Journal of Animal Ecology 2004
73, 1157–1167

Trends and cohort resonant effects in age-structured populations

OTTAR N. BJØRNSTAD*, ROGER M. NISBET† and JEAN-MARC FROMENTIN‡

**Departments of Entomology and Biology, The Pennsylvania State University, State College, Pennsylvania 16802, USA; †Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106, USA; and ‡IFREMER, Centre de Recherche Halieutique Méditerranden et Tropical, Boulevard Jean Monnet, BP 171, 34203 Sète cedex, France*

Summary

1. Trends and fluctuations in populations are determined by complex interactions between extrinsic forcing and intrinsic dynamics. As an example, the dynamics of many marine fish are characterized by age-structured dynamics forced by stochastic recruitment.
2. In this study we develop stochastic age-structured models for two case studies, the Atlantic bluefin tuna and the Atlantic cod. The former exemplifies intracohort interactions and density-dependent reproduction, the latter exemplifies density-dependent survival and intercohort interactions.
3. We use transfer functions and delay-coordinate models to study how the combination of age-structured interactions and stochastic recruitment can induce low-frequency variability. 'Cohort resonance', as we dub this effect, can induce apparent trends in abundance and may be common in age-structured populations.
4. Our study complements the theory of structured populations that focuses on cycles and chaos (high-frequency dynamics).
5. The innate low-frequency fluctuations we describe can potentially mimic or cloak critical variation in abundance linked to environmental change, over-exploitation or other types of anthropogenic forcing.
6. From a management and conservation viewpoint, it will be important to find ways to separate anthropogenic forcing from cohort resonant effects and/or to understand the way they interact.

Key-words: environmental stochasticity, fish populations, stochastic age-structured dynamics, stock-recruitment, transfer functions, trends.

Journal of Animal Ecology (2004) **73**, 1157–1167

Introduction

Trends and fluctuations in populations are determined by complex interactions between extrinsic forcing and intrinsic dynamics. For example, the dynamics of many marine fish are characterized by age-structured interactions and stochastic reproduction (Hjort 1926; Ricker 1954; Wooster & Bailey 1989). Age-structured interactions, such as asymmetric competition and/or cannibalism between sympatric cohorts, may be related to food and habitat limitations and predation risks (Wootton 1990). Depending on the species and the life cycle, the interactions among individuals lead to varying patterns of density-dependent population growth. Whenever competition induces enhanced mortality, regulation will be through density-dependent survival. In contrast, when competition leads to reduced growth, regulation will be through density-dependent reproduction as spawning is tightly linked to biomass (Wootton 1990).

A second axis to regulation in fish relates to the level of interactions between individuals of different age-classes and cohorts. In some species different age-classes have separate habitat preference and form separate shoals, in which case regulation is mainly through intracohort interactions. In other species habitat preferences overlap, in which case regulation is partly through interactions between cohorts. Such interactions are often asymmetric because of the heterogeneous

Correspondence: Ottar N. Bjørnstad, Departments of Entomology and Biology, The Pennsylvania State University, State College, Pennsylvania 16802. USA. Fax: 814 865 3048; E-mail: onbl@psu.edu

sizes of the interacting individuals. In species with iteroparous reproduction, there is invariably one additional 'intercohort interaction': the multiple age-classes that comprise the spawning stock all contribute to the size of the young-of-the-year (the so-called 'zero group').

A high level of stochasticity in recruitment appear to be ubiquitous in species with planktonic egg and larval stages (Eckert 2003), as the pelagic stage is affected by a suite of climatic and environmental factors. For instance, wind and oceanic currents may carry planktonic eggs and larvae to hostile offshore areas and phyto- and zooplankton availability may vary greatly among locations and between years to provide extremely variable resources (e.g. Cushing 1995).

We previously proposed a model incorporating age-structure, density-dependence and stochastic recruitment to account for the variability in populations of Norwegian coastal cod (Bjørnstad *et al*. 1999a). Simulations revealed that while the deterministic version of the model predicts either stability or variation at the few-generation scale (such as cyclic and chaotic oscillation), a more realistic stochastic model exhibits apparent trends in abundance that were overlaid on the 'deterministic variability' – even in the absence of directional changes in the environment. Preliminary analyses of the model led to the conjecture that the trends were caused by age-structured interactions 'echoing' the stochastic recruitment. This speculation is the focus of the current study. In what follows, we will refer to apparent or real trends as low-frequency variation and cyclic/ chaotic oscillation as high-frequency variation (e.g. Cohen 1995).

