ICES Journal of
Marine Science

Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery

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Independent of the effects of spawning-stock biomass (SSB), environmental variability in juvenile production, driven by factors such as temperature and food supply, have considerable potential to influence population resilience to fishing and depletion. Here, we analyse 18 time-series of Atlantic cod (*Gadus morhua*) stocks and empirically estimate this "environmental variability" in recruit-per-spawner (RPS) ratios. We then investigate the role of environmental recruitment variability on population resilience to fishing and ability to recover following depletion. To this end, cod population dynamics are simulated through a period of fishing, followed by a period of recovery, with alternative scenarios of recruitment variability and autocorrelation within it. The major effect of environmental recruitment variability is manifested through uncertainty. Firstly, the higher the recruitment variability, the shorter and less variable the time required for the population to decline below 15% of its carrying capacity, K. Secondly, higher variability leads to higher uncertainty in recovery time. Both these patterns are further strengthened by autocorrelation. Our findings suggest that increased environmental recruitment variability decreases resilience to fishing and increases uncertainty in recovery, thus challenging some traditional views that variability confers high productivity and rapid ability to recover from collapse.

Keywords: density-independent variation, environmental variation, *Gadus morhua*, juvenile production, reproduction, survival.

Introduction

Estimation of fish stock renewal ability is vital for projections about stock dynamics under alternative fishing strategies but it has also turned into one of the greatest challenges in fisheries research. Much of the traditional research in this respect has focused on the association between spawning stock size and recruit production, the so-called stock–recruitment relationship (e.g. Needle, 2002). In contrast to the patterns in recruitment attributable to population abundance and fishing, recruitment can also show temporal variation attributable to environmental conditions (e.g. Vert-pre et al., 2013). Temperature, predation, and food availability for juveniles have been identified as main environmental drivers (e.g. Brunel and Boucher, 2007; Olsen et al., 2011; Okamoto et al., 2012), and the magnitude and direction of the temperature effect has been further detected to differ between the edge vs. core areas within a species range (e.g. Planque and Fredou, 1999; Myers, 2001). Here, we define "environmental variability" in recruitment as the temporal variability in numbers of recruits exclusive of that generated by changes in spawning stock size.

In contrast to efforts to identify the causal mechanisms underlying environmental variability in recruitment, less attention has been focused on the implications of this form of variability on fish population dynamics and the ability of fish stocks to sustain harvesting. Recruitment variability has been identified as a much larger source of fluctuation in the abundance of a fished population than, for example, variation in natural or fishing mortality (Shelton and Mangel, 2011). Stochastic fluctuations in population dynamics are generally known to affect equilibrium abundance and increase extinction risk in depleted populations (Lande, 1993, 1998). Alternatively, it has been hypothesized that increased recruitment variability might reduce extinction probability and confer an ability to recover rapidly from collapse (e.g. Musick, 1999; Powles et al., 2000), based on the presumption that high recruitment variability is associated

with the production of unusually strong cohorts which will, in turn, enhance recovery.

Fishing-induced depletions of Atlantic cod (*Gadus morhua*), coupled with a lack of recovery in several regions despite reductions in fishing pressure, have rendered cod one of the best studied commercially fished species, with particular attention focused on stock renewal ability and potential correlates of stock recovery (Hutchings and Rangeley, 2011). In the North Sea, temperature and food supply have been reported to account for ~45% of the variability in cod recruitment, with spawning-stock biomass (SSB) accounting for additional 10% of the variation (Olsen *et al.*, 2011). Similarly, recruitment variation in several cod stocks has been suggested to co-vary with the North Atlantic Oscillation (NAO) index (Brander and Mohn, 2004). These observations suggest that stochastic environmental variability can play a significant role in cod recruitment dynamics.

In the present study, we explore how year-to-year environmental variation in cod recruitment, i.e. variability independent of changes in SSB, can affect population resilience to fishing and ability to recover from low abundance. To this end, we embed empirically quantified estimates of environmental recruitment variability into a process-based population model and simulate population dynamics under fishing, followed by a period of population recovery.

Methods

Environmental year-to-year variation in cod recruitment was quantified through the analysis of 18 stock-specific time-series (Table 1), using a hierarchical Bayesian modelling approach. The analyses focused on the recruit-per-spawner (RPS) ratios (number of recruits divided by the SSB) reported by Keith and Hutchings (2012). In their analyses, stock-specific RPS rations were standardized with respect to the stock-specific averages and units of standard deviation (s.d.) about them to facilitate comparison among stocks having

Table 1. Atlantic cod populations included in the environmental recruitment variability analysis (SD refers to standard deviation about the standardized RPS ratio).

