

LETTER

Does increasing mortality change the response of fish populations to environmental fluctuations?

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Abstract

Fluctuations of fish populations abundances are shaped by the interplay between population dynamics and the stochastic forcing of the environment. Age-structured populations behave as a filter of the environment. This filter is characterised by the species-specific life cycle and life-history traits. An increased mortality of mature individuals alters these characteristics and may therefore induce changes in the variability of populations. The response of a generic age-structured model was analysed to investigate the expected changes in the fluctuations of fish populations in response to decreased adult survival. These expectations were then tested on an extensive dataset. In accordance with theory, the analyses revealed that decreased adult survival and mean age of spawners were linked to an increase in the relative importance of short-term fluctuations. It suggests that intensive exploitation can lead to a change in the variability of fish populations, an issue of central interest from both conservation and management perspectives.

Keywords

Age-structured populations, climate-fishing interaction, demographic change, exploited fish stocks, frequency response, response to the environment.

Ecology Letters (2012) 15: 658–665

INTRODUCTION

Fish populations display fluctuations in abundance occurring over a large range of time scales, from the short (e.g. below the decade) to the long term (e.g. interdecadal to centennial), but understanding the origin of these fluctuations has remained elusive. Although intensive removals exerted by fisheries exploitation critically affect fish-stock biomass (Christensen *et al.* 2003), growing evidence has shown that long-term fluctuations in marine environments can force long-term changes in stock productivity (Beaugrand *et al.* 2003). However, this issue becomes even more complex considering that the effects of exploitation and climate may interact (Perry *et al.* 2010; Planque *et al.* 2010). By comparing theoretical expectations to empirical observations, this study presents new empirical evidence that such an interaction might be at play and that exploitation can affect the response of fish stocks to environmental variability.

The fluctuations of age-structured populations critically depend on the interplay between the structure of the species' life cycle (i.e. the skeleton of the underlying dynamical model) and the stochastic forcing of the environment (Bjørnstad *et al.* 1999; Bjørnstad & Grenfell 2001). Theoretical work has shown that age-structured populations behave as environmental filters that amplify and dampen environmental fluctuations at specific frequencies (Bjørnstad *et al.* 2004). The properties of such a filter, the frequency response, are largely determined by the life cycle and the life-history traits of populations. It has recently been shown that high mortality rates imposed on mature individuals, such as exploitation, can alter these characteristics and ultimately change the response of fish populations to their physical environment (Worden *et al.* 2010; Botsford *et al.* 2011; Rouyer *et al.* 2011). Therefore, understanding the life-history characteristics that determine the response of fish stocks to their environment is important for fisheries ecology, from both conservation and management perspectives.

Similar to the effects of the typical size-selectivity of fisheries that preferentially removes larger and older individuals (Law 2000; Hsieh *et al.* 2010), increased mortality caused by infectious diseases can also induce an age-selective removal of older individuals from fish populations (Price 1980; Ohlberger *et al.* 2011). A long-lasting selective removal of individuals from a population can lead to substantial demographic changes, which have important ecological implications. This process can indeed alter the capacity of populations to sustain long-term environmental fluctuations (Murphy 1968; Longhurst 2002; Ottersen *et al.* 2006), induce potentially long-term changes in life-history traits (Jørgensen *et al.* 2007), reduce the reproductive potential (Berkeley *et al.* 2004; Birkeland & Dayton 2005), affect fish-stock productivity (Conover & Munch 2002) and variability (Hsieh *et al.* 2006; Anderson *et al.* 2008; Stenseth & Rouyer 2008). The effect of increased adult mortality on the variability of fish stocks has mainly been studied through its magnitude, such as the coefficient of variation, whereas its other facet, its time scale, has received less attention. Knowledge about the effects of exploitation on the time scale of the response of fish stocks to climate is of critical importance for fisheries ecologists. Nevertheless, the literature specifically investigating this issue remains scarce and mainly theoretical (Worden *et al.* 2010; Botsford *et al.* 2011). In the context of current climate change and over-exploitation of marine resources, assessing whether fisheries affect the response of fish populations to their physical environment is a question of key interest.

In the present work, we investigated how the decreasing survival of mature individuals changes the frequency response of fish populations to their environment from both theoretical and empirical perspectives. Using a generic stochastic age-structured population dynamics model, we quantified how an increased adult mortality modified the frequency response of the population model to the stochastic environment. Following the methodology outlined in Bjørnstad *et al.* (2004) and in Worden *et al.* (2010), the transfer function of the model was computed

for different sets of adult mortality and life-history traits. Transfer functions describe the frequency composition of the spawning stock abundance as a function of the forcing by the environment at different frequencies. The characteristics of the transfer function obtained from the different sets of parameters provided the basis for our theoretical expectations, which were then confronted with empirical data. Two datasets of fish populations were then used to investigate the consistency between theoretical expectations and observations at the intra- and interpopulation levels using the power spectra of spawner-abundance time series. First, we investigated how increased adult mortality modifies the frequency response of fish populations over time. We selected three populations from marine and freshwater environments for which long time series were available that displayed contrasted periods of low and high adult mortality, induced by an elevated exploitation and an infectious disease. Second, we investigated whether or not such changes in the frequency response were detectable among stocks with different life-history traits and exploitation histories. Here, we used time series of spawner abundances for 24 commercially exploited fish stocks from the Northeast Atlantic.