Existing theory of population growth reveals many, often non-intuitive, effects of stochasticity. For instance, in the case of age-structured dynamics, describable by linear projection matrices, environmental stochasticity invariably results in lowered long-term growth rates (e.g. Tuljapurkar 1990; Caswell 2000). Even in static environments, demographic stochasticity can induce Allee effects (inverse density-dependence at low densities; Lande 1998). In the absence of stochasticity, non-linear interactions among age-, stage- or size-classes can lead to sustained high-frequency fluctuations in abundance (e.g. Oster & Takahashi 1974; Gurney & Nisbet 1980; Gurney, Nisbet & Lawton 1983; Nisbet & Onyiah 1994; Mertz & Myers 1996). Cannibalism can generate oscillations in which the survival alternates from high to low to high between consecutive cohorts to induce cyclic or complex dynamics (e.g. Diekmann *et al*. 1986; Hastings & Costantino 1991; Costantino *et al*. 1995). The effects of stochasticity on such non-linear dynamics are currently receiving increasing attention.

The current study seeks to complement previous work – by using transfer functions (e.g. Nisbet & Gurney 1982) and delay-coordinate models (e.g. Bjørnstad *et al.* 2001) – and discuss how the interplay of age-structured interactions and stochastic forcing determine population fluctuations over both long and short time-scales. Our main locus is on low-frequency variability that would be interpreted as a trend in abundance in all but the longest data sets. Trends and low-frequency variability are of obvious importance in management and conservation, because trends are often associated with environmental change (e.g. regime shifts), over-exploitation or other types of anthropogenic forcing. The variability that results from stochastic age-structured dynamics may wrongly encourage interventions in the face of natural low-frequency variability.

We show that – depending on the interactions within and among age classes – a population subjected to random environmental forcing on recruitment may exhibit low-frequency variability. In so doing, we provide a full analytical treatment of the conjecture by Bjørnstad *et al*. 1999a) that was dubbed the 'cohort resonance effect' in Bjørnstad & Grenfell (2001).

We analyse various life cycles that give rise to analogous effects and suggest that cohort resonant effects may be of general interest for age-structured populations. We place our results in the context of two case studies for which there exist exceptionally long time series: (1) the Atlantic bluefin tuna (*Thunnus thynnus* L.), which is regulated primarily by density-dependent reproduction, and (2) the Norwegian Skagerrak populations of Atlantic cod (*Gadus morhua* L.), which is regulated by density-dependent survival.

Focal species

Before embarking on the theoretical explorations, we outline the natural histories that motivate our models. A majority of marine fish are iteroparous and females produce many small eggs that develop, hatch and grow without parental care. The hatched fish larvae are typically pelagic, provisioned with a yolk sac, and have a relatively undeveloped body form (Wootton 1990). The time immediately following yolk resorption is known as the 'critical period' during which mortality is extremely variable from year to year because of environmental fluctuations in the pelagic ecosystem (e.g. Cushing 1990). After a period of growth, the larvae metamorphose into juvenile fish (adult-like but immature). Benthic ('ground-dwelling') and demersal (dwelling near the sea floor) juvenile fish eventually settle on or near the bottom, whereas pelagic ones stay in the water column. Depending on the species, the juvenile period extends from a few months to several years.

To understand the dynamics that may result from environmental stochasticity in recruitment we focus on two case studies, the East-Atlantic bluefin tuna and the Norwegian Skagerrak cod. These species are of interest because they display contrasting life histories, and we have exceptionally long time series of abundance data for both (Fig. 1). Intriguingly, the historical dynamics of both species are dominated by low-frequency variability that are only partially explained by human exploitation or climatic changes (Fromentin *et al.* 1998; Ravier & Fromentin 2001).