Location	Stock ID	Data years	SD
Northeast Arctic	CODNEAR	1946 – 2009	0.372
Georges Bank (Canada)	COD5Zjm	1978 – 2003	0.071
Eastern Scotian Shelf	COD4VsW	1970 – 2011	0.333
Western Scotian Shelf	COD4X	1983 – 2008	0.039
St Pierre Bank	COD3Ps	1977 – 2004	0.174
Northern Gulf of St Lawrence	COD3Pn4RS	1974 – 2008	0.072
Southern Gulf of St Lawrence	COD4TVn	1971 – 2009	0.106
Flemish Cap	COD3M	1988 – 2006	0.230
Southern Grand Banks	COD3NO	1959 – 2010	0.145
Georges Bank (US)	CODGB	1978 – 2007	0.094[a]
Celtic Sea	CODCS	1971 – 2007	0.139
Faroe Plateau	CODFAPL	1961 – 2009	0.076
Iceland	CODICE	1955 – 2003	0.136
Eastern Baltic	CODBA2532	1966 – 2008	0.175
Kattegat	CODKAT	1971 – 2005	0.278[b]
Irish Sea	CODIS	1968 – 2007	0.140
West of Scotland	CODVIa	1978 – 2007	0.337
North Sea	CODNS	1963 – 2009	1.542

[a]Stock closest to 25% quantile: low environmental recruitment variability scenario.
[b]Stock closest to 75% quantile: high environmental recruitment variability scenario.

different patterns of association between stock size and recruitment. Specifically, differences in the age at recruitment among stocks were accounted for through the standardization. Density-dependent variation in standardized RPS was controlled by considering SSB as a covariate, which was partitioned into discrete bins comprising 0–10, 10–20, 20–30, 30–40, 40–60, 60–80, and 80–100% of recorded SSB maxima, SSB_{max}. After controlling for the density-dependent variation, we quantified the amount of density-independent year-to-year variation about the standardized RPS. This variation was considered to primarily reflect environmentally driven variability in recruitment: an emerging pattern arising jointly from the effects of biotic and abiotic environmental drivers, such as predation, food availability, temperature, etc. Hereafter, we denote this joint amount of density-independent recruitment variability as "environmental recruitment variability". s.d. of the environmental recruitment variability were estimated for each stock separately as well as averaged across all stocks. The s.d. estimate obtained across all stocks was considered a proxy for the average amount of environmental recruitment variability in Atlantic cod. Additionally, the stock-specific s.d. estimates representative of the 25 and 75% quantiles for the magnitude of s.d. among stocks were considered indicative of low and high environmental recruitment variability, respectively. In our analyses, both the density-dependence of standardized RPS ratios and environmental variation about them (as reflected by the s.d. estimates) were implemented in a proportional manner, such that the analyses were not affected by the numeric values subjected to the standardizing method but only by the proportional magnitude of s.d. in relation to standardized RPS and the proportional changes in standardized RPS with respect to SSB.

To investigate how environmental recruitment variability affects the fishing and recovery of a cod stock, we simulated cod population dynamics, using an individual-based model. Given that the model and its parameterization are described in detail elsewhere (Kuparinen *et al.*, 2012, in press; Kuparinen and Hutchings, 2012), we provide only a brief description of the main model features relevant to the present work.

The core idea of the model is to describe life histories of individual fish, based on their von Bertalanffy (VB) growth trajectories $L(t) = L_\infty - (L_\infty - L_0)e^{-kt}$, where t is the age of a fish, $L(t)$ the length of a fish at age t, L_∞ the asymptotic body length, L_0 the average length at $t = 0$, and k the growth parameter that describes the rate at which an individual reaches its L_∞ (von Bertalanffy, 1938). Ranges and the relationship between L_∞ and k were estimated based on 258 empirically observed cod growth trajectories for the population inhabiting Ogac Lake in the Canadian Arctic (Hardie and Hutchings, 2011). In terms of VB parameters and length at maturity, this population is similar to cod populations at northern latitudes (e.g. Northeast Arctic cod, northern cod). The key advantage of the chosen population was that it reflects natural variability in life histories in a non-fished population at its equilibrium, rather than populations affected by fishing (see Kuparinen *et al.*, 2012, for further detail).