MATERIALS AND METHODS

Theoretical expectations: transfer functions

We used a simple age-structured population model, identical to the 'tuna model' in Bjørnstad *et al.* (2004), in order to represent a large range of fish life cycles. The general methodology and additional results on this model have been thoroughly documented in Bjørnstad *et al.* (2004) and only the material necessary to understand the following analyses is presented here. The reader seeking further details is referred to Bjørnstad *et al.* (2004), Worden *et al.* (2010) and the references therein.

The age-structured model is given by the following relationship:

$$N_{a,t} = Surv_a N_{a-1,t-1}, \quad a = 1, \dots, A_{\max},$$

where $N_{a,t}$ is the abundance at age a and time t and $Surv_a$ is the survival at age a .

The stock–recruitment relationship is given by:

$$N_{0,t} = \xi_t S_p^{(1-\beta)},$$

where ξ_t represents the stochastic forcing of the environment following a white noise process, β represents the parameter quantifying the degree of density dependence and S_p is the spawning stock abundance at time t .

Transfer functions were used to investigate how such an age-structured population model responds to environmental forcing on recruitment (Nisbet & Gurney 1982). Transfer functions describe the frequency composition of the output signal, here the spawning stock abundance, as a function of the input signal, here the forcing of recruitment by the stochastic environment at different frequencies. It describes how the stochastic forcing of the environment for different frequencies is amplified/dampened, therefore providing an adequate way to investigate the frequency response of the modelled population to its environment. To obtain the transfer function, one has to assume that the model has a locally stable equilibrium. Using log-transformed abundances, the equilibrium state of the model is determined and the model is linearised around this equilibrium. Then, the transfer function is obtained by Fourier

transforming the linearised system. The transfer function of the model is given by:

$$TF(f) = \frac{\sum_{k=A_{50}}^{k=A_{\max}} \left[e^{-2\pi ijk} \frac{Surv^k}{\sum_{j=A_{50}}^{j=A_{\max}} Surv^j} \right]}{1 - (1 - \beta) \sum_{k=A_{50}}^{k=A_{\max}} \left[e^{-2\pi ijk} \frac{Surv^k}{\sum_{j=A_{50}}^{j=A_{\max}} Surv^j} \right]}$$

where f is the frequency, β the density-dependence parameter, $Surv$ the survival, A_{50} the age at 50% maturity and A_{\max} the maximum age of the population. It has to be noted that here $Surv$ is not an age-specific variable.

To quantify the relative importance of low/high frequencies, the slope of the transfer function in log-coordinates was calculated for a broad range of values for β and $Surv$, as well as for different sets of A_{50} and A_{\max} . The slope of the power spectrum in log-coordinates has already largely been used to quantify the relative importance of low and high frequencies in environmental and biological signals (Halley 1996; Halley & Stergiou 2005). Its simple interpretation, the more negative the slope the more dominated by low frequencies is the signal, eases the following comparisons between theoretical and empirical results.

Intrapopulation comparisons

First, we investigated how an increasing adult mortality modifies the frequency response of populations over time, i.e. on an intrapopulation basis. Studying the spectral composition of a signal necessitates long-term time series, a constraint that became even more stringent because the spectral composition within one stock had to be compared between contrasted periods of adult mortality. The Northeast Arctic cod stock (*Gadus morhua*), has displayed long, consistent and contrasted periods of low and high exploitation and is thus well suited for this analysis (Table 1). Data for the Northeast Arctic cod were obtained from the Virtual Population Analysis (VPA) performed by the International Council for the Exploration of the Sea (ICES) stock assessment group, which were completed back in time (until 1913) by the long-term VPA performed by Hysten (2002). This economically important stock displayed substantial changes in exploitation and age structure as the fishing mortality sharply increased in the late 1940s (see Hysten 2002 and Rouyer *et al.* 2011). The analysis of this stock was complemented by using data for two freshwater populations of perch (*Perca fluviatilis*) in the north and south basins of Windermere, a glacial valley lake in the English Lake District (UK). Windermere is divided into a mesotrophic north and a eutrophic south basin by islands and shallows (Le Cren 2001). The perch populations in the two basins are independent according to capture–mark–recapture and genetic data (Kipling & Le Cren 1984; Bodaly *et al.* 1989). Perch population abundances were obtained from a recent estimation of age-specific population numbers that were fitted to a long-term time series of catch and effort data from Windermere (Langangen *et al.* 2011). The original catch data were taken from a scientific monitoring programme of the lake that started in the early 1940s and continues today with very little changes in gear

Table 1 Species, stock and temporal extent of the time series in the database used for the interpopulation analysis