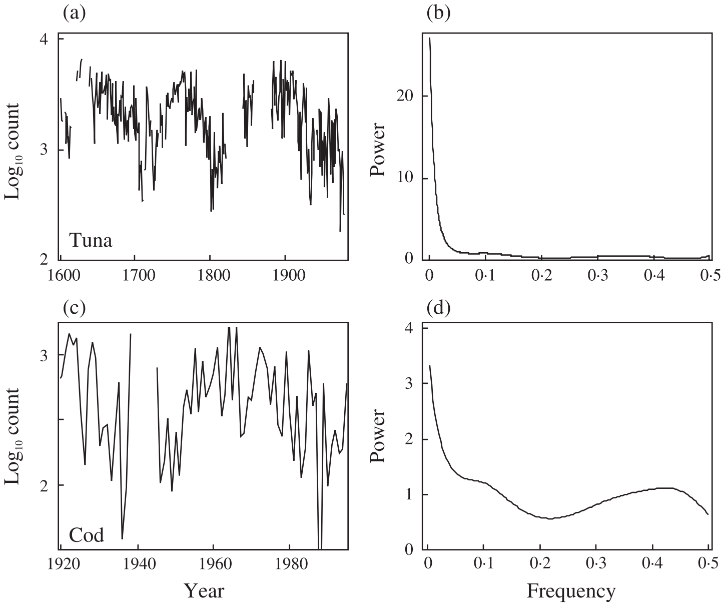

Fig. 1. Time series and power spectra of bluefin tuna (a, b) from traps in Sicily (Ravier & Fromentin 2001) and coastal cod (c, d) from the Skagerrak (Fromentin *et al.* 1997; Bjørnstad *et al.* 1999b). The power spcctra were estimated using logspline spectra (Kooperberg, Stone & Truong 1995) applied to the Lomb periodogram for incomplete time series (Lomb 1976).

Bluefin tuna is a large, pelagic and highly migratory fish, with migration between its spawning sites (restricted to a few spots in the Western Mediterranean Sea) and its feeding grounds (covering the North Atlantic). Some juveniles stay in the Mediterranean Sea, while others migrate into the North Atlantic (Mather, Mason & Jones 1995). Most members of a juvenile shoal come from the same age-class. East-Atlantic bluefin tuna mature after about 4 years, can live for at least 20 years, and can reach a substantial size (> 3 m long and 500 kg; Fromentin & Fonteneau 2001). Density-dependent mortality has not been documented in tuna species. However, reproduction is highly size-dependent, so density-dependent growth will translate into density-dependent fecundity.

Atlantic cod, in contrast, is demersal with life-history traits that vary between local populations. The populations of the Norwegian Skagerrak coast are non-migratory and spawn in March. The pelagic larval phase is about 5 months and the young-of-the-year settle to a demersal life style during the summer and grow for around 2 years before maturing. The two juvenile age-classes (the young-of-the-year and the 1-year-old) have similar habitat preferences and are sympatric (Stenseth *et al.* 1999). As a consequence there is competition for habitat and food among individuals in the same cohort and density-dependent cannibalism by individuals of the older cohort (e.g. Bjørnstad *et al.* 1999b; Fromentin *et al.* 2001). Two- and 3-year-olds constitute about 75% of the spawning stock biomass in these coastal populations and life span rarely exceeds 6 years. This is short compared to other cod stocks (Stenseth *et al.* 1999). The Skagerrak cod is thus characterized by density-dependent survival and interactions between cohorts.

Transfer functions for age-structured dynamics

THE GENERAL MODEL

The interplay of stochastic forcing and age-structured interactions shapes the dynamics of each cohort as well as the dynamics of groups of cohorts. Many aspects of the dynamics can be understood with the aid of transfer functions (Priestley 1981; Nisbet & Gurney 1982) that relate fluctuations in the 'output' – for example, the number of individuals in the reproductive stock – to the stochastic 'input', represented by variable per capita reproduction rates (see Horwood 1983; Ripa, Lundberg & Kaitala 1998, for related ecological applications).

Consider an annually reproducing species with age-structure and stochastic per capita reproductive rates. Let $N_{0,t}, \dots, N_{d,t}$ denote the abundances of the young of the year and the subsequent d age classes. The growth of cohorts older than the young-of-the-year is generally given by the relation:

$$N_{j+1,t} = N_{j,t-1}\lambda_j(N_{0,t-1}, \dots, N_{d,t-1}), \quad j = 0, 1 \dots, d \qquad \text{eqn 1}$$

where λ_j is the (possibly density-dependent) survival of age-class, j. Recruitment into the $0th$ age-class is through reproduction by the stock (the sum across adult age-classes, $S_t = N_{m,t} + N_{m+1,t} + \dots + N_{d,t}$ where m is the age at maturity). Recruitment may be density-dependent and is also influenced by a multiplicative stochastic forcing function denoted by ζ_t. With these assumptions, the dynamics of the young-of-the-year (age < 12 months) can be written in the form:

$$N_{0,t} = \zeta_t S_t F(S_t), \qquad \text{eqn 2}$$

where $F()$ is the (possibly density-dependent) fecundity function. We note that while it may seem mathematically extraneous to have a 'half time step' equation – the annual time subscripts are the same on the left-hand side and right-hand side of eqn 2 – we employ this as a biologically motivated intermediate step, because many key density-dependent and density-independent interactions occur during the transitions from the metamorphosis from the egg and larval phases. In the age-structured calculations that follow, we retain order by back-substituting for the right-hand side of eqn 2 before analysis.