In previous studies, the model has been used to describe the evolution of fish life histories (e.g. Kuparinen *et al.*, 2012). However, our preliminary analysis indicated that environmental recruitment variability had no effect on cod life-history evolution either in the absence or in the presence of fishing. As a consequence, we focus here on the ecological effects of environmental recruitment variability in the absence of life-history evolution. To this end, VB growth curves of fish were drawn randomly in our simulations from a

pool of individuals that had been recorded from the simulations during a 30-year period in a non-fished, fully adapted population. Thus, the pool reflected natural variability in cod life histories and the distribution of life histories did not change during the course of the simulations.

Being an individual-based model, the model tracks individuals in a population through time and records the state of the population at each time-step. Demographic processes are modelled at the level of the individual, and demographic stochasticity is described by drawing random numbers from appropriate distributions. At each time-step, the model simulates whether an individual survives or not: the instantaneous rate of natural mortality, M, is assumed to be 0.12 for immature individuals and 0.22 for mature individuals. These mortality estimates were obtained by calibrating the model to best predict the empirically observed lengths-at-age and, thus, to mimic environmental conditions experienced by this unfished population.

Although individuals that survive grow along their VB growth trajectories, their annual growth increment negatively depends on population density, such that each length increment corresponds to an increase in t given by $e^{15-17.6c}(1 + e^{15-17.6c})^{-1}$, where c is the ratio of population biomass to carrying capacity (Kuparinen *et al.*, 2012). Individuals whose body length exceeds 66% of L_∞ are considered sexually mature (Jensen, 1997). Mating occurs randomly and juvenile production is modelled to depend on female body size; the number of eggs produced is given by $(0.48 \times ((\text{female weight} + 0.37)/1.45) + 0.12) \times 10^6$ (Hutchings, 2005), where weight $= 3.52 \times 10^{-6} \times \text{length}^{3.19}$ (Kuparinen *et al.*, 2012). Survival from the egg stage to the 3-year-old recruit stage was estimated to be 1.13×10^{-6} (Hutchings, 2005). To characterize density-dependent effects on recruitment, juvenile production (as described above) was scaled up or down in proportion to the density-dependence of standardized RPS ratio estimates for cod, derived from Keith and Hutchings (2012; assuming compensatory population dynamics). These scaling factors and associated % of SSB$_{max}$ bins were: 1.30 (0–10%); 0.979 (10–20%); 0.807 (20–30%); 0.702 (30–40%); 0.647 (40–60%); 0.544 (60–80%); and 0.450 (80–100%). Here, SSB was compared directly with K (approximated to a first degree by SSB$_{max}$); juvenile production at 30–40% of K was considered the baseline [this is the approximate level of SSB$_{max}$ at which the previously mentioned relationship between body size and juvenile production was estimated by Hutchings (2005) for Newfoundland's northern cod]. For example, at SSB levels corresponding to 20–30% of K, body size–juvenile production relation was increased by 15% (using the scaling factor $0.807/0.702 = 1.150$; see Kuparinen *et al.*, in press, for further detail).

Environmental recruitment variability was embedded into the same scaling by drawing a random number each year from a normal distribution having a mean of zero and an s.d. matching one of the environmental recruitment variability scenarios: low variability, average variability, high variability (Table 1). These were further contrasted with simulations that excluded environmental recruitment variability. The drawn random number was then added to the SSB-specific standardized RPS ratios given above, such that recruitment was either increased or decreased owing to the year effect. For example, if the random number describing annual recruitment success was 0.2, then the juvenile production at 20–30% of K was increased by 43.4% from the body size–juvenile production relation given above $[(0.807 + 0.2)/0.702 = 1.434]$. The same annual random number was applied across all individuals that reproduced in a given year.

Investigation of the stock-specific time-series of the standardized RPS rations suggested that 8 of 18 stocks exhibited autocorrelation at a lag of 1 year ($p < 0.05$ in Pearson's tests) with correlation coefficients being ~ 0.4. To address the consequences of such a level of autocorrelation among years, we repeated the above simulation design with a scenario of autocorrelated recruitment variability. To this end, we simulated year-to-year environmental recruitment variability through an autoregressive process with a lag of one time-step (year) and 0.4 correlation between the subsequent time-steps (generic formulation: $X[t] = 0.4 \times X[t - 1] + \varepsilon$). The random variation term (ε) was drawn similarly as above, from a normal distribution having a mean of zero and an s.d. matching one of the considered environmental recruitment variability scenarios.

