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Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations

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Hjort (1914. Fluctuations in the great fisheries of northern Europe. Rapport et Procès-Verbaux des Réunions du Conseil Permanent International pour l'exploration de la Mer, XX: 1–228) identified two important aspects of the early life of fish as being important determinants of fluctuations in year-class strength: changes in nutrition and transport. He dismissed a third possible influence, changes in the abundance of the reproductive stock. Here, we describe how a recently discovered characteristic behaviour of age-structured populations termed *cohort resonance*, which does involve changes in adult abundance, can have a substantial effect on fluctuations in fished populations. Cohort resonance involves selectively greater sensitivity of age-structured populations to generational frequencies and to very low frequencies in the environmental signal influencing a population. This frequency-dependent selectivity has been shown to increase with fishing, as do the total amounts of variability in recruitment, egg production, and catch. Cohort resonance differs from other recent model mechanisms proposed to explain the observed increase in variability with fishing in that it does not require over-compensatory density-dependence. It stems from the compensatory ascending limb of the egg–recruit relationship, and is a characteristic of a stable population driven by a random environment. We demonstrate the differences in frequency selectivity and increases in variability with fishing among three different Pacific coast species with different longevity: coho salmon (*Oncorhynchus kisutch*; ∼3 years), Pacific hake (*Merluccius productus*; ∼25 years), and Pacific Ocean perch (*Sebastes alutus*; ∼90 years). The shortest lived, coho salmon is the most sensitive to environmental variability, but variability in egg production and catch both increase more rapidly with fishing in the longer-lived species. Understanding cohort resonance will aid in anticipation of predicted potential changes in the frequency content of the physical environment with changing climate (e.g. more frequent El Niños), and it provides a warning regarding the possible confounding of increasing sensitivity to slow change due to fishing with actual slow change of population parameters due to climate change. Our understanding of the role of cohort resonance in population variability will be enhanced by further identification of empirical examples. We describe some of the challenges in this effort.

Keywords: age structure, environmental variability, fishing, frequency response, stochastic models.

Introduction

The problems facing Hjort and his fishery science colleagues in 1914, even in the early years of fisheries science, involved the same topics as those facing fishery scientists in 2014. We still seek to understand the causes of fluctuations in fished populations, but with added concern for anticipated effects of a changing climate due to increasing CO_2 concentrations in the atmosphere. Hjort (1914) presciently defined this field as we know it by focusing research on the early lives of fish, and by proposing two reasons for dramatic variability in their survival: nutrition and transport. These have had a great effect on fisheries research since then, leading to two of the dominant mechanisms proposed to underlie interannual variability in recruitment (Houde, 2008). The former has become well known as the "match–mismatch" mechanism (Cushing, 1990), and the latter underlies the "stable retention" mechanism (Iles and Sinclair, 1982).

Here, we describe a mechanism related to a conclusion by Hjort (1914) that is less well remembered. In the paragraph preceding his description of the nutrition and transport effects, he considered the role of variability in egg production by adults as an effect on variability in recruitment. He concluded that, "it is difficult to avoid the conclusion that the actual quantity of eggs spawned is not a factor in itself sufficient to determine the numerical value of a year class." Currently, we, of course, include an underlying effect of stock on recruitment, and take careful note of maternal effects, but we seldom focus on their role in interannual variability. However, here we describe the developing understanding of cohort resonance (Bjørnstad *et al.*, 2004; Worden *et al.*, 2010), a mechanism that has a substantial influence on the annual fluctuations in the number of recruits in a year class, and does involve variability in annual egg production. Our results indicate why it is not surprising that Hjort (1914) concluded that the amount of egg production each year had no influence on the dynamics of interannual variability in cohort abundance. This mechanism also involves another aspect of population dynamics on which Hjort recommended more research, age structure, though his interest lay in the prediction of yield from older ages based on the abundance of the young, rather than in the role of age structure in population dynamics.

Cohort resonance was described as an integrated, whole mechanism by Bjørnstad *et al.* (2004), though various aspects had been alluded to earlier. They showed that the peaks at low frequencies (i.e. decadal scale variability) and frequencies near 0.4 cycles per year seen in the calculated spectrum of the catches of cod in the Skagerrak were not dominant frequencies of the variable environment, rather they were peaks in the sensitivity of the age-structured cod population to environmental variability. This meant that populations could be viewed as filters that are more sensitive to some frequencies of environmental variability than others (Greenman and Benton, 2005). In particular, models of age-structured populations exhibit peaks in sensitivity to low frequencies and generational frequencies when driven with white noise (i.e. equal variance at all frequencies). The term “sensitivity” in this context refers to the ratio of the variance at a certain frequency in an output, such as abundance or recruitment, to the variance at that same frequency, in the input being varied by the environment, such as survival at age 1. This sensitivity is a function of frequency [or equivalently, a function of period $= 1/(\text{frequency})$]. They drew attention to the consequences of sensitivity to low frequencies because that would emphasize slowly varying (decadal) trends, which would confound efforts to detect actual slowly developing changes to life history rates due to climate change (i.e. the *cloaking effect* of cohort resonance). To be clear, we use the term “cohort resonance” here to refer only to sensitivity to: low frequencies and frequencies near $1/(\text{generation time})$, i.e. our definition does not include variability at frequencies near $1/(2 \times \text{generation time})$, which were also discussed in Bjørnstad *et al.* (2004). Such cycles of period 2 generations have been discussed extensively elsewhere (see Botsford and Wickham 1978; Botsford 1997, and references therein).

The cohort resonance effect was elevated in importance when it was found that both the selective sensitivity to low frequencies and generational frequencies identified by Bjørnstad *et al.* (2004) and the overall sensitivity to environmental variability increased with declining survival. Such a decline in survival could be caused, for example, by fishing or a long-term decline in environmental conditions influencing larval or juvenile survival (Worden *et al.*, 2010). This finding suggested that a better understanding of cohort resonance could address some of the current questions regarding the synergistic effects of fishing and climate change (e.g. Perry *et al.*, 2010; Planque *et al.*, 2010; Hollowed *et al.*, 2011). It could also help to explain the growing empirical evidence of increased population variability with fishing, as seen in time-series of abundance, egg production (Hsieh *et al.*, 2006), and recruitment (Brander, 2005; Ottersen *et al.*, 2006). Cohort resonance could possibly shed light on the various roles of proposed causal factors such as the selective greater reduction in older ages due to fishing, i.e. age truncation (Brander, 2005; Ottersen *et al.*, 2006; Anderson *et al.*, 2008; Planque *et al.*, 2010; Shelton and Mangel, 2011a), maternal effects (Brander, 2005; Ottersen *et al.*, 2006; Planque *et al.*, 2010), and selection for changes in life history by fishing (Law, 2000; Planque *et al.*, 2010).

The prevailing view of the cause of the increase in variability with fishing is that it arises from unstable behaviour of fish populations (Shelton and Mangel, 2011b; Sugihara *et al.*, 2011). Anderson *et al.* (2008) sought to explain the observation that time-series of annual egg production from a number of fish species off the west coast of the United States showed greater variability in fished species than unfished species (Hsieh *et al.*, 2006). They introduced two effects proposed qualitatively to arise from the truncation of an age structure by size-selective fishing, into their non-age-structured model: (i) better tracking of the environmental signal by the population, and (ii) a change in the intrinsic rate of population increase, *r*. From analysis based on fitting general functional forms of the time-series (S-map analysis), and a discrete time model of the dynamics of total abundance having the familiar Ricker (1954) form, they concluded there was limited evidence for the increased tracking as a cause, and strong evidence for changing dynamics due to increased rate of increase, *r*.

In a later study, Shelton and Mangel (2011a) addressed the question of how increased fishing increases variability using a discrete time model of the dynamics of lumped total biomass, with a Ricker (1954) stock–recruit relationship representing the recruits added each year. They noted that literature-based values of the parameters of their model for 45 fish species indicated that models of the species dynamics were typically in regions of parameter space where the populations would not be stable. They showed that in these models: (i) fishing increased variability, (ii) populations were more sensitive to environmental variability in recruitment than in adult mortality, and (iii) temporal correlation in environmental variables played a vital role in determining population variability.