To analyse the stochastic dynamics we first assume that the density-dependence in recruitment (eqn 2) and/or survival (eqn 1) leads to an equilibrium state that is locally stable. We then linearize the equations about this equilibrium, and use the linearized equations to study the response to forcing (Appendix A). Nisbet & Gurney (1982) discuss in detail the strengths and limitations of this approach, drawing heavily on the study by Nisbet, Gurney & Pettipher (1977). The take-home message is that for many models with a single, locally stable, equilibrium, linearized analysis provides a remarkably good characterization of even quite large population fluctuations. The approach is much less robust for systems with multiple equilibria, and is of course inapplicable to systems with chaotic dynamics. The power of analyses based on linearized dynamics has also been exploited to understand community dynamics (e.g. Ripa *et al.* 1998; Ives, Gross & Klug 1999; Ripa & Ives 2003), while some limitations of the approach for systems near the edge of chaos were discussed by Pascual & Mazzega (2003).

In what follows, it is convenient to work with the sequence of vectors of log-transformed abundances, $\{\log \mathbf{N_t}, t = 1, 2, \ldots\}$. The linearization around the equilibrium log-abundance of each cohort, $\{\log \mathbf{N}^*\}$ will then take the form

$$\mathbf{x}_t = \mathbf{J}\mathbf{x}_{t-1} + \mathbf{A}\alpha_t \qquad \text{eqn 3}$$

where $\mathbf{x_t} = \log \mathbf{N_t} - \log \mathbf{N}^*$ is the vector of deviations of log-abundance from equilibrium, **J** is the Jacobian 'stability' matrix for the system, **A** is the vector that describes the influence of the stochastic forcing on the growth of each state variable, and α_t is the deviations of $\log \zeta_t$ from its expectation (see Appendix A for details).

Transfer functions specify how the interactions in the life cycle amplify or attenuate stochastic forcing at different frequencies, f (Nisbet & Gurney 1982). Fluctuations with a frequency of 0·5 or 0·25 represents a 2-year and 4-year cycle, respectively. Fluctuations with very low frequencies would be indistinguishable from trends in all but the longest time series, thus representing 'apparent trends'. The power spectrum (sometimes called spectral density or simply spectrum), $h_j(f)$, of the fluctuations in age class j is related to the power spectrum, $\Gamma(f)$, of the stochastic forcing function by the relationship

$$h_j(f) = |T_j(f)|^2\,\Gamma(f) \qquad \text{eqn 4}$$

where the transfer function, $T(f)$ is given by (Appendix B):

$$\mathbf{T}(f) = (\mathbf{I} - e^{-2\pi\iota f}\mathbf{J})^{-1}\mathbf{A}, \qquad \text{eqn 5}$$

where **I** is the identity matrix, and ι is the complex constant.

Several details in this relation were laid bare in Nisbet & Gurney (1982: chs 2–4). In addition, the transfer function has a particularly useful interpretation when moving from the state-space model (i.e. eqns 1–2) to its delay-coordinate equivalent that is a powerful tool in ecological time series analysis (Royama 1992; Bjørnstad, Falck & Stenseth 1995). The latter describes the dynamics of any one of the state variables (e.g. the stock) in terms of patterns of 'statistical density dependence' (Royama 1992) and the historical values of that particular variable at times $t - 1, t - 2, \ldots, t - d$ (e.g. Royama 1992; Bjørnstad *et al.* 2001). For the present models, the delay-coordinate representation shows how the age-structured interactions induce delays in population regulation (see Bjørnstad *et al.* 1999a). In particular, the delay-coordinate model:

$$\begin{aligned} x_t = c &+ \underbrace{a_1 x_{t-1} + a_2 x_{t-2} + \ldots + a_d x_{t-d}}_{\text{autoregression}} \\ &+ \varepsilon_t + \underbrace{b_1 \varepsilon_{t-1} + \ldots + b_q \varepsilon_{t-q}}_{\text{moving averaging}}, \end{aligned} \qquad \text{eqn 6}$$

has a transfer function of the form:

$$T(f) = \frac{1 + b_1 e^{-(2\pi\iota f)} + \ldots + b_q e^{-(2\pi\iota f)q}}{1 - a_1 e^{-(2\pi\iota f)} - \ldots - a_d e^{-(2\pi\iota f)d}}. \qquad \text{eqn 7}$$