To explore how recruitment variability affects population resilience to fishing and its ability to recover from a low abundance, we simulated cod population dynamics during a period of fishing followed thereafter by a period of recovery. Fishing pressure was set to $F = 0.2$ and size-specific fishing selectivity followed a logistic curve estimated for bottom-trawled cod (Kuparinen and Hutchings, 2012). Populations were first simulated in equilibrium dynamics (no fishing) for 50 years, followed by a period of fishing that ended once abundance had declined below 15% of K, after which fishing mortality was zero and the population was allowed to recover. The choice of the 15% threshold was done to facilitate investigation of the role of recruitment variability in isolation from density-dependent processes at low abundance, such as the Allee effects or compensation (Kuparinen *et al.*, in press). The total number of simulated time-steps (years) for each run was 300. The simulation design was repeated with the four environmental recruitment variability scenarios (no/low/mean/high variability) under the presence/absence of autocorrelation, each simulation scenario with 50 replicated runs. All the simulations and analyses were conducted in R 2.15.0 (R Development Core Team, 2012).

Results

The s.d. of year-to-year environmental (i.e. density-independent) variation in standardized RPS averaged 0.165 across all analysed stocks. However, environmental recruitment variability also differed considerably among stocks, such that the 25 and 75% quantiles of stock-specific values varied threefold, being ~ 0.094 and 0.278, respectively (Table 1). We denoted these as low and high environmental recruitment variability scenarios, respectively.

When implemented to the simulation model, the average environmental recruitment variability increased fluctuations in population characteristics, as reflected by increased fluctuations in population abundance, life-history traits (such as age at maturity), and per capita population growth rate, r (Figure 1). Notably, owing to density-dependent mechanisms that limited population growth, fluctuations about population abundance were not symmetric: the highest observed abundances were no more than 2–3% greater than the equilibrium abundance (96–97%) of K, whereas the lowest abundances could be as low as 85% of K. Incorporation of environmental recruitment variability to the simulation model (through scaling of juvenile production) appeared to mimic the empirically observed environmental recruitment variability very well: at equilibrium, the coefficient of variation (CV) for the RPS ratio in the simulated populations ranged between 0.304 and 0.314 (across ten replicated simulation runs), whereas the CV for standardized RPS
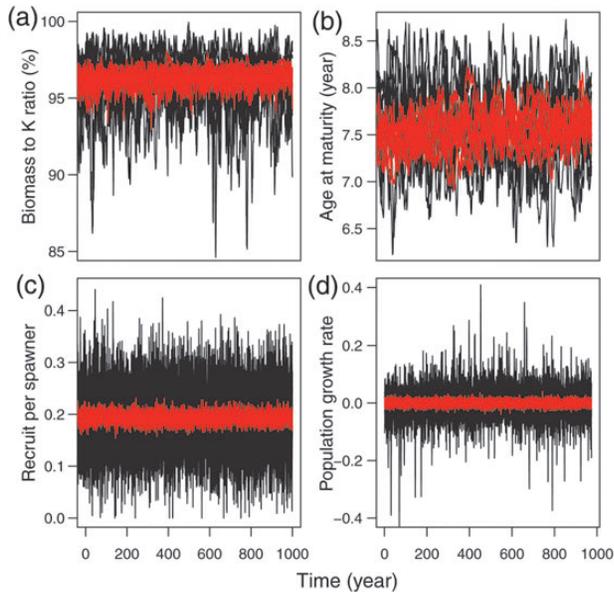
Figure 1. Dynamics of a non-fished population under the scenarios of average (black) and absent (red) environmental recruitment variability: (a) biomass to carrying capacity (K) ratio, (b) mean age at maturity, (c) RPS ratio (recruitment at the age of 3 years), (d) per capita population growth rate. Individual lines represent replicated simulation runs, ten runs for both the environmental recruitment variability scenarios.

derived from the empirical analyses was 0.367 for abundances corresponding to 80–100% of SSB_{max}.

