, however, and our simulations suggested that genetic diversity losses occur sooner in such species. A 10% loss of allelic richness occurred within five generations for effective population sizes near 3000 and within fifteen generations for effective sizes near 10 000 (Fig. 1b). In both the discrete and the overlapping generation scenarios, allelic richness was still declining after 30 generations (Fig. 1).

The above simulations for allelic richness were for a sample size of 50 individuals, similar to the data we analysed in our meta-analysis. When we examined the decline of allelic richness in the full population, however, we found a much more rapid loss (Fig. 2). In particular, a 10% loss of alleles occurred within a

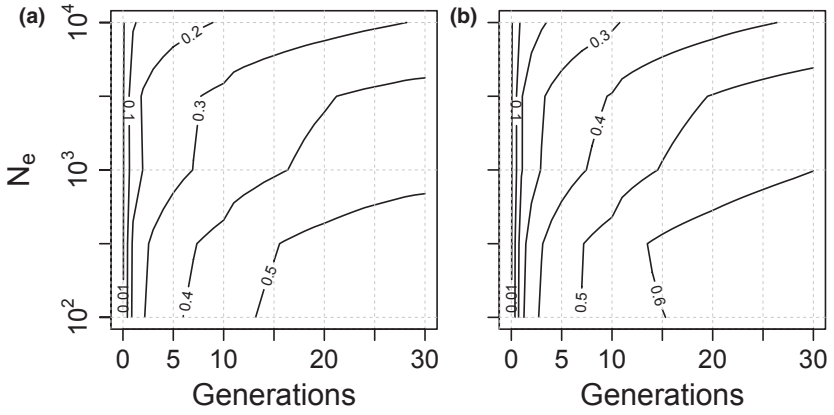


**Fig. 2** Expected loss of allelic richness in the entire population. Graphs show simulated bottlenecks of 90% in a species with discrete generations (a) or overlapping generations (b). See legend of Fig. 1 for other notes.

generation or two of a 90% decline in population size, even for effective sizes of 10 000. After only five generations, more than 20% of alleles were lost for any populations with effective sizes under 6000. We also found 30% losses after ten generations for populations with effective sizes of 3000. These lost alleles were primarily the rare alleles that could drift to extinction relatively easily.

When we simulated bottlenecks in discrete generation populations connected by gene flow, declines of allelic richness occurred over similar time frames and effective sizes for 0.1% or 1% immigration rates (Figs S3 and S4, Supporting information). However, allelic richness declined substantially more slowly for an immigration rate of 10%. Heterozygosity also declined more slowly, and even a 1% loss was unlikely for effective population sizes of more than 3000. If only the focal population experienced the bottleneck, diversity declined more slowly (Fig. S4, Supporting information) than in a scenario where all populations experienced the bottleneck (Fig. S3, Supporting information), but the difference was relatively minor. We also examined mutation rates five times higher or lower and found that our results were relatively insensitive to these differences (compare Fig. 1 to Figs S5 and S6, Supporting information).

Finally, we tested the statistical power to detect a loss in genetic diversity with sampling before and after a 90% decline in abundance. We selected three bottleneck scenarios from our simulations that produced declines in genetic diversity similar to those detected in our meta-analysis (i.e., ~10% loss of allelic richness and 0–2% loss of heterozygosity). Across 1000 simulated data sets, our calculations suggested that statistical power to detect a 10% loss of allelic richness was low unless twenty or more loci were examined, while substantially more than twenty loci were needed to reliably detect a decline in heterozygosity (Fig. S7, Supporting information).

## Discussion

While previous studies on individual species have reached conflicting conclusions about whether overfished marine species suffer a reduction in genetic diversity, our analysis across 32 overfished species and 128 closely related species suggests that being overfished reduced genetic diversity by a small but measurable amount in most species. Our simulations suggested that these observed declines were possible for populations with effective sizes up to 10 000, but were most likely in species with overlapping generations, with effective sizes in the low thousands and with <10% gene flow from outside populations. Our simulations also suggested that the loss of rare alleles throughout the entire population (rather than in a sample of individuals) could be two to three times greater than we detected.