Species	Stock	Temporal extent
Cod (<i>Gadus morhua</i>)	Baltic Sea (subd. 22–24)	1970–2008
	Baltic Sea (subd. 25–32)	1966–2008
	Northeast Arctic	1913–2006
	Faroe	1961–2008
	Iceland	1955–2009
	North Sea	1963–2008
Haddock (<i>Melanogrammus aeglefinus</i>)	Irish Sea	1968–2007
	Celtic Sea	1971–2007
	Northeast Arctic	1950–2008
	Faroe	1957–2008
Herring (<i>Clupea harengus</i>)	North Sea	1960–2008
	Norwegian Spring-spawning	1907–2006
	West Scotland (subd. Via)	1957–2008
Plaice (<i>Pleuronectes platessa</i>)	North Sea	1957–2008
	Irish Sea	1964–2007
Saithe (<i>Pollachius virens</i>)	Northeast Arctic	1960–2008
	Faroe	1961–2008
	North Sea	1967–2008
Sole (<i>Solea solea</i>)	North Sea	1957–2008
	Irish Sea	1970–2006
	Western Channel (subd. VIIe)	1969–2007
	Celtic Sea	1971–2007

type and fishing methods (Le Cren 2001). In 1976, the outbreak of a perch-specific pathogen was observed in Windermere, which induced a dramatic mortality with much higher prevalence among large, mature individuals compared to small, immature ones (Bucke *et al.* 1979). The high mortality among adult perch severely truncated the population age structure for many years after 1976 (Edeline *et al.* 2008; Ohlberger *et al.* 2011). The perch populations were fished until 1948 in the north and until 1965 in the south basin, but they are not exploited by a commercial fishery today (Le Cren *et al.* 1977). Because no estimate of the spawning stock abundance was available, time series of catches of mature individuals were used to check the consistency of the results.

For each of these stocks, the power spectra of the spawning stock abundance for the cod stock, and the total abundance for the perch populations, were computed. In order to obtain a robust estimate of the power spectrum and to analyse as many frequencies as possible, the wavelet methodology was used (Cazelles *et al.* 2008). The wavelet approach decomposes the variance of time series over time and by frequency. The relative importance of frequencies for each time step may then be represented in the time/frequency plane that forms the wavelet power spectrum. Averaging the wavelet power spectrum over a given time period provides an unbiased estimator of the power spectrum. To compare the power spectrum of time series between periods of low and high adult mortality, this approach was preferred to the classical Fourier decomposition. Fourier decomposition involves the analysis of each period and is constrained by their length. In contrast, the wavelet analysis is applied to the whole time series and therefore allows the analysis of lower frequencies. Averaging the wavelet power spectrum over each period thus provides an analysis over similar frequencies that can be compared directly. For each case, the wavelet power spectrum of the spawning

stock or population abundance time series was therefore averaged over the period of low and high adult mortality and the two resulting power spectra were then compared. In order to obtain comparable and consistent estimates of the power spectra, for all time series the maximum time scale analysed was set to be equal to one-third of the length of the shortest time series, i.e. 20 years.

Interpopulation comparison

Time series of 24 stocks from the Northeast Atlantic each comprising more than 35 years of data were extracted (Table 1) from the latest reports available from the relevant ICES working groups (<http://www.ices.dk/indexfla.asp>). For each stock, the time series of spawning stock abundance was obtained from age-structured matrices of maturity and abundance. Potential demographic changes were quantified through time series of mean age in the spawning abundance, calculated as the mean of the ages weighted by the proportion of the spawning stock abundance within each age class. The mean age of spawners for each stock was then estimated as the median of the distribution across years. The magnitude of changes in age structure over time was estimated by the difference in the median of the distribution between the second and the first half of the time series.

The complete dataset of 24 stocks was then used to investigate the relationships between the variability in slopes of the power spectra and (1) the average mean age of the population, and (2) the magnitude of change in the age structure over time. To do so, the power spectrum of the spawning stock abundance was estimated using the wavelet power spectrum averaged over time. The maximum scale analysed was set to be equal to the third of the length of the spawning abundance time series. The slope was estimated based on the log-transformed power spectrum with a robust linear regression procedure using iterated re-weighted least squares (function “rlm” from the package MASS in the statistical software R; Venables & Ripley 2002). This method was used to diminish the effects of peaks in the power spectrum on the estimate. No effect of the length of the time series was found on the spectral estimates. A linear model was then used to investigate whether a change in age structure affected the relationship between the slope of the power spectrum and the mean age of spawners. The stocks displayed various degrees of changes in age structure that were modelled by a categorical variable, introduced in interaction with the mean age of spawners. With this structure, the model estimated the effect of the mean age of spawners on the slope of the power spectrum for each level of the categorical variable. The categorical variable was defined with four levels, each containing six stocks, which were obtained from the quartiles of the distribution of changes in mean age over time.

All computations were performed using R (ver. 2.12.0, R Development Core Team, 2010; Available at <http://www.R-project.org>).