Under simulated fishing mortality, increased recruitment variability affected population resilience in two ways. First, the greater the recruitment variability, the shorter the time required for the population to decline below 15% of K (Figure 2a–d), as reflected by differences between median fishing period lengths among the recruitment variability scenarios, particularly between the scenarios with and without recruitment variability (no variability: 66.0 years, low: 61.5 years, average: 55.5 years, high: 51.5 years; Figure 2e). In the absence of recruitment variability, the fishing period before abundance decreasing to 15% of K was ~28% longer than that associated with high recruitment variability. Second, increased recruitment variability decreased variability about the duration of the fishing period, as shown by the reducing heights of the boxplots in Figure 2e.

An opposing pattern was evident in the number of years required for the population to rebuild its biomass to 50% of K after the end of the fishing period. Although median recovery times did not differ between the recruitment variability scenarios (12 years for each scenario), uncertainty associated with the duration of the recovery period increased with increasing recruitment variability (Figure 2f).

Inclusion of the autocorrelation to the recruitment variability strengthened substantially the patterns seen in the simulations without the autocorrelation (Figure 3a–d). Again, fishing period length becomes shorter (medians, with no variability: 63.0 years, low: 61.5 years, average: 50.0 years, high: 49.5 years; Figure 3e) and less variable along with increasing recruitment variability (Figure 3e). In contrast, uncertainty about the recovery times increased along with increasing recruitment variability (Figure 3f), yet median recovery times did not substantially differ between the scenarios (12–13 years).

Discussion

The dynamics of Atlantic cod populations during fishing, followed by a period of biomass recovery simulated under differing levels of environmental recruitment variability and autocorrelation within it, suggest that rather than affecting the duration of fishing and recovery periods directly, environmental recruitment variability manifests itself at the level of uncertainty. The greater the environmental recruitment variability, the more certain it is that a population will be unable to sustain a specific level of fishing mortality for a long period (Figure 2e) and the less certain the recovery period following a cessation of fishing (Figure 2f). This pattern was further strengthened by incorporating autocorrelated environmental recruitment variability among years (Figure 3e and f).

Increased environmental recruitment variability decreases resilience to fishing and increases uncertainty of recovery. This is at odds with the perception that increased variability confers rapid ability to recover from collapse (e.g. Musick, 1999; Powles *et al.*, 2000), an assumption grounded in the notion that high recruitment variability is associated with the production of unusually strong cohorts that will enhance recovery. One logical difficulty in this perception, of course, is that high recruitment variability also translates into unusually weak year classes. Especially if such years come in sequences owing to autocorrelation of environmental variation, they can retard population biomass development and reduce population resilience to fishing.

We also find that increased environmental recruitment variability leads to increased uncertainty in recovery, although the average recovery period is unaffected. This result draws attention to the general importance in fisheries science of exploring variability in addition to averages: risks associated with overfishing, such as population collapses or unexpectedly slow recovery, are typically extreme events rather than properties of average population behaviour (Minto *et al.*, 2008). The role of stochasticity in population dynamics can become pronounced, especially at low levels of abundance, such that outcomes can be inherently difficult to predict (Lande, 1993, 1998).

Models are necessarily simplifications of the true complexity of natural populations. In the present study, the model incorporated simplifying assumptions that should be accounted for when interpreting the results. The applied modelling approach is suited for a relative comparison of simulation scenarios and exploration of general patterns, such as the decrease/increase in uncertainty owing to environmental variability in recruitment, but the model is not designed to produce numeric projections of any particular cod stock. This is because the model was calibrated to reflect the generic species-level properties of an unfished population; the model lacks stock-specific features such as a consideration of predator–prey interactions and demographic differences among the stocks. Properties of the model formulation and parameters are discussed elsewhere (Kuparinen *et al.*, 2012, in press; Kuparinen and Hutchings, 2012), so in the following we focus on the implementation of environmental recruitment variability and its limitations.