Theory predicts that drift acts more quickly and severely on allelic richness than on heterozygosity because the former is more sensitive to rare alleles (Maruyama & Fuerst 1985), a finding confirmed by our simulations and consistent with our observation of stronger reductions in allelic richness than in heterozygosity. The small difference in heterozygosity that we detected therefore appears to indicate a recent rather than ancient bottleneck.

The other patterns that we detected in our genetic diversity data set were largely consistent with previously published results. In particular, we found a positive relationship between global fisheries catch and genetic diversity, as well as a negative but much weaker relationship between body size and diversity. McCusker & Bentzen (2010) found similar patterns, including the weaker relationship with body size, and concluded that both catch and size are proxies for long-term abundance. The lower diversity we detected in cross-species amplifications of microsatellites also matches previous reports (Rico *et al.* 1996).

One important question is whether marine fishes have effective population sizes consistent with the declines in genetic diversity that we detected. The effective size of marine fishes has been much debated and remains an important area of research (Poulsen *et al.* 2006; Hare *et al.* 2011). Despite very large census population sizes, some authors have suggested that effective population sizes for many marine fishes may be in the thousands, and even lower in some cases (Hauser *et al.* 2002; Poulsen *et al.* 2006; Laurent & Planes 2007). Variance in reproductive success, family-correlated survival, population fluctuations through time and skewed sex ratios are all common traits of marine species that tend to reduce effective size below census size (Hauser *et al.* 2002). Even for some of the most abundant species such as sardine (Clupeidae) and anchovy (Engraulidae), modelling suggests that high variance in reproductive success can, under some circumstances, produce effective sizes in the thousands (Gaggiotti & Vetter 1999), while empirical work has also suggested low effective sizes (Laurent & Planes 2007). Some of the smallest estimates of effective sizes in marine fishes (tens to hundreds) have been questioned for methodological reasons (Hare *et al.* 2011), but even studies generally sceptical of low effective-to-census size ratios in marine fishes have concluded that effective sizes in the thousands may be reasonable (Poulsen *et al.* 2006; Therkildsen *et al.* 2010). Interestingly, our simulations also suggested that effective sizes in the thousands are consistent with the decline in genetic diversity that we detected, particularly when overlapping generations were considered.

While our simulations revealed that high levels of gene flow (10% immigration) could offset the impacts of a bottleneck, these levels seem unlikely between distinct fish stocks. Migration rates of 10% would tend to synchronize population dynamics (Hastings 1993), and it would be unlikely that two subpopulations connected by such high levels of dispersal would be identified as separate stocks in the first place. Given that a 90% decline from prefishing biomass is reasonable to expect for heavily overfished marine species (Worm *et al.* 2009), our simulations implied that loss of genetic diversity may be a common outcome when harvest causes dramatic and prolonged declines in abundance. Our simulations also suggested that these declines continue to deepen with time.

If these declines in genetic diversity are common, however, it is perhaps curious that a number of studies have not detected such declines, even with direct before and after sampling around a large reduction in population size (e.g. Ruzzante *et al.* 2001; Poulsen *et al.* 2006; Therkildsen *et al.* 2010; Jakobsdóttir *et al.* 2011). One possibility is that the statistical power of these tests was low when conducted with the relatively few loci that have been available to date. Previous researchers have pointed out the low power of bottleneck tests when conducted with ten or fewer loci (Cornuet & Luikart 1996; Antao *et al.* 2011; Peery *et al.* 2012), and our simulations confirmed similar findings for before–after sampling of allelic richness and heterozygosity with twenty or fewer loci. The ability to examine many loci across many species was one advantage of our meta-analytical approach. However, direct detection provides the strongest evidence for genetic bottlenecks, and we recommend that future temporal studies genotype substantially more loci than have been examined in the past (though we fully recognize the difficulties of doing so with historical genetic material). Single-nucleotide polymorphism (SNP) genotyping (e.g. Therkildsen *et al.* 2013) and next-generation sequencing provide promising technologies for overcoming many of these problems in the future.