Here, we first describe what cohort resonance adds to the current view of the issues Hjort was addressing. We then note how cohort resonance provides an alternative to the prevailing explanation of the observed increases in variability with fishing. We characterize an important way in which cohort resonance will vary with species, the dependence on longevity. We do this by illustrating the effects of fishing on frequency selectivity and overall variability in three species from the California Current, with different longevity: Pacific ocean perch (*Sebastes alutus*; POP), Pacific hake (*Merluccius productus*; a.k.a. whiting), and coho salmon (*Oncorhynchus kisutch*).

Basic model and previous analyses

To represent the behaviour of these age-structured populations, we used a linear age-structured matrix model with a non-linear egg–recruit relationship. For the iteroparous species (POP and Pacific hake), the model has the form

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ s_1(t)x_1(t) \\ s_2x_2(t) \\ \vdots \\ s_{n-1}x_{n-1}(t) \end{pmatrix}, \qquad (1)$$

where $x_i(t)$ is the number of individuals in age class *i* at time *t*.

For the semelparous species (coho salmon), the model takes the form

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ (1-p_1)s_1(t)x_1(t) \\ (1-p_2)s_2x_2(t) \\ \vdots \\ (1-p_{n-1})s_{n-1}x_{n-1}(t) \end{pmatrix}, \qquad (2)$$

where the multiplicative $(1-p_i)$ terms account for the fact that spawning is an additional source of mortality in a semelparous species.

For both of these, $P(t)=\sum_{i=1}^{n} p_i f_i x_i(t)$ is the annual egg production resulting from the age-specific probability of spawning, p_i, and the age-specific fecundity rates, f_i. Recruitment is a Beverton and Holt (1957) function of egg production, multiplied by lognormal random noise,

$$R[P(t)] = \frac{\alpha P e^{-\xi t}}{1+\beta P} \qquad (3)$$

with random values of ξ chosen from a Gaussian distribution with the mean 0.0 and standard deviation σ_R. Survival is a function of instantaneous natural mortality, M_R (age 1) or M (constant over ages >1 year), and age-dependent fishing mortality, F_i', and is given by $s_i = \exp(-M - F_i')$. The methods used to calculate survivals and fecundities are shown in the Supplementary data along with all parameter values.

While we present the model of semelparous coho salmon explicitly in terms of the linked spawning and mortality, in the subsequent analyses presented here none of the differences between species' behaviour is due to the differences between their semelparous and iteroparous life histories. Thus, the responses of the coho salmon here would be the same as those of an iterparous species with the same pattern of the amount of spawning at age.

In previous analyses, we obtained equilibrium conditions for these models and analysed deterministic stability (Worden *et al.*, 2010). Population stability depends on the slope of the egg–recruit relationship at equilibrium. Because we are using a Beverton–Holt stock–recruitment model, whose slope is always positive, the population will always be stable about its equilibrium. It will not display the kind of unstable behaviour in the models currently proposed to be the cause of increasing variability with fishing (Shelton and Mangel, 2011b; Sugihara *et al.*, 2011). Stochastic analysis of this model, however, shows that this locally stable population model can be continuously perturbed away from equilibrium by environmental variability, and will display the sensitivity to specific frequencies of environmental variability characteristic of cohort resonance: low frequencies and generational frequencies (i.e. with period equal to the generation time; Worden *et al.*, 2010). This is an important distinction between cohort resonance and other population dynamic mechanisms underlying cyclic behaviour. Cycles with period 2 generations are caused by over-compensatory density-dependence (i.e. a negative slope in the stock–recruit relationship), and the cyclic state is unstable about the equilibrium. These are the inter-cohort cycles described in Bjørnstad *et al.* (2004), whereas cohort resonance cycles are the intra-cohort cycles.

Qualitative explanation of cohort resonance

The mechanistic basis for cohort resonance, and the way it is related to the studies of Hjort (1914) can be understood based on two graphical representations (Figures 1 and 2). Changes in the long-term equilibrium values of recruitment due to long-term changes such as increased mortality due to fishing are contained in the well-known condition for equilibrium of an age-structured population with density-dependent recruitment (Figure 1, Sissenwine and Shepherd, 1987; Botsford, 1997). This graphical version of the equilibrium condition states that the equilibrium value of recruitment will be at the intersection of the egg–recruit relationship and a straight line through the origin, with slope equal to the inverse of lifetime egg production (LEP, Figure 1). As fishing increases (or survival declines for other reasons), the equilibrium moves the unfished equilibrium [e.g. point (a)] to lower annual egg production and lower recruitment [e.g. point (b)], until the LEP has been reduced to the inverse of the slope at the origin of the egg–recruit relationship, at which point [point (c); and beyond], the equilibrium is zero. For our purposes here, note that as the equilibrium declines, the local slope of the egg–recruit relationship itself becomes steeper with the Beverton–Holt model.

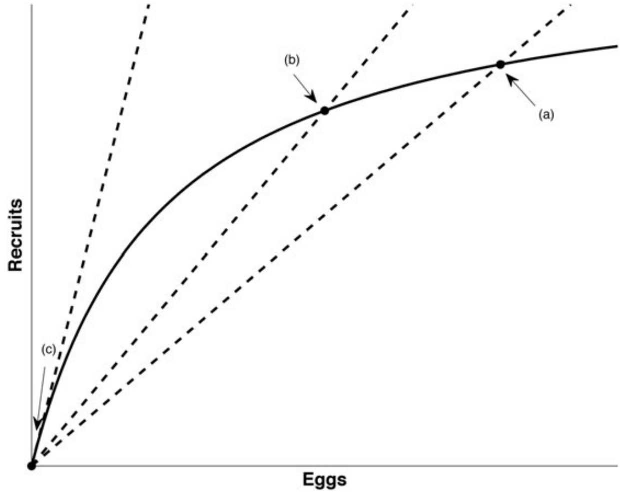

Figure 1. Graphical representation of the equilibrium condition for an age-structured population with density-dependent recruitment. The solid line is the annual number of recruits produced from the annual number of eggs produced. The dashed lines have slope equal to 1/LEP, where LEP is the lifetime egg production of females in the population. For increasing rates of fishing, the slope increases. For example, point (a) could represent the unfished equilibrium, and point (b) an equilibrium with fishing. When the population is fished at a rate that causes the slope to be greater than or equal to the slope of the egg–recruit relationship at the origin, the equilibrium recruitment will be zero [point (c)].

The dynamic behaviour underlying the greater sensitivity of cohort resonant populations to environmental signals on generational time-scales can be understood by considering the case in which the survivals at each age in Equations (1) and (2) are not time varying, and environmental variability is solely in recruitment [Equation (3)]. In that case, the variation in egg production $P(t)$ from its equilibrium value is the weighted sum of past variations in recruitment from the equilibrium recruitment, with the constant weighting factors being the amount of spawning per recruit at that age (i.e. survival to each age times the fecundity at that age; Worden *et al.*, 2010).