RESULTS

Theoretical expectations

The expected change in the frequency response of the populations to an increased adult mortality was investigated using the transfer function of a typical fish life cycle, constructed for a large range of values for the age at maturity, the maximum age, the density-dependence parameter and the survival. The change in the relative

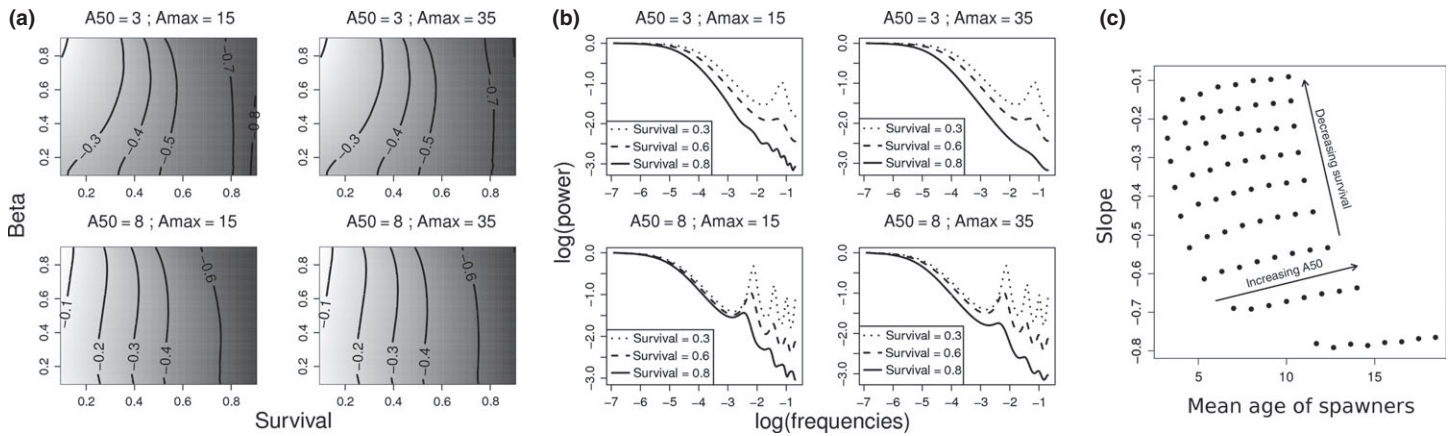


Figure 1 (a) Slopes of the transfer function, regression between $\log(\text{spectrum})$ and $\log(\text{frequencies})$, against survival and density dependence for different age at maturity (A_{50}) and maximum age (A_{max}). The slopes are in a grey scale, the darker the more negative the slope and the more dominant are the long-term fluctuations, contours indicate the different levels. (b) Power spectra in log-coordinates for different survival values and for the different sets of A_{50} and A_{max} . Density dependence was set to 0.4. (c) Slopes of the transfer function against the mean age of spawners for survival ranging from 0.1 to 0.9 and A_{50} ranging from 3 to 10. A_{max} was fixed to the asymptotic value of 50 years, whereas density dependence was fixed at 0.4.

importance of frequencies with decreasing adult survival was quantified using the slope of the resulting transfer function in log-coordinates. The more negative the slope, the more dominant are the low frequencies, that is, the long-term fluctuations, in the signal. The variability of the slope was then investigated for different ages at maturity and maximum ages, over a large range of parameter values for density dependence and survival (Fig. 1a). The slopes were overall negative indicating a general dominance of the low frequencies over the shorter ones. Whereas density dependence did not show a strong effect on the relative importance of frequencies, a decrease in adult survival was always associated with an increase in the slope. This pattern was apparent in the actual transfer functions, which were more flattened at higher than at lower adult mortality for any set of parameter values inspected (Fig. 1b), suggesting that populations with higher adult mortality are less dominated by long-term fluctuations.

The slope estimates did not depend on the maximum age of a stock, but the slopes did depend critically on the number of spawning age classes, which was affected by survival and by the age at maturity. The slope estimates displayed a negative association with the mean age of spawners, with steeper slopes associated with higher survival (Fig. 1c). Increasing age at maturity was positively associated with the slope estimates, but with a weaker effect than survival (Fig. 1c).

Intrapopulation comparison: changes over time

Changes in variability between the two contrasted periods of adult mortality could be directly visualised in the time series (Fig. 2a). For instance, the relatively smooth spawning stock abundance time series of the Northeast Arctic cod displayed stronger short-term fluctuations over the high adult mortality period, a pattern that was also clear for the two perch populations. This visible increase in short-term variability was further associated with a substantial decrease in the mean age, suggesting a truncation of the age structure of the populations. The power spectra of the three populations were plotted and the periods of low and high adult mortality were compared (Fig. 2b). In order to facilitate the comparison, the ratio between the power spectra obtained for the periods of high and low adult

mortality was computed. Positive values indicate an increase whereas negative values indicate a decrease in the relative importance of the corresponding frequencies. All the populations displayed a flatter power spectrum during the period of high adult mortality and their ratio was always positive for the higher frequencies. Whereas the populations displayed a power spectrum dominated by low frequencies during the periods of low adult mortality, this pattern disappeared or became weaker during the periods of higher adult mortality. The perch stocks illustrated a particularly strong pattern as the power spectra for the periods with high adult mortality were nearly flat, indicating a signal whose variance was explained in a comparable amount by short- and long-term fluctuations. Analysing the catch per unit effort of mature individuals (not shown) for the two perch populations displayed less drastic changes but nevertheless indicated an increase of the relative importance of high frequencies in the signal. This suggested that the observed frequency changes were neither an artefact of the model used to estimate the abundance, nor linked to the use of total abundance instead of spawning abundance.