We assumed that the magnitude of environmental recruitment variability was independent of SSB. This decision was supported by the observation that empirical s.d. estimates were very similar for abundances up to 60% of SSB_{max}, but at abundance levels of 60–100% of SSB_{max} the s.d. were ~20% smaller (Bartlett's test with $p = 0.02$). However, abundances higher than 60% of SSB_{max} were not relevant for the present simulation design (as we focused
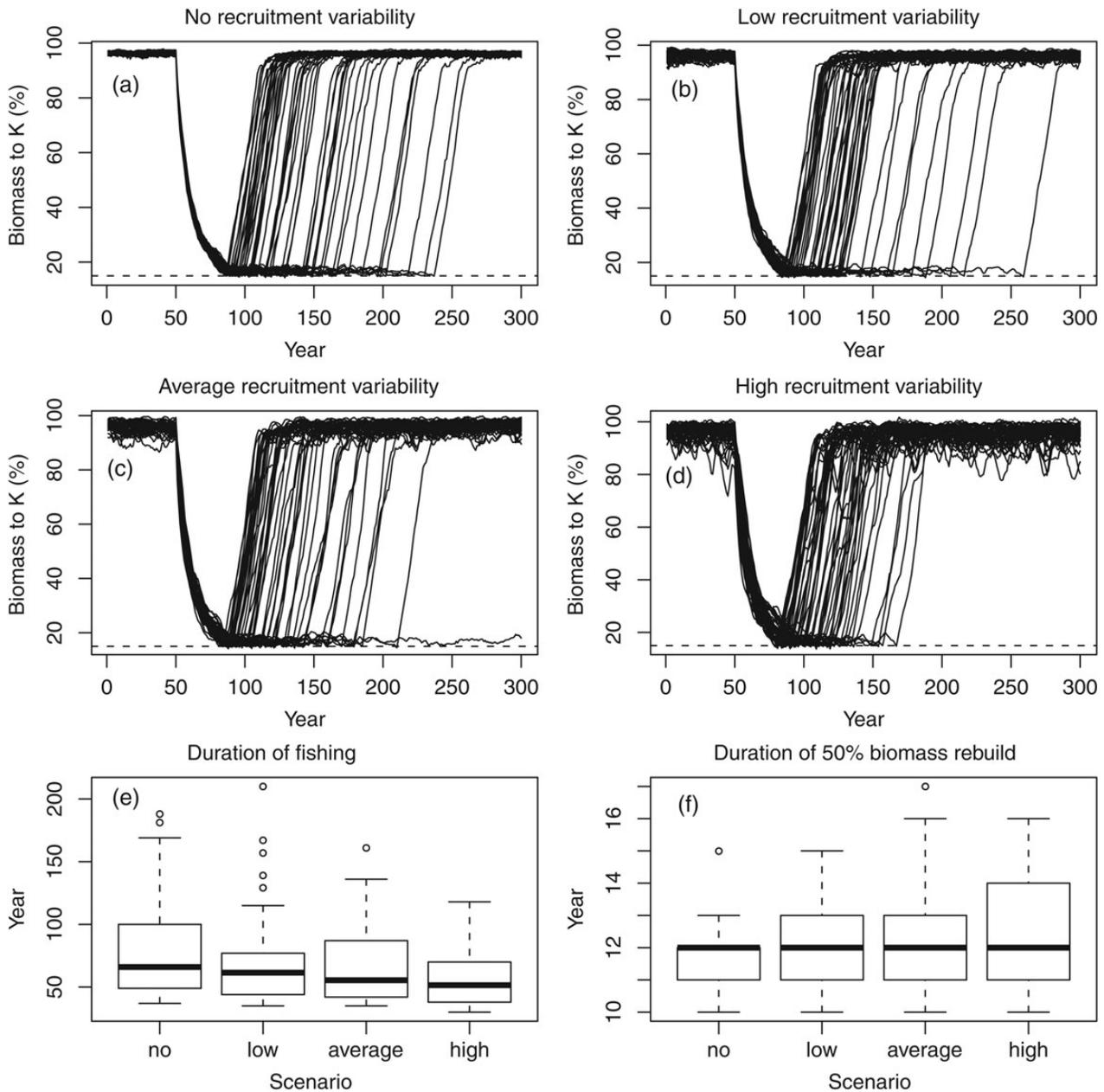
Figure 2. Changes in population biomass during fishing and recovery under four scenarios of non-autocorrelated environmental recruitment variability: (a) no; (b) low; (c) average; and (d) high. Fishing is initiated at year 50 and continued until the population had declined below 15% of carrying capacity (K). After the end of fishing, the population is allowed to rebuild and simulations are continued until year 300. Solid lines show replicated simulation runs, 50 for each environmental recruitment variability scenario. Durations of the fishing period and the biomass recovery period (biomass level 50% of K) are summarized across the replicates in (e) and (f), respectively. Boxes span the interquartile range, and whiskers encompass values less than 1.5 box lengths away from the box. Outliers are marked with open circles. In the presence of an average level of environmental recruitment variability, one replicate did not decline below 15% of K within the simulation period and was omitted from the boxplots.