With that in mind, we can graphically portray the ways in which variability is transformed as it flows through the population for both the unfished (Figure 2a) and the fished (Figure 2b) case. The recruitment signal (the red signal in the lower left of Figure 2a and b) is a

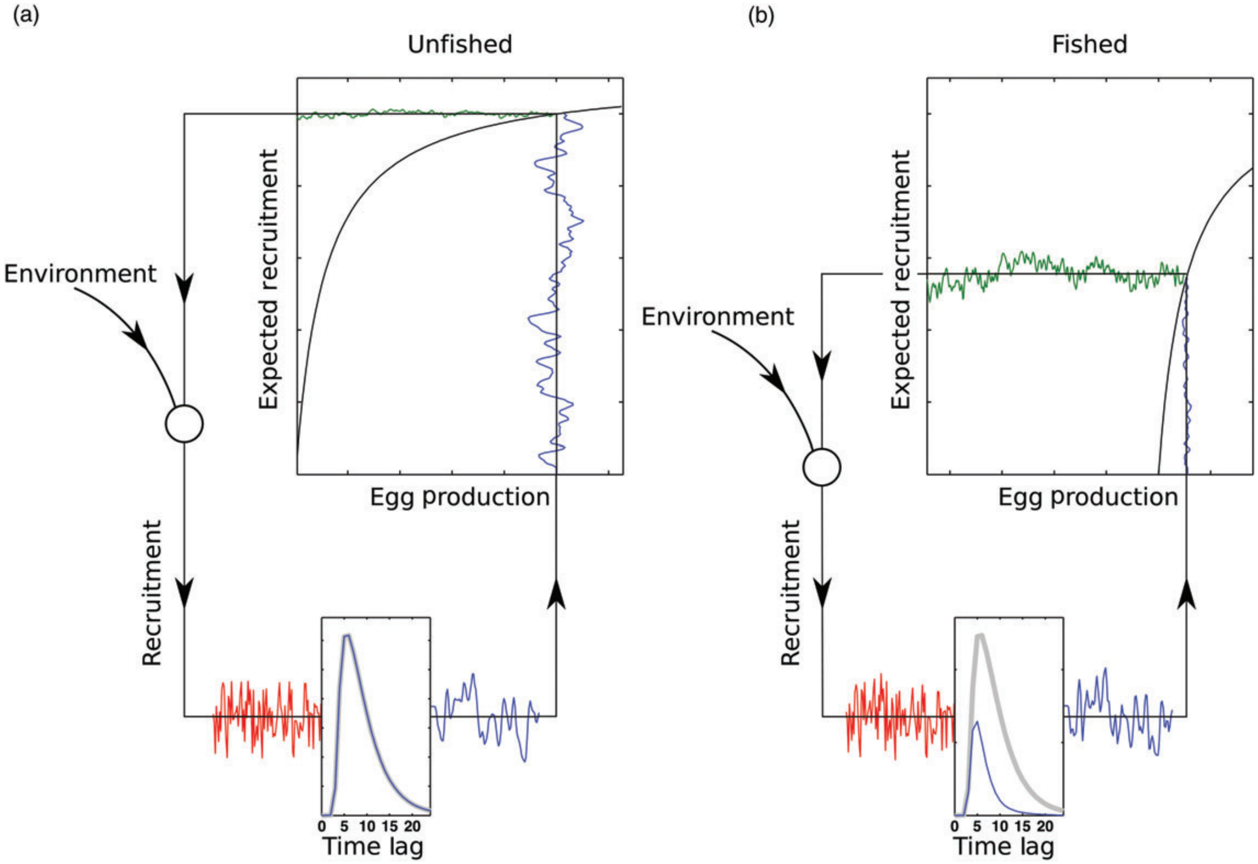

Figure 2. Schematic representation of the variability about equilibrium of signals involved in the cohort resonance mechanism for the unfished case (a) and the fished case (b). In the unfished case (a), the slope of the egg–recruit relationship is shallow, so the variability in expected recruitment can be less than that in egg production. The introduction of environmental variability into this signal produces the highly "noisy" recruitment (red signal) that would be observed empirically. Egg production (purple signal) is the weighted sum of past recruitments. The weighting function, i.e. the product of survival to age times fecundity at age, is shown in the box in the lower part of (a) and (b). The fished case (b) differs in two ways: (i) the slope of the egg–recruit relationship is steeper at the lower equilibrium (as explained by Figure 1), hence the signal is "amplified", and (ii) the distribution of reproduction over age is truncated, leading greater reinforcement of frequencies near the inverse of the peak reproductive age.

combination of the expected recruits from egg production (the green signals in Figure 2a and b) and the multiplicative noise from the environment [Equation (3)]. The egg production time-series (the purple signal in Figure 2) will be less variable than recruitment signal (red) because it will be a weighted sum of the noisy recruitment time-series. The weighting function (spawning at age) is shown in the lower boxes in Figure 2a and b. The effect of that variability in egg production (i.e. the purple signal in the upper part of Figure 2) on recruitment in each later year depends on the slope of the egg–recruit relationship at equilibrium (i.e. the amplification from the purple signal to the green signal will be greater with a steeper slope).

The sensitivity to generational frequencies in the cohort resonant effect arises when the environmental signal has a substantial periodic component with period T, where T is the generation time (contained in the weighting function in the lower boxes of Figure 2). For example, consider the example of a survival time-series that consisted of pulses of favourable recruitment conditions every T years. Signals with that periodicity would tend to be reinforced because the high recruitment from each pulse of high survival would be augmented by the high egg production from the previous pulse T years earlier (i.e. pulses in the green signals in Figure 2 would coincide with new pulses in the environment). One can see intuitively that this effect will be stronger under certain conditions. One condition is when the width of an individual's spawning-at-age distribution (i.e. the function in the box in the lower left) is narrow. This will concentrate the future effects of recruitment into a narrower range of ages, thus focusing the effect increasingly on a single age. The second is when the slope of the egg–recruit function at equilibrium is steep. This will amplify the magnitude of fluctuations (going from the blue to the green signal in the top part of Figure 2). Both the narrowness of the age span of reproduction and the steepness of the slope of the egg–recruit relationship at the origin become stronger as fishing increases; the former is due to age truncation, and the latter is due to the equilibrium moving down to points with steeper slope on the ascending limb of the egg–recruit function. Comparing these effects in the fished case (Figure 2b) with the unfished case (Figure 2a), the narrower spawning age distribution in Figure 2b focuses egg production in fewer ages, and a steeper slope at equilibrium causes variability in egg production (i.e. the purple signal in the top part of Figure 2b) to produce greater relative variability in recruitment (i.e. the green signal).

The other peak in the frequency-dependent sensitivity of cohort resonance, sensitivity to low frequencies, can be viewed as an effect arising from a low level of density-dependence. As fishing increases and the slope of the dashed line in Figure 1 becomes steeper, the population will increasingly resemble a Leslie Matrix (Caswell, 2001) with no density-dependence, i.e. Figure 1 would resemble two straight lines, one with the slope of 1/LEP, and the other with slope equal to the constant egg-to-recruit survival at low abundance. Such a matrix would not have a non-zero equilibrium. If it were subject to random environmental variability in recruitment, it would display the behaviour of a neutrally stable system with λ near 1.0, i.e. it would vary about a constant level on time-scales near the generation time for a while, then wander slowly to a different constant level and vary similarly about that level for a while, etc. Slight random changes in early survival could have a great effect on recruitment if they lasted long enough to produce something like the geometric growth characteristic of these matrices. If they lasted a shorter time, values of λ slightly greater than, and slightly less than 1.0 would tend to cancel. Thus, the population becomes sensitive to lower frequencies. Note that this sensitivity to low frequencies is a consequence of the population having little density-dependence, and λ being near 1.0, thus it is not directly related to the resonance phenomenon.

Expected cohort resonance from three fished species

We can obtain some sense of what to expect from cohort resonance by examining expected results from three fished species with different longevities. These expectations can then be compared with empirical population time-series over the last several decades. Here, we examine three species fished off the US west coast: coho salmon (*Oncorhynchus kisutch*; ∼3 years), Pacific hake (*M. productus*; ∼25 years), and POP (*S. alutus*; ∼90 years), where the value in parentheses is the approximate maximal age. We first outline the differences in spawning age structure and response to fishing, then show how these lead to differences in the frequency responses between species with different longevities. Because of the interest in how variability increases with fishing (Anderson *et al.*, 2008; Shelton and Mangel 2011a, b; Sugihara *et al.*, 2011), we then compare how variability in recruitment, egg production, and catch increase with fishing.