Notice that the denominator of the transfer function reflects the regulatory delays and implies a particular form for the autoregressive component of the delay-coordinate model (Priestley 1981: ch. 4). In contrast, the numerator details how stochasticity may, depending on the specific life cycle, have both immediate and delayed effects as reflected in the coefficients of the moving average component. Furthermore, the Cayley–Hamilton theorem ensures that for any linear model (such as eqn 3), there exists a unique delay-coordinate representation (viz. eqn 6) (see, for example, Akaike 1974 and Aoki & Havenner 1991). This is a one-way equivalence, meaning that a given delay-coordinate model may arise from a number of different state-space models. The state-space/delay-coordinate equivalence is central to understand how age-structured interactions may interplay with stochasticity to induce apparent trends in fish populations. In the Supplementary material we supply a concise Mathematica workbook that details the calculations involved in the transfer functions, power spectra and delay-coordinate representations. With this general background in mind, we turn to the two case studies.

DENSITY-DEPENDENT FECUNDITY

The tuna life cycle, reviewed above, motivates the following age-structured model for each of the j juvenile cohorts (four in the case of bluefin) and $d - m$ adult cohorts (around 15–20) that comprise the spawning stock:

$$N_{0,t} = \zeta_t S_t F(S_t) \qquad \text{eqn 8}$$

$$N_{j,t} = \lambda_j N_{j-1,t-1} \quad j = 1, \ldots, d \qquad \text{eqn 9}$$

$$S_t = N_{m,t} + N_{m+1,t} + \ldots + N_{d,t}$$

Notation follows that of the General Model section. The annual survival, λ_j, is around 0·75 for juvenile age classes (i.e. for $j = 1, \ldots, m - 1$) and around 0·9 for adults (ICCAT 1997). With this mortality schedule, 95% of the individuals that survived through the planktonic phase will be dead by age 20, and a very small fraction of the spawning stock is comprised of older individuals. The size of the cohort decays (approximately geometrically) with age. Due to senescence there may be an upper age-limit, d. We focus on the results assuming finite life span, but also present the mathematics for the limit as $d \to \infty$ (negligible senescence). For relatively low senescence (high value of d), the results are indistinguishable.

The function $F(S_t)$ describes density-dependent recruitment. For mathematical simplicity we use the Compertz model ($F(S) = \exp(-\beta \log S) = S^{-\beta}$) but the conclusions generalize to the more commonly used Beverton–Holt model (Bjørnstad, Nisbet and Fromentin, unpublished results). For this life cycle, representative forms for the transfer functions of individual cohorts and that of the whole spawning stock (Table 1) are depicted in Fig. 2. This figure shows that in the presence of white-noise stochastic forcing (i.e. temporally uncorrelated stochastic forcing), the spectrum of each cohort is also approximately 'white' (i.e. a flat power spectrum). In contrast, the spawning stock spectrum is heavily 'red-shifted' (i.e. dominance of low frequency variation; Cohen 1995) compared to the individual cohorts. The degree of red-shifting increases with number of cohorts in the stock (Fig. 2), so that more than 30% of the variation in the stock is in the very low frequency range ($0 < f < 0{\cdot}05$) compared to 5% for each cohort. This red-shifting cannot be accounted for by the slight increase in mean ages of reproduction (given in Fig. 2 legend) that result from the increase in number of adult cohorts. Rather, the delay-coordinate representation of the model can elucidate the mechanism behind this conspicuous difference.

For any of the individual cohorts, j, the delay-coordinate representation for the dynamics is:

$$x_{j,t} = c + \underbrace{(1-\beta)\sum_{k=m}^{d} P_k x_{j,t-k}}_{\text{delayed regulation}} + \alpha_t, \qquad \text{eqn 10}$$

where c is a constant, P_k is the proportion of the stock in age-class k at equilibrium, and x is as defined in the General Model section above. The variable α_t is the deviation of $\log \zeta_t$ from its expectation (see Appendix A). Assuming lognormal recruitment, α_t will be a sequence of zero-mean normal variates (that need not necessarily be independent).