on population dynamics under fishing and early recovery) and, thus, environmental recruitment variability was simplified to be uniform across abundances. Similarly, we explored non-autocorrelated as well as autocorrelated (though stationary) environmental recruitment variability and found patterns consistent across these two scenarios. However, in reality, recruitment is further affected by productivity regimes that can arise from temporal variation in factors such as temperature and food availability (Brander and Mohn, 2004; Olsen *et al.*,

2011). Such regimes are highly population and ecosystem-specific and it is not straightforward to detect those, such that they fall beyond the generic, empirically defendable approach of the present study. Nonetheless, the impacts of such regimes constitute an important avenue of future research, to gain a more complete picture of environmental impacts on recruitment dynamics.

The estimates of year-to-year recruitment variability applied here were empirically based and, thus, provide a realistic basis for
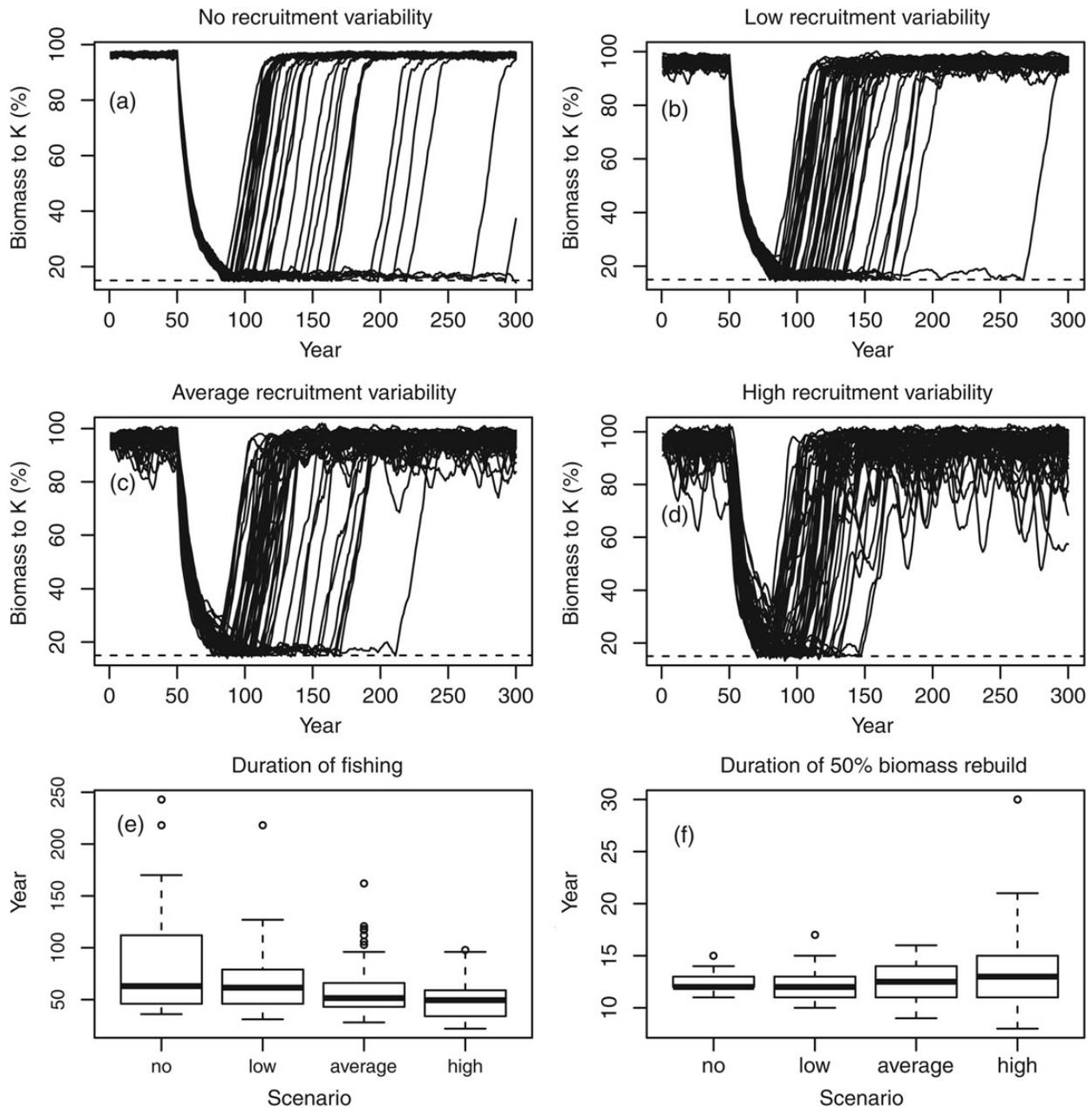
Figure 3. Population biomass development during fishing and recovery in the presence of autocorrelated environmental recruitment variability, under the four scenarios of (a) no; (b) low; (c) average; and (d) high variability. Autocorrelation occurs at the lag of one time-step (year) and the correlation among subsequent steps is set to 0.4. Otherwise, simulation design and figure elements are the same as in Figure 2.