Interpopulation comparison

The slopes of the power spectrum of the spawning abundance computed for the 24 Atlantic stocks displayed a weak and negative association with the mean age of spawners. This negative relationship was in general accordance with the theoretical expectations (Fig. 1c). However, a few stocks with a relatively high mean age of spawners displayed less negative slopes (Fig. 3a). The investigation of the magnitude of the changes in mean age of spawners over time showed that the latter stocks underwent important changes in age structure, which coincided with periods of elevated fishing mortality (Fig. 3b). Classifying the stocks in four levels based on the magnitude of the change in age structure over time (see methods) revealed that these stocks belonged to the level where the most important and longer-term changes were observed. A decrease > 0.7 years was observed for these stocks, suggesting that they underwent age truncation. In fact, no substantial long-term change in age structure due to elevated fishing mortality could be detected among the other stocks. The linear

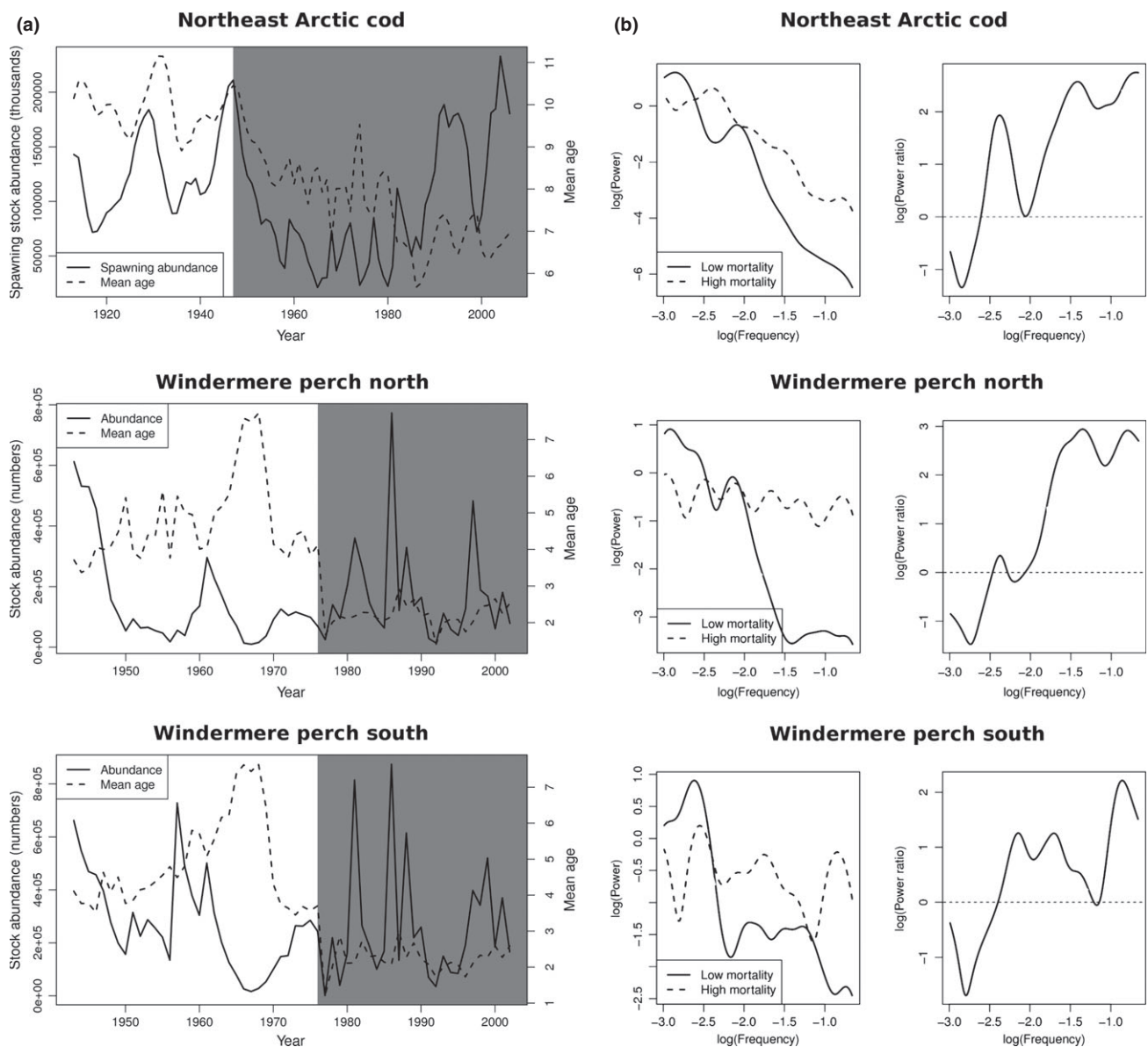


Figure 2 Changes in the variability of time series over time. (a) Time series of spawning stock abundance and mean age of spawners for the Northeast Arctic cod (top), and the north (middle) and south (bottom) stocks of Windermere perch. The grey areas represent the period of increased adult mortality. (b) Power spectrums for the period with low (solid line) and high adult mortality (broken line) were computed for each population (left plot). Log of the ratio between the power spectra for high and low adult mortality (right plot). Negative values therefore indicate a decrease in the relative importance of corresponding frequencies, whereas positive values indicate an increase in their relative importance.