The density-dependence in reproduction, as quantified by β, induces a distributed delay in regulation that corresponds to the ages of the spawning individuals, from the time-lag representing maturation, m, to the time-lag of maximum age, d. The importance of each delay is

Table 1. Transfer functions for individual cohorts, j, the stock, S, and young-of-the-year, 0, for the tuna model with density-dependent fecundity (eqns 8–9) and the cod model with density-dependent survival (eqns 12–14): the weights, P_k, are quantified as $\lambda_s^{k-m}/\Sigma_{k=m}^{d}\lambda_S^{d}$. The limits in the absence of senescence ($d \to \infty$) are also given. The limits are for $m = 3$ (top) and $m = 1$ (bottom)

Density-dependent fecundity:	
$T_j(f) = \dfrac{1}{1-(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}$	$\xrightarrow[d\to\infty]{\lim} \dfrac{1}{1-\dfrac{e^{-6\pi\iota f}(1-\beta)(1-\lambda_s)}{e^{2\pi\iota f}-\lambda_s}}$
$T_S(f) = \dfrac{\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}{1-(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}$	$\xrightarrow[d\to\infty]{\lim} \dfrac{e^{-6\pi\iota f}(1-\lambda_s)}{1-\dfrac{e^{-6\pi\iota f}(1+\beta)(1-\lambda_s)}{e^{2\pi\iota f}-\lambda_s}(e^{2\pi\iota f}-\lambda_s)}$
$T_0(f)$ same as $T_j(f)$	
Density-dependent survival:	
$T_j(f) = \dfrac{(1-\beta)e^{-2j\pi\iota f}}{1+\gamma e^{-2\pi\iota f}-(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}$	$\xrightarrow[d\to\infty]{\lim} \dfrac{(1-\beta)e^{-2j\pi\iota f}}{1+\gamma e^{-4\pi\iota f}-\dfrac{e^{-2\pi\iota f}(1-\beta)(1-\lambda_s)}{e^{2\pi\iota f}-\lambda_s}}$
$T_S(f) = \dfrac{(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}{1+\gamma e^{-2\pi\iota f}-(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}$	$\xrightarrow[d\to\infty]{\lim} \dfrac{(1-\beta)(1-\lambda_s)e^{-2j\pi\iota f}(e^{2\pi\iota f}-\lambda_s)^{-1}}{\left(1+\gamma e^{-2\pi\iota f}-\dfrac{e^{-2\pi\iota f}(1-\beta)(1-\lambda_s)}{e^{2\pi\iota f}-\lambda_s}\right)}$
$T_0(f) = \dfrac{1+\gamma e^{-2\pi\iota f}}{1+\gamma e^{-2\pi\iota f}-(1-\beta)\sum_{k=m}^{d} e^{-2k\pi\iota f} P_k}$	$\xrightarrow[d\to\infty]{\lim} \dfrac{1+\gamma e^{-2\pi\iota f}}{1+\gamma e^{-2\pi\iota f}-\dfrac{e^{-2\pi\iota f}(1-\beta)(1-\lambda_s)}{e^{2\pi\iota f}-\lambda_s}}$