A reduction in genetic diversity among overfished species could be caused by selection or by genetic drift. Fishing can exert strong selective pressures on target species (Law & Grey 1989; Jørgensen *et al.* 2007), with two potential consequences for genetic diversity. On the one hand, selection for particular variants at specific loci can create regions of the genome with anomalously low or high diversity (Foll & Gaggiotti 2008). Obvious outlier loci that might signal the action of natural selection in our overfished species were not readily apparent in our data, though formal statistical tests were not possible and we cannot entirely discount this process. In addition, strong selection can reduce genome-wide effective population size by increasing the variance in reproductive success among individuals (Hare *et al.* 2011). The latter demographic process has similar effects to a reduction in effective population size caused by overharvest. Both processes can drive genetic drift to erode diversity throughout the genome (Frankham *et al.* 2002; Hauser *et al.* 2002; Hare *et al.* 2011), and both could be acting on these species.

As explored in part by our simulations, the degree to which these processes reduce diversity depends on many factors, including initial effective population size, the length of time and the degree to which effective population size is reduced, and the amount of gene flow (Frankham *et al.* 2002; Allendorf *et al.* 2008; Flight 2010). We expect, for example, that taxa with more severe overfishing will suffer a greater loss of diversity. These factors, in addition to sampling variance and between-species and between-population differences in life history and demography, may help to explain the variation across taxa that we observed in Table 1. Our statistical model accounted for a number of factors, but did not, for example, examine different magnitudes of overfishing. Future work on this issue will be helpful for understanding how to balance fishing against the maintenance of genetic diversity.

Once lost from a population, genetic diversity can be rebuilt through mutation or through immigration from refugia. Mutation will rebuild genetic diversity over many generations, but the process will be very slow. While immigration can act over faster timescales, it may not quickly reverse the consequences of a bottleneck. For six of our overfished species (including *Brevoortia tyrranus* and *Cynoscion regalis*), the entire species is considered one stock, leaving no potential refugia. For other species, we expect that relatively few refugia with high genetic diversity remain because fishing tends to target the largest populations first (Sethi *et al.* 2010). When we examined the RAM Legacy stock status database (Ricard *et al.* 2012), we found that all stocks (100%) with known status had been overfished for 28 of the 32 overfished species in our data set. It appears that, when one stock is overfished, others in the same species are likely to suffer similar declines. Over longer time periods, however, rare immigration events from genetically divergent and locally adapted populations may help diversity recover (Pukk *et al.* 2013). More broadly, even if an overharvested species is allowed to recover demographically, it appears that its evolutionary trajectory may be altered for a substantially longer period of time (Law & Grey 1989; Enberg *et al.* 2009).

The ability of a species to evolve and survive in future conditions depends on the alleles present within the genome and the traits conferred by them, particularly in rapidly changing environments (Allendorf *et al.*

2008). While the relationship between genetic diversity and adaptive capacity is complex (Willi *et al.* 2006), our results suggest that genetic drift in marine fishes is strong enough to remove alleles at neutral or weakly selected loci across the genome, including those that may be critical for adaptation to future environmental conditions. If being overfished amplifies genetic drift across many species, as our data suggest, it may drive the loss of important alleles from a large number of populations (Ryman *et al.* 1995). Loss of 10% of the alleles at any one locus may not exert a strong fitness effect, but our results and simulations suggest that this is a genome-wide loss in many heavily fished species. Loss of just one allele at thousands of loci in a species could substantially reduce adaptive capacity, particularly under future climate conditions that species rarely encounter today.