model, which estimated the effect of the mean age of spawners on the slope of the power spectrum for each of the four levels corresponding to the different magnitude of changes in age structure, confirmed these observations (Fig. 3a). The model explained 64% of variance and displayed significant negative effects of the mean age of spawners on the slopes of the power spectrum for each level (Table 2). Hence, stocks with higher mean age of spawners generally displayed spawning abundance time series with stronger low-frequency fluctuations. However, the relationship became weaker for the two levels representing the more pronounced changes in age structure and particularly for the level composed by age-truncated stocks (Fig. 3a), suggesting that changes in age structure were associated with a shift towards high frequencies in spawning abundance time series. These results were generally in accordance with the theoretical expectations

obtained from the transfer function, which showed that a higher mean age of spawners was associated with steeper negative slopes while an increased adult mortality was associated with less negative slopes (Fig. 1c).

DISCUSSION

Fish populations behave as an environmental filter and its modification through exploitation constitutes a main pathway through which fisheries effects interact with climate (Perry *et al.* 2010; Planque *et al.* 2010). The present study compared the frequency response predicted by a generic model to observations made on an extensive dataset to provide evidence that increased adult mortality can change the time scale of the response of fish stocks to their environment. Our results

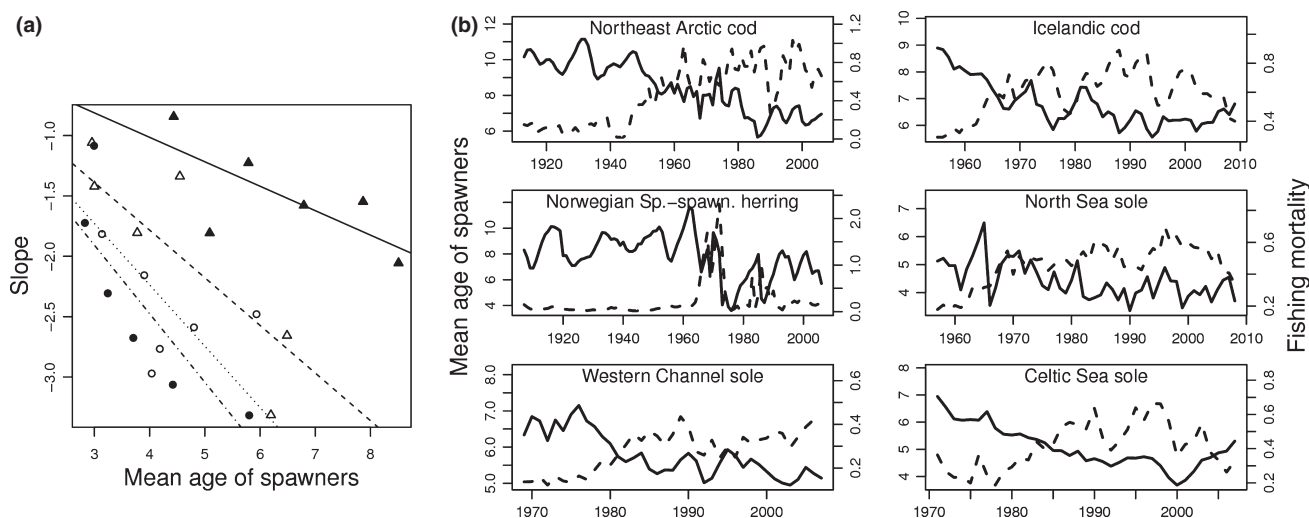


Figure 3 (a) Slope of the power spectrum of the spawning stock abundance time series for 24 stocks from the Northeast Atlantic against the mean age of spawners. Symbols and lines refer to stocks displaying a slight increase (white circles, dotted line), no change (black circles, dot-dashed line), slight decrease (white triangles, dashed line) and strong decrease (black triangles, solid line) in the mean age of spawners over time. (b) Time series of mean age of spawners (solid lines) and fishing mortality (dotted lines) for the six stocks that displayed the most pronounced changes in age structure.