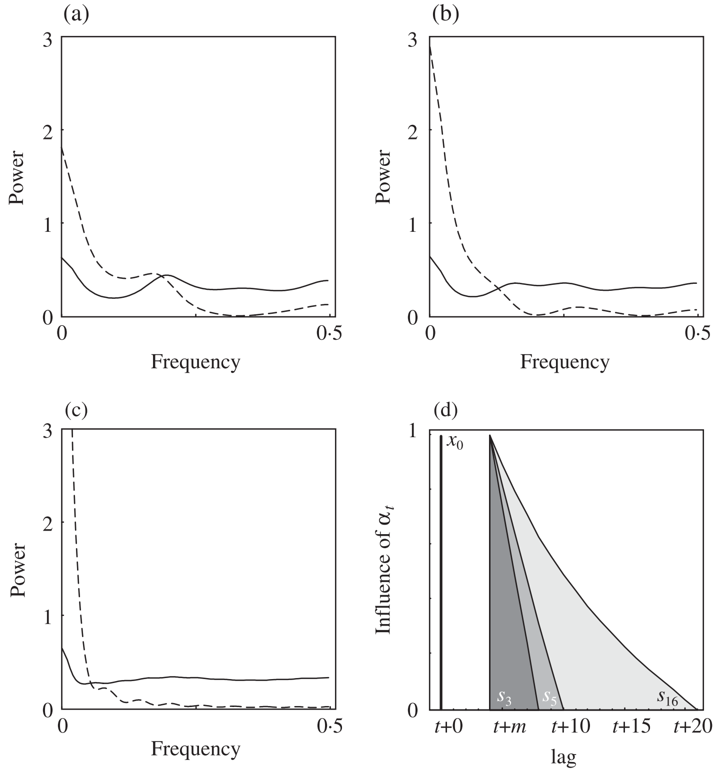

Fig. 2. The theoretical power spectra for individual cohorts (solid line) and the total stock size (dotted line) of the generic tuna model (eqns 8–9) as a function of number of cohorts in the stock. (a) Three adult cohorts (generation time: 4·9 years), (b) five adult cohorts (generation time: 5·8 years) and (c) 16 adult cohorts (generation time: 9·1 years). (d) The effect of the stochastic reproduction on an individual cohort (the-young-of-the-year) and the reproductive stock (for three, five and 16 adult) cohorts as measured by the scaled cross-covariance between the stochastic reproduction and abundance as a function of time lag (see text for details: x_0). The maximum covariance is scaled to one to ease comparison. Model parameters are: $m = 4$, $\beta = 0{\cdot}7$, $\lambda_S = 0{\cdot}9$, $\lambda_J = 0{\cdot}75$ and $\alpha^* = \log(10)$.

given by the equilibrium proportion of the stock in each age-class. Note that the $(1 - \beta)P_k$ coefficients in eqn 10 represents the strengths of 'statistical density-dependence' in ecological time series parlance (e.g. Royama 1992).

The corresponding equation for the log-spawning stock, s, takes an analogous form to eqn 10 except for the nature of the stochastic component:

$$s_t = c + \underbrace{(1 - \beta)\sum_{k=m}^{d} P_k s_{t-k}}_{\text{delayed regulation}} + \underbrace{\sum_{k=m}^{d} P_k \alpha_{t-k}}_{\text{distributed noise}}. \qquad \text{eqn 11}$$

Comparing eqn 10 to eqn 11, the difference in dynamics – notably the degree of red-shifting of the stock dynamics (Fig. 2) – arises because of the way the stochastic forcing is echoed in a distributed fashion within the stock, but not in the individual cohorts. This conspicuous difference leads to the different numerators of the two transfer functions (see Table 1). In the presence of stochasticity we can therefore expect any individual cohort to vary mildly around the equilibrium. The stock, in contrast, will exhibit apparent long-term trends. Because the low-frequency variation is associated with 'echoing' of the stochasticity by the age-structured interactions, we dub this the 'cohort resonance' effect. We note that similar effects also appear in models of biomass except that the weights, P_k, then represent the proportion of the stock biomass rather than numbers.

One way to intuit about the cohort resonance effect is to consider the temporal signature of the stochastic reproduction on the stock and on individual cohorts. Obviously, the effects on the young-of-the-year is instantaneous, that of the 1-year-old will be with a 1-year time lag, etc. A good way to visualize this signature is to consider the covariance between the stochastic reproduction and abundances as a function of time lag. We calculated these covariances according to Priestley (1981: ch. 3·5). For individual age-classes, this function has a spike at the appropriate lag (i.e. lag 0 for the young-of-the-year, x_0) and will be zero for all other lags. For the stock, in contrast, the effect is distributed across several time lags (Fig. 2d).

DENSITY-DEPENDENT SURVIVAL

The life cycle of the Skagerrak cod motivates the following age-structured model (Bjørnstad *et al*. 1999a; Stenseth *et al*. 1999; Fromentin *et al*. 2001):

$$N_{0,t} = \zeta_t S_t \qquad \text{eqn 12}$$

$$N_{1,t} = N_{0,t-1} e^{-\beta v(N_{0,t-1})} e^{-\gamma w(N_{1,t-1})} \qquad \text{eqn 13}$$