We compare these three species in terms of their manifestation of the cohort resonance mechanism, in a way that focuses on the effects of differences in age structure. We project the different behaviour of these three species using an age-structured model with different parameters for each species from recent stock assessments (see equations and parameter values in the Supplementary data). Because the cohort resonance mechanism of interest here (i.e. sensitivity to generational frequencies and low frequencies) depends only on the ascending, compensatory part of the stock–recruitment curve, we use a Beverton–Holt egg–recruit relationship (Beverton and Holt, 1957). Stock–recruitment relationships for some species may, of course, have a descending, over compensatory limb at high stock values. Small signal behaviour about equilibria on that declining part of the curve could lead to locally unstable populations with cycles of period 2 generations, and could also exhibit more complex, chaotic behaviour (Hassel *et al.*, 1976; Botsford, 1992). We do not address that possibility here because our purpose is to show that such unstable behaviour is not required for variability to increase with fishing. This contrasts with the explanations of the observed increase in variability with fishing by others (Shelton and Mangel, 2011b; Sugihara *et al.*, 2011). For the purposes of comparing the effects of the different age structures, we apply the same lognormal random variability in recruitment survival to all three species. The Beverton–Holt egg–recruit relationships are parameterized so that they all have the same asymptotic maximal value of recruitment, and the slope parameters are specified such that the equilibria of the three species will be at the same point when the species have the same value of the fraction of lifetime recruitment (FLEP). FLEP is the ratio of current LEP to unfished LEP, essentially the same as spawning potential ratio in other fishery publications (Goodyear, 1993; Mace and Sissenwine, 1993; O'Farrell and Botsford, 2005). Values of FLEP convey the same information as the values of LEP involved in the equilibrium condition depicted in Figure 1, but they are normalized by dividing by the value of LEP in the unfished condition. This is commonly done to put the persistence of populations of different species on a common, comparable basis, regardless of differences in fecundities, larval survivals, etc. Using FLEP, rather than LEP, also involves the presumption of some greater degree of generality in persistence mechanisms described by FLEP than by the actual values of LEP. Here, we chose the value of the slope at the origin [α in Equation (3)] of the Beverton–Holt function so that all three populations collapse at $\mathrm{FLEP_C} = 0.1$, a reasonable value both locally (Dorn, 2002) and globally (Myers *et al.*, 1999).

The cohort resonance effect is determined by the age distribution of reproduction, and the way that distribution changes with fishing (Figure 3a–c). The spawning age distributions of POP, Pacific hake, and coho salmon along the west coast of the United States are dramatically different, but all are truncated by increased fishing, which reduces lifetime reproduction and slightly diminishes the dominant age of spawning.

Lifetime reproduction decreases with increased fishing more rapidly in longer-lived species (Figure 3d) This means that for the Beverton–Holt egg–recruit relationship (Beverton and Holt, 1957), which does not involve over-compensation, fishing will reduce equilibrium recruitment sooner for longer-lived species (Figure 1). Here we compare behaviour of these three species at different values of FLEP, rather than different values of fishing mortality, *F*, to focus more directly on dynamic differences due to age structure, rather than confounding them with differences in equilibrium (which are static, long-term effects, also due to age structure as shown in Figure 3d). Each fishing level is identified by its Exploitation Index, EI ($\mathrm{EI} = (1 - \mathrm{FLEP})/(1 - \mathrm{FLEP_C})$), where $\mathrm{FLEP_C}$ is the value at which equilibrium recruitment collapses to zero, here assumed to be 0.1 for all three species (Sissenwine and Shepherd, 1987). Thus, EI is a convenient common measure of fishing level for the three species, ranging from no fishing ($\mathrm{EI} = 0$) to population collapse ($\mathrm{EI} = 1.0$).

Differences in spawning age structure lead to differences in the environmental frequencies to which different species are sensitive. This effect is demonstrated here with the dominant form of environmental variability found in marine fish, high variability in recruitment survival [Equation (3); Figure 4]. The forcing signal used here was chosen to have equal variance at all frequencies, i.e. it was white noise. Because of that, the quantity plotted in Figure 4 is a measure of how sensitive the populations are to each of the different frequencies of variability in the environment. Our measure of sensitivity here is the ratio of the variance of the particular variable (recruitment, egg production, catch) about its equilibrium value to the variance of the variable that is being forced by the environment (here recruitment survival), about its mean. This variable is the same as what is referred to elsewhere as the power spectrum. Since these are not electrical signals, they do not represent power, so we refer to this variable as frequency-dependent sensitivity of variance.

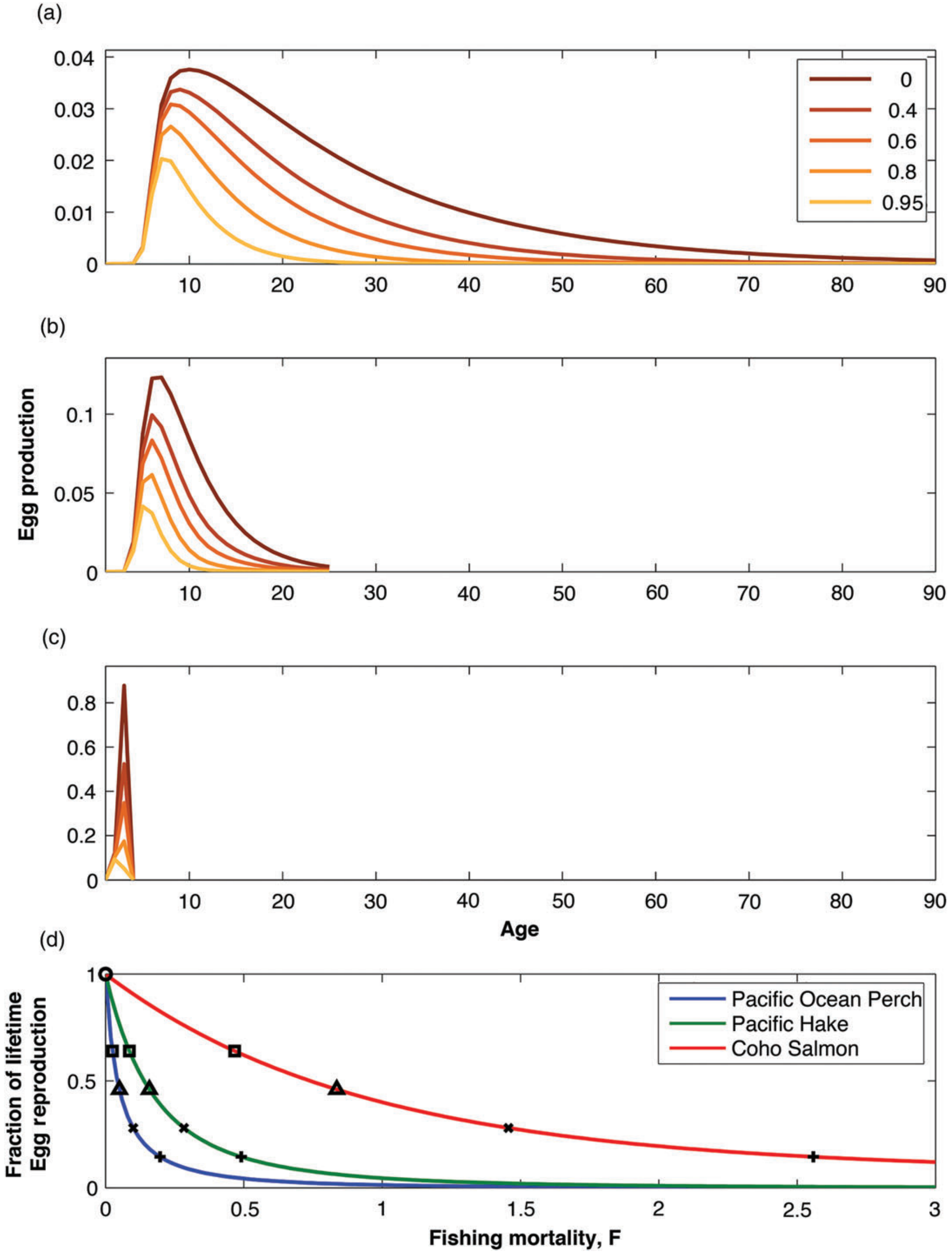

Figure 3. The probability distributions of egg production over age with no fishing for (a) POP, (b) Pacific Hake, and (c) coho salmon along the west coast of the United States, and the diminished distributions at four different levels of fishing. Each is identified by their Exploitation Index, EI ($\mathrm{EI} = (1 - \mathrm{FLEP})/(1 - \mathrm{FLEP}_C)$), where FLEP is the fraction of unfished lifetime reproduction (thus lower $\mathrm{EI} =$ lower fishing), and FLEP_C is the value at which equilibrium recruitment collapses to zero, here assumed to be 0.1 for all three species for the ease of comparison of the effects of age structure. (d) The different values of fishing mortality rate and FLEP that produces the five values of EI for each species in (a)–(c) with the circle indicating $\mathrm{EI} = 0$, the squares indicating $\mathrm{EI} = 0.4$, the triangles indicating $\mathrm{EI} = 0.6$, the *x*'s indicating $\mathrm{EI} = 0.8$, and the $+$'s indicating $\mathrm{EI} = 0.95$. The value of EI declines from 1.0 to 0.0 as fishing increases from no fishing to the point at which the population would collapse (i.e. $\mathrm{FLEP} = 0.1$).