Fisheries managers have long documented and responded to the demographic and ecological impacts of overharvest, but they have rarely managed for genetic diversity (though see calls to do so in Jørgensen *et al.* 2007; Smith 1994). This lack of attention may stem from uncertainty about the generality of genetic impacts from overfishing. Our results, however, provide evidence that overfishing has reduced genetic diversity in a wide range of abundant marine fishes and that these effects will probably continue unless populations are allowed to recover.

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M.L.P. and S.R.P. conceived and designed the study and wrote the paper. M.L.P. collected and analyzed the data and designed the simulations.

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## Data accessibility

Genetic diversity database, modified BOTTLESIM source code and R code for bottlenecks in stepping-stone populations: DRYAD entry doi:10.5061/dryad.jt683 (Pinsky & Palumbi 2013).

## Supporting information

Additional supporting information may be found in the online version of this article.

**Table. S1** Species and references used in our meta-analysis. The Overfished column indicates whether any populations of the species were known to be overfished.

**Table. S2** Summary of sample size (in total number of species and in number of overfished species), allelic richness ($A$), and expected heterozygosity ($H$) for loci that are not cross-species amplifications. Data are reported separately for overfished populations ($A_{OF}$ and $H_{OF}$) and for those that were not overfished ($A_{NO}$ and $H_{NO}$).

**Fig. S1** Simulated bottlenecks of 50% in a species with discrete generations (a, c) or with overlapping generations (b, d). Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b) or proportion of heterozygosity lost (c, d). Initial effective population size ($N_e$) is indicated along the $y$-axis, and generations postbottleneck are indicated along the $x$-axis.

**Fig. S2** Expected loss of allelic richness in the entire population. Graphs show simulated bottlenecks of 50% in a species with discrete generations (a) or overlapping generations (b). See legend of Fig. S1 for other notes.

**Fig. S3** Simulations for populations linked by immigration rates of 0.1% (a, d), 1% (b, e) or 10% (c, f). All populations experienced a bottleneck of 90%. Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b, c) or proportion of heterozygosity lost (d, e, f). Initial effective population size ($N_e$) is indicated along the $y$-axis, and generations postbottleneck are indicated along the $x$-axis.

**Fig. S4** Simulations for populations linked by immigration rates of 0.1% (a, d), 1% (b, e) or 10% (c, f). Only the focal population experienced a bottleneck of 90%. Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b, c) or proportion of heterozygosity lost (d, e, f). Initial effective population size ($N_e$) is indicated along the $y$-axis, and generations postbottleneck are indicated along the $x$-axis.

**Fig. S5** Simulations initialized with mutation rates of $1 \times 10^{-3}$. Simulated bottlenecks of 50% (a,c) or 90% (b, d) in a species with discrete generations. Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b) or proportion of heterozygosity lost (c, d). Initial effective population size ($N_e$) is indicated along the $y$-axis, and generations postbottleneck are indicated along the $x$-axis.

**Fig. S6** Simulations initialized with mutation rates of $1 \times 10^{-4}$. Simulated bottlenecks of 50% (a,c) or 90% (b, d) in a species with discrete generations. Contour lines indicate proportion of allelic richness lost in a sample of 50 individuals (a, b) or proportion of heterozygosity lost (c, d). Initial effective population size ($N_e$) is indicated along the $y$-axis, and generations postbottleneck are indicated along the $x$-axis.

**Fig. S7** Statistical power to detect declines in a) allelic richness or b) heterozygosity with samples taken before and after a 90% decline in population size. Parameter sets for the simulations were a pre-bottleneck $N_e$ of 1000 and samples taken three generations postbottleneck (solid line); $N_e$ of 3162 and five generations (dashed line); and $N_e$ of 10 000 and 15 generations (dotted). These parameter sets were chosen to produce declines in genetic diversity consistent with our meta-analysis results (i.e., 10% decline in allelic richness, 0–2% decline in heterozygosity).