Table 2 Results of the linear model investigating the relationship between the slope of the power spectrum of the spawning stock abundance time series and the mean age of spawners for different levels of changes in age structure

Effect	Estimate	P-value
Intercept	-0.2	0.6
Mean age:D1	-0.51	< 0.0001
Mean age:D2	-0.57	< 0.0001
Mean age:D3	-0.39	0.0002
Mean age:D4	-0.2	0.0038
R^2	0.64	

D1–D4 represent the four levels of changes in age structure, where D4 is the level for which the stronger declines over time occurred.

show that the age structure has important consequences for the variability of fish populations. As it is affected by both the age at maturity and the survival of mature individuals, the mean age reflects important properties of the population and thus of the environmental filter. The results from the theoretical model showed that an elevated mean age of spawners was associated with steeper slopes of the transfer function of the spawning stock abundance, which indicate relatively smooth time series, i.e. dominated by long-term fluctuations (Fig. 4a). However, it also indicated that an elevated adult mortality reduced the mean age of spawners and changed the transfer function towards flatter slopes, which indicate more prevalent short-term fluctuations in the spawning abundance (Fig. 4b). The interpopulation analysis was consistent with these findings as negative relationships were found between the mean age of spawners and the slopes of the power spectrum (Fig. 3a). This pattern was weaker for the stocks that underwent age truncation, suggesting that changes in age structure induced by exploitation changed their frequency response towards more prevalent short-term fluctuations (Fig. 3a). In accordance with theoretical results, the elevated adult mortality experienced by these stocks may have led to a change in their age structure (Fig. 3b) inducing relatively higher short-term fluctuations in the signal, i.e. less steep slopes of the power spectrum, than for the other stocks.

The slopes were obtained by a linear approximation to the power spectrum, which allowed us to compare the relative importance of low and high frequencies in the power spectra in a synthetic fashion. However, this approach has the drawback to be affected by peaks in the power spectrum, calling for a robust estimation procedure to diminish their potential impact. Although no suitable solution was available to completely overcome this limitation, the difference in the slopes observed between the age-truncated and the other stocks suggests that it was not an artefact of the estimation procedure. Such a change in the frequency response associated with a higher adult mortality and a truncated age structure was also suggested by the intrapopulation analysis. The time series for the three examined populations displayed a flatter power spectrum during periods of elevated mortality, which also indicated an increase in the relative importance of short-term fluctuations (Fig. 2).

We have investigated whether changes in age structure induced by elevated adult mortality could lead to changes in the frequency response of fish stocks to the environment. This hypothesis was used to explain the changes in the time scale of population variability, but it is not the sole hypothesis. Age truncation may have several, non-mutually exclusive consequences for population dynamics. As the mortality of adult individuals increases, the population variability becomes increasingly dominated by recruitment dynamics, which changes the variability towards more prevalent short-term fluctuations. In addition, age truncation is also likely to undermine bet-hedging strategies, which can cause a change in recruitment variability itself by nonlinear amplification of the stochastic forcing of the environment (Hsieh *et al.* 2006; Anderson *et al.* 2008). Whether such a process occurs in the populations studied here has not been investigated. It should also be noted that substantial evidence suggests that fish dynamics may be nonlinear and unstable, and this hypothesis should be considered (Hsieh *et al.* 2005; Anderson *et al.* 2008; Glaser *et al.* 2011). In the case of nonlinear and unstable dynamics, our theoretical results, obtained assuming that the model has a single and locally stable equilibrium, would not allow us to explain the observed changes in variability.