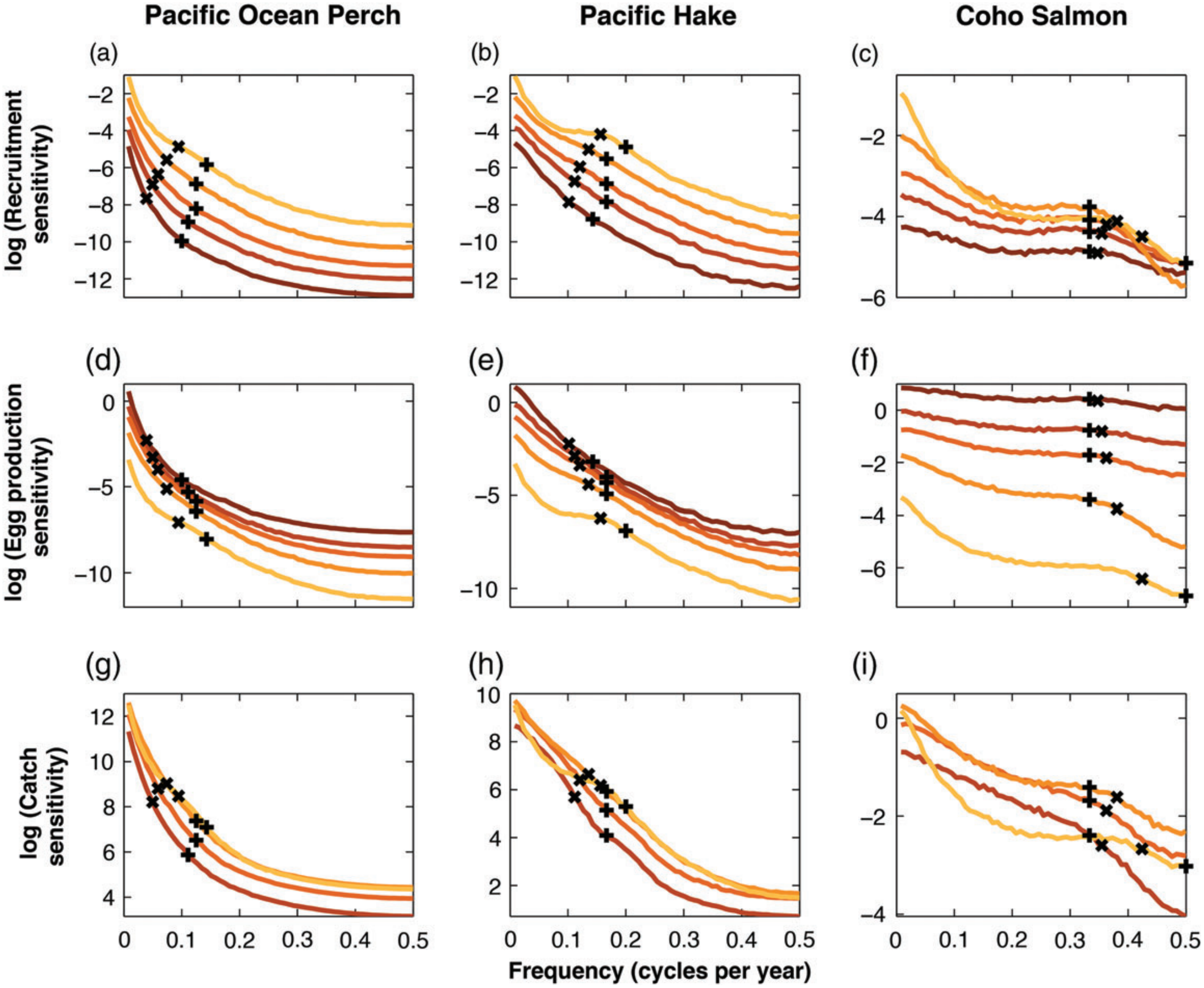

Figure 4. Sensitivities of species and variables to the frequencies of variability in the environmental variable affecting survival. The sensitivity is the ratio of the variance in the variable about its equilibrium value to the variance in the variable that is being forced by the environment (here recruitment survival), about its mean. The sensitivity of recruitment expected from the egg–recruit relationship (a–c, i.e. the green line in Figure 2), egg production (d–f, i.e. the purple signal in Figure 2), and catch (g–i) in POP (a, d, and g), Pacific hake (b, e, and h), and coho salmon (c, f, and i) to frequencies of environmental variability at different levels of fishing are indicated the same as in Figure 3. The *x*'s indicate the inverses of the means and the +'s indicate the inverses of the modes of the spawning age distributions in Figure 3.

These patterns of sensitivity to different frequencies illustrate the differences in the characteristics of cohort resonance among species with different longevities, and how they change with fishing. The primary feature in these is greater sensitivity to frequencies near the inverse of the means (*x*'s) and modes (+'s) of the spawning age distributions in Figure 3 (Bjørnstad *et al.*, 2004; Worden *et al.*, 2010), which is most obvious in the recruitment signal that results from the egg–recruit relationship (Figure 4a–c). These peaks are stronger in shorter-lived species (e.g. hake and coho salmon), and become stronger with greater fishing (Worden *et al.*, 2010). Note that the magnitudes of the sensitivity of recruitment over all frequencies actually increase with fishing. That effect is subsequently occluded by the added large random variability, hence it is not present in the spectra of annual egg production (Figure 4d–f) and catch (Figure 4g–i). These latter variables are relatively more responsive to low frequencies, even in the unfished case. This is because these two variables are sums over multiple cohorts, hence over multiple past values of random recruitment, which has the effect of smoothing out the high frequencies in environmental variability seen in recruitment. However, they also show a small effect of the resonant peak at generational time-scales in salmon, and in the heavily fished case for Pacific hake. The order of the sensitivities in catch signals at different levels of fishing is not the same as the order in egg production because equilibrium catch first increases, then decreases as fishing increases.

The important characteristic of cohort resonance here in the context of Hjort (1914) is that the fluctuations in recruitment to a population do not simply follow the variability in survival through the recruitment stage, as would occur if egg production was relatively constant as commonly assumed [and was posited by Hjort (1914)]. Rather, as explained in Figure 2, variable recruitment survival multiplies the result of *variable* egg production, which varies due to the effects of past recruitment. That effect is demonstrated in Figure 5, where the expected recruitment signal from the egg–recruit relationship is relatively constant in the unfished case, but as fishing increases, it becomes a lagged, smoothed version of past recruitment, with increasing resemblance to past