the investigated simulation scenarios. Nonetheless, it is notable that even the high recruitment variability scenario is only representative of the 75% quantile rather than extreme conditions; in reality, we would expect 25% of cod stocks to exhibit environmental recruitment variability of this magnitude or higher. Therefore, the chosen low and high environmental recruitment variability scenarios were generally conservative; individual stocks can show much higher levels of recruitment variability than those examined here. Among the investigated stocks, unusually high amount of recruitment variability was detected in North Sea cod (Table 1). This might relate to the fact that the stock was associated with unusually high RPS values in the 1960s and 1970s, which might have

contributed to large magnitude of variation about the standardized RPS estimates.

Regarding the generality of our findings to other species, we note that cod is highly fecund, which positively correlates with the magnitude of recruitment variability (Rickman *et al.*, 2000). On the other hand, the high longevity of the species is linked to lower levels of recruitment variability (Longhurst, 2002), a predicted consequence of the species' bet-hedging life-history strategy (Hutchings and Rangeley, 2011). In addition, although the magnitude of environmental recruitment variability is likely to be highly species- and population-specific and to depend on prevailing productivity regimes (Vert-pre *et al.*, 2013), there are few reasons to assume

that the qualitative way in which environmental recruitment variability translates into uncertainty about resilience and recovery would not apply to species other than cod.

The roles that environmental recruitment variability play in fish stock resilience to fishing and recovery ability have several implications for fisheries management and conservation planning. Environmental uncertainty has been projected to increase with global warming and climate change (IPCC, 2013), which is likely to translate into variability in cod recruitment and, as suggested by the present work, lead to diminished resilience to fishing and increased uncertainty of recovery. Any such changes are forecasted to be particularly pronounced at the southern edge of the species range, where stocks (e.g. North Sea cod) are considered to be inhabiting suboptimal conditions and are sensitive to temperature change (Planque and Fredou, 1999; Beaugrand *et al.*, 2003; Pörtner and Peck, 2010). Environmental conditions experienced by the southern stocks are likely to become increasingly unfavourable leading to the prediction that conditions promoting good year class production will become increasingly infrequent (O'Brien *et al.*, 2000).

Apart from the direct effects of increasing environmental variation, another indirect aspect affecting variability in cod recruitment is the reduction in the age and size of adult cod, as predicted by Hutchings and Myers (1993) (see also Olsen *et al.*, 2004; Swain *et al.*, 2007; Swain and Mohn, 2012). Earlier maturation leads to reduced longevity, a pattern linked to increased recruitment variability (Longhurst, 2002). Additionally, lack of old large individuals decreases the seasonal duration of spawning, predicted to lead to higher variability in egg and larval survival among years (Hutchings and Myers, 1993; Minto *et al.*, 2008), a pattern that can be further strengthened by increasing temporal environmental variability. Although currently observed changes in population age and size structure are primarily hypothesized to be the result of predation (Swain and Mohn, 2012) and fishing (Kuparinen and Merilä, 2007), similar trends are also projected under increasing temperatures (Cheung *et al.*, 2013).

The present study draws attention to the impacts of environmental recruitment variability on resilience to fishing and recovery following depletion. We show that increasing environmental fluctuations in reproductive success reduce resilience to fishing and increase uncertainty about recovery, a finding in accordance with observations from many fisheries, where collapses have often occurred surprisingly rapidly and for which the recovery rate has been slow (Hutchings and Reynolds, 2004; Neubauer *et al.*, 2013). The omission of environmental variation from stock productivity projections can lead to unduly positive perspectives about the sustainability of fishing strategies.

Acknowledgements

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Handling editor: Valerio Bartolino