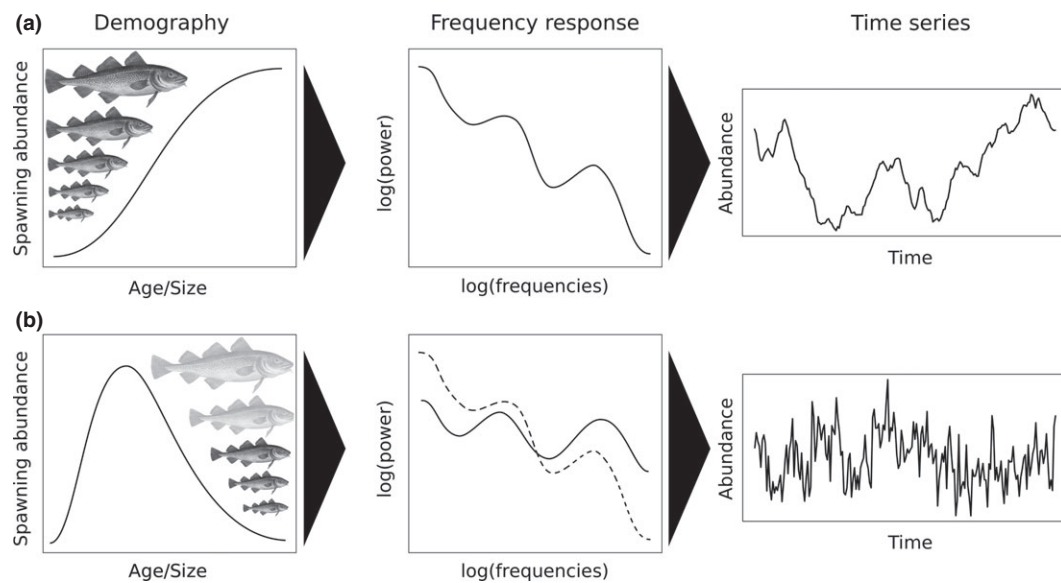


Figure 4 Schematic illustration representing the effect of changing demography on the frequency response of fish stocks. (a) In the pristine state, the demographic structure is dominated by older/larger individuals, which translates into a dominance of the low frequencies in the signal yielding relatively smooth time series of spawning abundance. (b) A high adult mortality leads to a dominance of younger/smaller fishes in the spawning abundance, which translates into a more balanced composition of the signal between low and high frequencies, yielding less smooth time series.

Our results also rest upon the theoretical model used, whose simplicity did not allow a precise description of the diversity of life cycles in our database. This choice was justified by the large number of populations analysed and the substantial differences in their life cycles. The few assumptions in our model were reasonable for many populations and made its results relevant to a wide range of cases. However, it is expected that, for particular cases, studies using more accurate models will provide more precise insights about the underlying mechanisms. For instance, feedback processes can produce fluctuations at higher frequencies, which may affect the general pattern of increasing short-term variability with increasing adult mortality (e.g. see the ‘cod model’ in Bjørnstad *et al.* 2004). Particularly, cannibalism is a process known to affect the dynamics of many of the stocks studied here, for instance cod and perch. Including such processes into the model has a large potential to help understanding observed patterns of variations in wild populations. Such a framework provides a suitable platform to address other important questions in fisheries ecology, for instance to investigate how parental effects (e.g. Berkeley *et al.* 2004) alter the population dynamics of fishes.

As in Bjørnstad *et al.* (2004), the environmental forcing on recruitment was made according to the assumption of a white noise process, corresponding to uncorrelated time series. This does not affect the calculations of the transfer functions, but temperature in marine ecosystems rather follows a red noise than a white noise process, for which the variance of the signal is dominated by long-term fluctuations (Vasseur & Yodzis 2004; Rouyer *et al.* 2010). Such red noise processes can tinge the observed power spectrum of populations and increase the relative importance of low frequencies in population fluctuations (Bjørnstad *et al.* 2004). This phenomenon is consistent with previously documented links between the long-term fluctuations in temperature and in population abundances, as shown for the Northeast Arctic cod and the Norwegian Spring-spawning herring stocks (Tøresen & Østvedt 2000; Godø 2003).

However, the increased sensitivity to shorter-term environmental fluctuations due to an elevated adult mortality can change this response, which may also explain the increasing effect of temperature on those two stocks for the period of decreased mean age of spawners (Rouyer *et al.* 2011). The combination of red noise in marine environments and the selective removal of older individuals can have serious consequences for marine fish stocks. Our results demonstrate that populations exhibiting a truncation of their age structure were associated with shorter-term fluctuations in time series, which suggests an increased sensitivity to the short-term changes in the environment. In addition, the selective removal of older individuals has important biological consequences as it can alter the natural ability of fish stocks to withstand environmental changes (Longhurst 2002) and reduce their reproductive potential (Berkeley *et al.* 2004; Birkeland & Dayton 2005). For instance, the over-exploitation of the North Sea cod reduced its spawning biomass to a few young age classes and warmer-than-average temperatures during the past two decades are likely to have driven the stock to consecutive years of poor recruitment and to its current low level (O’Brien *et al.* 2000).

An increasing importance of short-term fluctuations is generally considered as an undesirable state from both management and conservation perspectives as it can affect biological reference points, extinction risk, economic markets and precautionary measures (Beddington & May 1977; May *et al.* 1978; Ludwig *et al.* 1993; Hsieh *et al.* 2006). We therefore emphasise that the dynamical consequences of demographic changes should be accounted for when developing management schemes (Botsford *et al.* 2011).

ACKNOWLEDGEMENTS

Funding for T. R. was provided by the Norwegian Research Council through the ARCWARM Project (#178239). J. O. was funded by the Norwegian Research Council (#185000). We thank Ian Winfield,

Janice Fletcher, Ben James and other colleagues for undertaking the field and laboratory work of the Windermere monitoring programme, and we are grateful to the Freshwater Biological Association for their joint stewardship of the long-term Windermere data. This work was supported by the EUR-OCEANS Consortium.

AUTHORSHIP

Tristan Rouyer performed the analyses and wrote the paper; Alexander Sadykov performed the linear analysis of the model; Jan Ohlberger helped with data analysis and wrote the paper; Nils Chr. Stenseth wrote the paper.

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Editor, Boris Worm

Manuscript received 19 October 2011

First decision made 28 November 2011

Manuscript accepted 16 March 2012