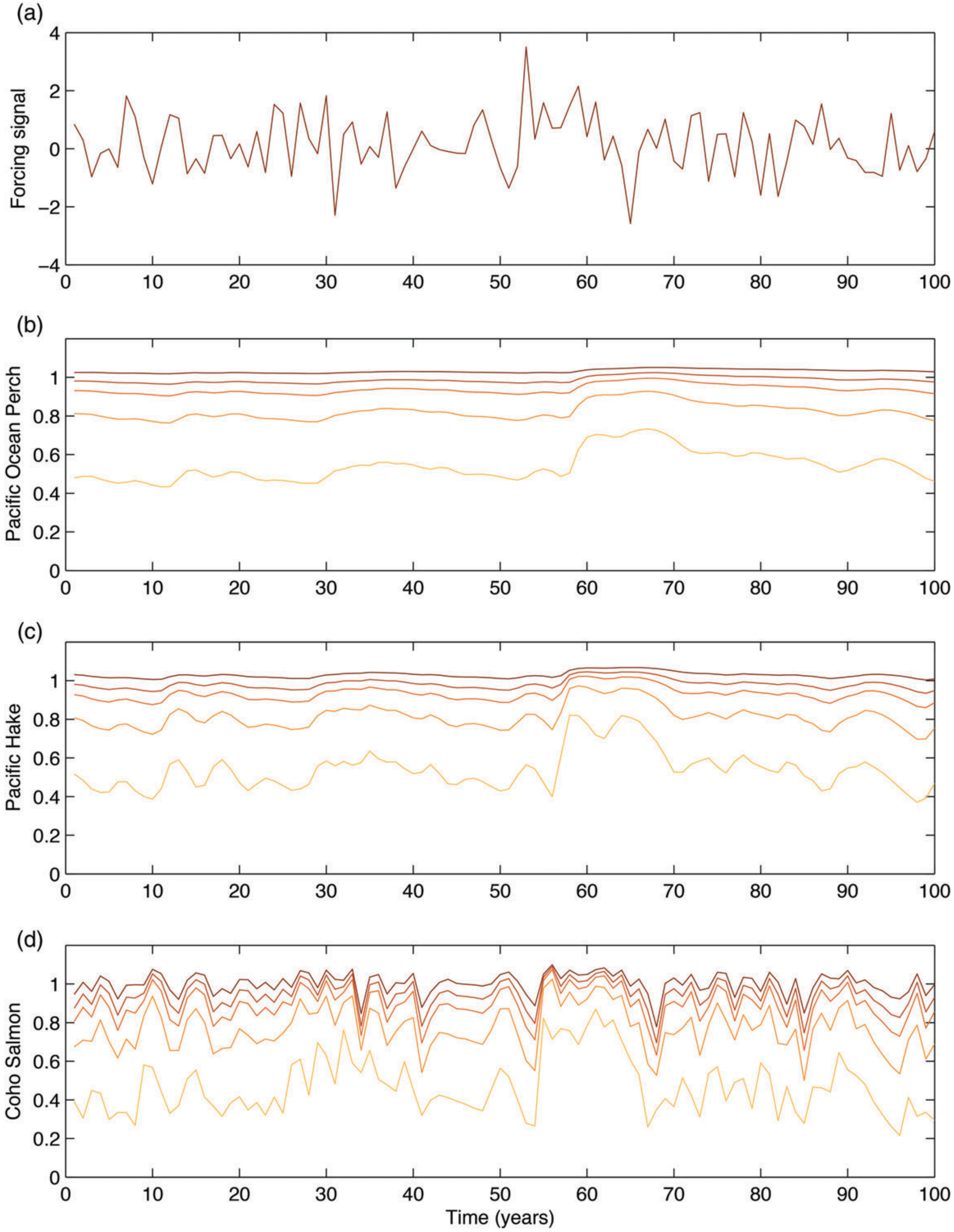

Figure 5. The effects of past recruitment on current recruitment through variability in egg production. The recruitment signal we can observe empirically is the product of current random recruitment survival (a) and current expected recruitment from the egg – recruit relationship (i.e. the green signals in Figure 2) for POP (b), for Pacific Hake (c), and for coho salmon (d), which all depend on the effects of past recruitment through current egg production. The different values of the exploitation index are indicated in (b), (c), and (d) in the same way as in Figures 3 and 4.

recruitment as the cohort resonance effect becomes stronger. For example, the dip in recruitment survival at year 51 becomes a dip in expected recruitment near year 58 for POP (a lag of 7 years), a similar dip in expected recruitment near year 56 for Pacific hake (a lag of 5 years), and a dip during years 53 and 54 (a lag of 2–3 years) for coho salmon. These are important because they serve to reinforce temporal variability in the environment on generational time-scales (see explanation of lower part of Figure 2). It must be emphasized that fishery biologists [e.g. Hjort (1914) and others] could not have seen the signals in Figure 5 because actual sampling of recruitment occurs after the addition of variability in survival (i.e. the red signal in Figure 1), which occludes the signal seen in Figure 5.

Empirical observations of an increase in variability with fishing have been made in terms of variables such as egg production (Hsieh *et al.*, 2006) and catch (Bjørnstad *et al.*, 2004). Here, we show how the coefficient of variation (*CV*s) of recruitment measured at two points in the life history, and the *CV*s of egg production and catch change with fishing (Figure 6). These plots of the *CV*s arising from environmental variability that is white noise in recruitment survival show how the relative amount of variability in various quantities in fish populations would increase with fishing (Figure 6a–d). Unfished variability in the recruitment resulting from the egg–recruit relationship (Figure 6a, the green signals in Figure 2, and the time-series shown in Figure 5b–d) is greatest in the shortest lived species, but increases more rapidly in the longer lived. Unfished variability in observed recruitment (Figure 6b, the red signals in Figure 2) is quite similar for the three species because they are dominated by the same multiplicative lognormal white variability in survival. There is little increase in observed recruitment variability with fishing, except near collapse (Figure 6b). This lack of an observable increase is also due to recruitment observations being made just after the introduction of environmental variability experienced during the larval stage. Any increase in variability of this relatively small signal from the egg–recruit relationship is occluded by the large, constant magnitude of the environmental noise, until just before collapse. With no fishing, the *CV*s of both egg production (Figure 6c) and catch (Figure 6d) are less than those of observed recruitment (Figure 6b), because they are sums over current age classes, thus weighted sums over past random recruitments. This smoothing effect is greater for longer-lived species because they sum over the results of a greater number of past random recruitments. However, importantly, as fishing increases, the *CV* of egg production increases more rapidly in the longer-lived species as seen in Figure 6a. This difference is due primarily to age truncation reducing the number of past random recruitments influencing egg production each year, thus reducing the smoothing of variable recruitment (Figure 2). The *CV* of catch varies slightly differently because equilibrium catch at first increases then declines as fishing increases. However, similar to the *CV* of egg production, the *CV* of catch increases more steeply with fishing in the longer-lived POP than in salmon and hake.

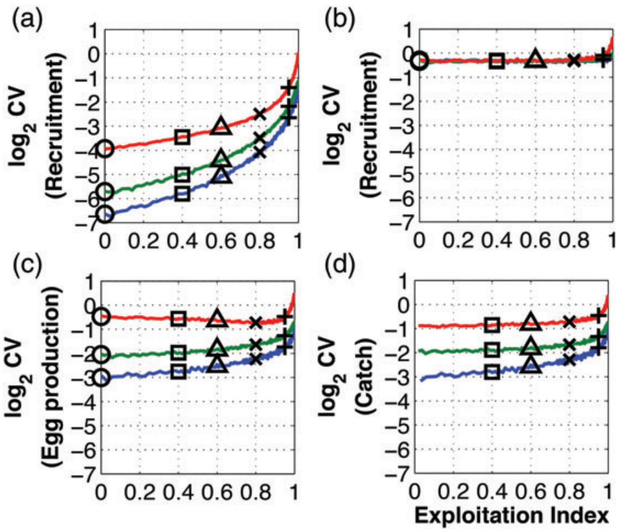

Figure 6. The effects of different levels of fishing on the variability (coefficient of variation) in recruitment expected from the egg–recruit relationship (a, the green signals in Figure 2), the recruitment after variability is added (b, the red signals in Figure 2), egg production (c, the purple signals in Figure 2), and catch (d) depend on fishing as it varies from no fishing (EI = 0) to the collapse point (EI = 1.0) for coho salmon (light grey line, or red line online), Pacific hake (dark grey line, or green line online), and POP (black line, or blue line online). The symbols indicate the same values of FLEP as in Figure 3. Note that the logarithms here are to the base 2 to allow easy comparison of doubling.

The empirical spectra of each these species (Figure 7) are consistent with these findings regarding the order of magnitudes of expected responses, but they require care in interpretation (Greenman and Benton, 2005). The observed signals are the product of the frequency selective sensitivity of each species and the frequency content of the actual environment over the past several decades, so would not necessarily be expected to match the frequency selectivity exactly. However, we can expect from Figures 4 and 6 that of these three species, coho salmon would be the most likely to exhibit peaks on generational time-scales, and they would be near period 3 (Figure 4). Therefore, the spectrum of spawning abundance for Oregon Coast Natural coho salmon (Rupp *et al.*, 2012) displayed significant variability in spawning abundance near period 3 from 1980 through the mid-1990s. It also has substantial variability on time-scales near 20 years, but that is not identified as significant by the wavelet analysis, and is outside the cone of significance due to series length. The *CV* of this spawner abundance time-series is 0.41. The spawning-stock biomass of Pacific hake displays substantial variability between 8 and 16 years from the late 1970s through the end of the series, but most of this is outside the cone of significance due to the series' length. The *CV* for this time-series is 0.31. The spawning-stock biomass for POP shows greater variance near a period of 10 years throughout the series from the 1970s to the year 2000, with a *CV* of 0.31 also.

Discussion

Cohort resonance is a recently discovered mechanism that contributes substantially to variability in fluctuating fish populations. It is an interaction between the fluctuating age structure of a fish population and the density-dependence in the early lives of fish. The life history of a species determines its response to environmental variability in early life, notably with greater sensitivity to specific frequencies. Cohort resonance is named for the *resonance* mechanism underlying the inherent sensitivity of age-structured populations to generational frequencies, i.e. it consists of noise exciting a natural frequency of a system. The mechanism underlying sensitivity to low frequencies is different, having more to do with the wandering behaviour of linear populations with weak density-dependence.

Species differences

A key feature of cohort resonance illustrated here is that its relative effect on a species depends critically on the species longevity.

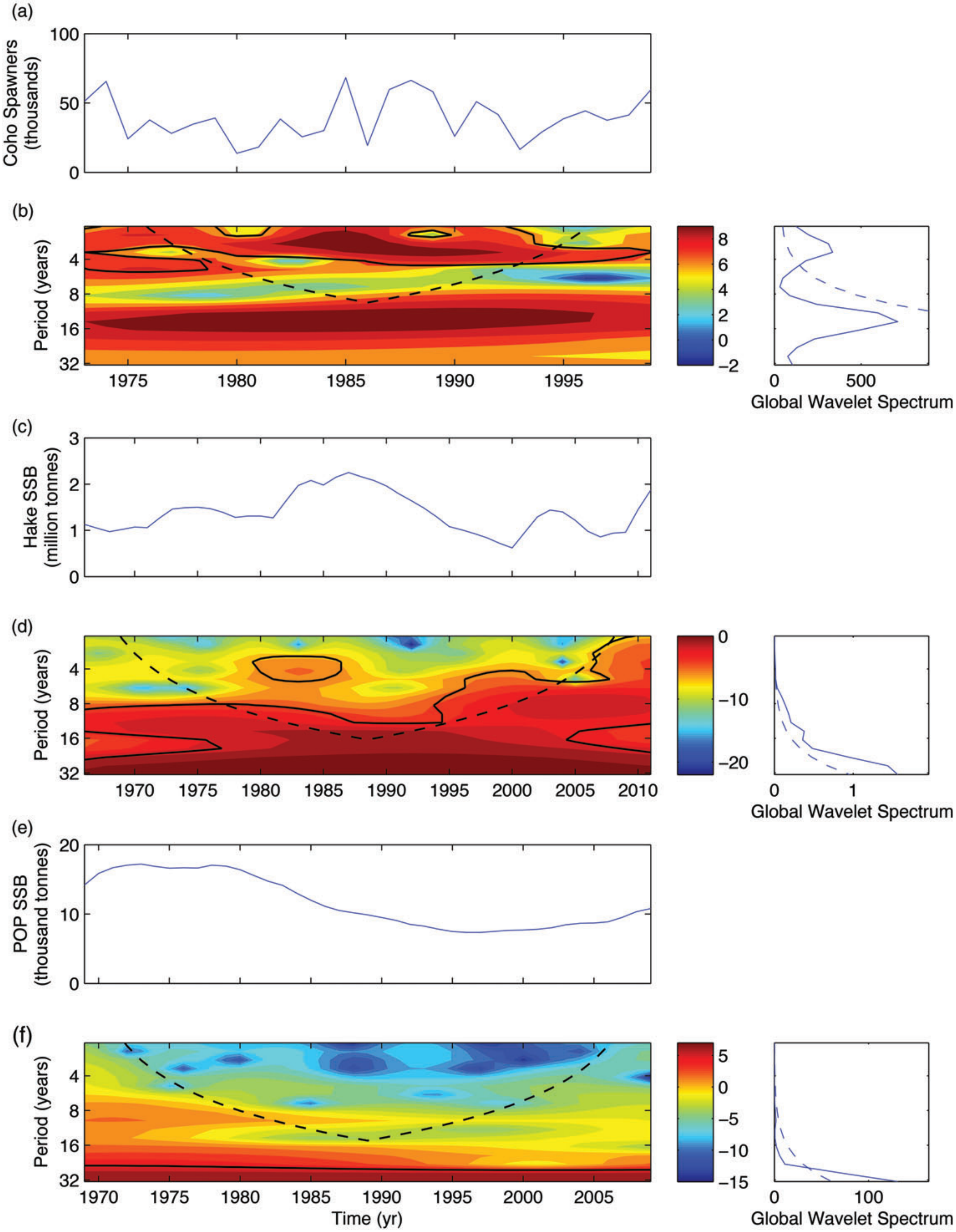

Figure 7. Spectra of the species analysed. Time-series (a, c, and e) and wavelet spectra (b, d, and f) for coho salmon, Pacific hake, and POP. In the wavelet spectra, the dashed lines indicate the "cone of significance" due to limited series length, i.e. only results at periods less than the period indicated are significant (Torrence and Compo, 1998). Bold lines indicate significance by a different criterion, whether they are significantly different from an AR2 process with the same intra-series correlation. The colour bars indicate the logarithms to the base 2 of the variance density. The Global Wavelet Spectra each represent the wavelet spectrum of each complete series.

Shorter-lived fish are much more sensitive to environmental variability than longer-lived species. Here unfished coho salmon, which live 3 years, were approximately six times as variable as unfished POP (~90 years), and unfished Pacific hake (~25 years) were twice as variable (Figure 6c, where actual exact values at EI = 0 are 0.126:0.235:0.712).

Increased variability with fishing

A second key feature of cohort resonance illustrated here is that variability in several population variables increases with fishing at rates that depend on longevity. While without fishing, coho salmon egg production and catch were more sensitive to environmental variability than the other two species, as fishing increased, the sensitivities to environmental variability of the longer-lived species (hake and POP) increased more rapidly than in coho salmon, so that under heavy fishing (i.e. EI = 0.95), the environmental sensitivity of egg production in the longest lived species was about half that of the shortest lived. Associated with these increases in overall sensitivity to the environment was a frequency selective increase in sensitivity to slow changes in the environment and variability on generational time-scales (Figure 4).

The predominant proposed explanations of increasing variability with fishing have involved unstable behaviour of over-compensatory models (Anderson *et al.*, 2008; Shelton and Mangel, 2011a), and while details are the subject of ongoing debate (Shelton and Mangel, 2011a; Sugihara *et al.*, 2011), these authors agree that unstable models are a key to their explanations. Both of these models depend on the well-known ability of population models with over-compensatory density-dependence in the egg-to-recruit relationship with display highly variable, possibly chaotic behaviour (Hassel *et al.*, 1976; Botsford, 1992), which cohort resonance does not. In most fish populations, it is difficult to determine whether the egg–recruit relationship is truly over-compensatory (Dorn, 2002; Zhou, 2007). Yet most fish populations show the compensatory decline in slope as abundance increases from very low values, which is the form driving the cohort resonance effect.

If cohort resonance is the dynamic mechanism responsible for increasing variability with fishing, the analyses here would shed light on the roles of various proposed biological factors. For example, age truncation is certainly a central factor in cohort resonance (Figure 3), but maternal effects would not be necessary for variability to increase with fishing. Also, selection for changes in life history parameters could exacerbate variability, but again, they would not be necessary.

Empirical observations

Future usefulness and understanding of cohort resonance will depend on identification of empirical examples. One example is the recent demonstration that an extreme form of cohort resonance explains the "cohort dominant" cycles in sockeye salmon (i.e. cycles consisting of a single spawning run of high abundance followed by several smaller runs, Ricker, 1997; Myers *et al.*, 1998; White *et al.*, 2014). The conditions that would allow the cohort resonance effect to cause decades of cycles similar to the cohort dominant cycles in sockeye salmon were: narrowness of the spawning age distribution, low persistence with regard to the stock–recruit relationship, and high variability in juvenile survival (White *et al.*, 2014). More important to us here perhaps, this investigation also led to the realization of a somewhat unique characteristic of cohort resonance: since it arises from environmental forcing of a *stable* population, a population may satisfy the conditions for cohort resonance, yet not actually display the characteristic behaviour of cohort resonance simply because it has not recently been excited by an appropriate environmental signal. This is contrary to the expectations when analysing population data to evaluate the presence of cycles due to a mechanism involving actual instability.

Another empirical example is the recent investigation by Rouyer *et al.* (2012) of the effects of fishing on the spectra of population variability in 24 North Atlantic fish stocks, including the herring and cod stocks in Hjort (1914). The slope of the variance spectrum was shown to be shallower (i.e. include more high frequencies) in stocks for which the mean age had declined, consistent with expectations from cohort resonance.

The three species examined here are further examples of empirical observations of cohort resonance. Because the frequency-dependent filtering is only part of what produces these observed signals, they would not be expected to be exactly the same as the theoretical projections. The *CV*s of the empirical egg production time-series for coho salmon, Pacific hake, and POP in Figure 7 were 0.41, 0.31, and 0.31, respectively, or ratios of 1.0:0.76:0.76, when compared with the predicted values at EI = 0.8 in Figure 6c of ~1.0:0.5:0.3. The spectra showed high variance near the generational frequency for the species for which it was expected to be strongest, coho salmon, and in general, the rates of decline of variance with frequency in the global wavelet spectra (Figure 7b–f) loosely followed those expected from Figure 4.

Analysis of these time-series illustrates some of the challenges in detecting the spectral sensitivities in cohort resonance. One is that long time-series are necessary, especially for long-lived species. In our wavelet analyses (Figure 7), we have shown periods out to 32 years to illustrate the presence of variance at low frequencies, but even periods >8 years for salmon and 16 years for the other two species lie outside the cone of significance. Longer time-series will be necessary to detect such long periods. A second challenge is that much of the available data may only be the results from fitting stock assessment models. The frequency content would be influenced by the model used in the fitting. In Figure 7, this was the case for Pacific hake and POP, which are taken from stock assessments, but could not affect coho salmon, for which abundances are direct observations rather than model products. A third challenge in detecting cohort resonance effects is the previously mentioned fact that population time-series depend on environmental variability in the recent past, as well as the population sensitivity we are trying to detect.

It is interesting that empirical evidence of the effects of cohort resonance was not detected by Hjort (1914), nor anyone else, during the 90 years from 1914 to 2004. This is likely due to two reasons: (i) detection from early life history data would have involved examining recruitment, which is dominated by environmental noise that would overwhelm any cohort resonant variability from the egg to recruit relationship (Figure 6b when compared with Figure 6a) and (ii) most results in 1914 were presumably based on relatively lightly fished, reasonably long-lived species, in which cohort resonant effects are weaker. For example, Hjort (1914) was mainly concerned with herring and cod off the coast of Norway, which had lifespans near 10 years.

Although cohort resonance would have been difficult to detect empirically, one might further ask why the cohort resonance phenomenon was not discovered earlier by those working in population dynamics? The answer is, at least in part, because cohort resonance occurs in stable populations. Mathematical ecologists working in population dynamics tend to look for instabilities when trying to answer questions regarding large fluctuations. An example of locally unstable cycles in fisheries due to over-compensatory density-dependence in stock recruitment is the cyclic variability of period $2T$ in some marine populations (e.g. Ricker, 1954; Botsford and Wickham, 1978).

Mechanisms that are similar to, or are a part of, cohort resonance have been identified empirically in previous quantitative analyses. For example, a meta-analysis of variability in early survival of fish indicated greater variability in populations fished to low abundance, and suggested that the mechanism was stochastic density-independent mortality in the egg and larval stages, followed by compensatory (not over-compensatory) density-dependent mortality in the juvenile stage (Myers, 2001; Minto *et al*., 2008).

Theoretical considerations

The theoretical basis for cohort resonance ties it to a broad range of other topics in population dynamics. The analysis demonstrating cohort resonance employs a model of how the population varies with respect to its equilibrium value (e.g. Worden *et al*., 2010). This model has essentially the same form as a Leslie matrix, which means that its dominant behaviour is geometric growth, which in the stable case, would return the abundance to equilibrium. It also means that the next largest mode of behaviour is a cyclic approach to equilibrium, mathematically the same cyclic transients one sees when a simulation of a Leslie matrix starts from an arbitrary initial age structure (Sykes, 1969). These are essentially the same kind of transients one could see when a population is placed under the protection of a marine protected area (White *et al*., 2013). This also means that one can glean information regarding which life history characteristics will lead to greater propensity for cycling at period T from studies of that same topic for other species (e.g. Taylor, 1979, for insects).

Another valuable link to theory is the fact that the increase in variance and change in frequency response with fishing due to cohort resonance are similar to the increases in variance and autocorrelation being investigated as Early Warning Signs (EWS) of deleterious changes in ecosystem state. The increase in variance due to cohort resonance near the population collapse point is illustrated in Figure 6, and the increase in autocorrelation follows from the increasing sensitivity to low frequencies with fishing in Figure 4. In more general settings, the role of increasing variance and autocorrelation as leading indicators of tipping points or regime shifts has been a subject of great recent interest (Scheffer *et al*., 2009, 2012; Boettiger *et al*., 2013). In the population models of the cohort resonance effect, we do not have a saddle–node bifurcation, which is commonly the focus in EWS research, but instead, we have what is known as an exchange of stability. Cohort resonance is quite similar to the experimental system examined by Drake and Griffen (2010) who analysed the response of a laboratory population of Daphnia to reduced food levels for signs of increased variance in the abundance time-series before extinction. What is different and interesting about cohort resonance is the role played by age structure in generating the increased variance in a system where stochasticity is important. The recent finding that an increase in catch variability preceded collapses in North Pacific crab fisheries is a suggestion that cohort resonance may have been involved (Litzow *et al*., 2013). Much work remains in relating our results to the growing EWS literature and developing rigorous approaches to using these signals to forecast shifts (Boettiger and Hastings, 2012).

Climate change

The existence of cohort resonance in age-structured fish populations has important implications for the effects of climate change on marine ecosystems (Botsford *et al*., 2012). It provides information regarding the effects of possible changes in the frequency content of environmental signals (e.g. changes in the frequency of El Niños). Such changes in El Niños have been observed empirically in the past (Cobb *et al*., 2003) and are also predicted by global climate models in the future (Timmermann *et al*., 1999). A second implication for climate change is identification of the confounding of potential slow changes in abundance due to fishing or climate change, with increasing sensitivity to low frequencies due to cohort resonance [the "cloaking" effect of Bjørnstad *et al*. (2004)].

In summary, the phenomenon of cohort resonance seems to be a valuable addition to the search for greater understanding of fluctuations in fished populations which Hjort initiated 100 years ago. Further analyses and continued comparison with empirical data will likely produce results that could be useful in fisheries management and anticipating the effects of climate change. Additional work is needed to compare the expectations of cohort resonance to empirical data.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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