$$N_{j,t} = \lambda_S N_{j-1,t-1} \quad j = 2, \dots, d \qquad \text{eqn 14}$$

$$S_t = N_2 + \dots + N_d.$$

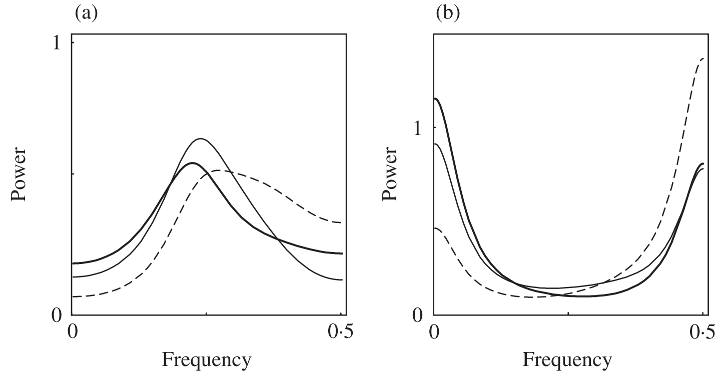

Fig. 3. The normalized power spectra of the model (eqn 12) in the parameter range resulting in (a) asymptotically stable overcompensation cycle (parameters $\beta = 1{\cdot}6$, $\gamma = 0{\cdot}4$, $\lambda = 0{\cdot}4$) and (b) (asymptotically stable) single-generation cycle (parameters $\beta = 0{\cdot}4$, $\gamma = 0{\cdot}3$, $\lambda = 0{\cdot}4$). The former represents a two-generation cycle. Full line represents the young-of-the-year, the dashed line represents age 1, and bold lines represents the stock. The peak in power at high frequency represents the cycle. Note also the peak in the low-frequency end of the spectrum of (b).

The strictly positive functions $v()$ and $w()$ determine the functional forms of how competition (within-cohort interactions) and cannibalism (between-cohort interactions), respectively, affect survival. The parameters β and γ measure the strength of these respective processes. The parameter λ_S represents the annual survivorship of mature individuals (around 0·4 in the Skagerrak cod populations; Julliard *et al.* 2001). The maximum life span, d, appears to be around 5–6 years (less than 3% of the stock are older than 5 years). As in the case of density-dependent fecundity, we focus on the results pertaining to finite life spans but also present the mathematics for the limit as $d \to \infty$. Empirical studies indicate that the density-dependence in survival is approximately log-linear [i.e. $v(N_0) = \log(N_0)$ and $w(N_1) = \log(N_1)$; Bjørnstad *et al.* 1999b]. The skeleton (i.e. the deterministic analogue) of the model (eqns 12–13) (Table 1) with only one adult cohort is discussed by Nisbet & Onyiah (1994). [However, in their detailed study, density-dependence was assumed of be of the Ricker form (i.e. $v(N_0) = N_0$ and $w(N_1) = N_1$)] This model can, in addition to the overcompensation (two-generation) cycles seen in the presence of density-dependent fecundity, also exhibit single-generation cycles when intercohort interactions are strong.

The transfer functions associated with the life cycle (eqns 12–13) (Table 1) are shown in Fig. 3. In addition to the cycles, the young-of-the-year and the spawning stock are predicted to show low-frequency fluctuations for certain parameter values (Fig. 3b). The delay-coordinate representation for the first age class (see equations) is:

$$x_{1,t} = \underbrace{\underbrace{c - \gamma x_{1,t-1}}_{\text{cannibalism}} + \underbrace{(1-\beta)\sum_{k=2}^{d} P_k x_{1,t-k}}_{\text{competition}}}_{\text{delayed regulation}} + \alpha_t. \qquad \text{eqn 15}$$

The variable α_t is, again, deviation of $\log \zeta_t$ from its expectation (see Appendix A).

The corresponding equations for the age-zero cohort and the spawning stock take an analogous form to eqn 15 except for the stochastic component:

$$x_{0,t} = \underbrace{c - \gamma x_{0,t-1} + (1-\beta)\sum_{k=2}^{d} P_k x_{0,t-k}}_{\text{delayed regulation}} + \underbrace{\alpha_t + \gamma\alpha_{t-1}}_{\text{distributed noise}}, \qquad \text{eqn 16}$$

and

$$s_{0,t} = \underbrace{c + (1-\beta)\sum_{k=2}^{d} P_k s_{0,t-k}}_{\text{delayed regulation}} + \underbrace{(1-\beta)\sum_{k=2}^{d} P_k \alpha_{t-k}}_{\text{distributed noise}}, \qquad \text{eqn 17}$$

respectively. Comparing eqns 16 and 17 to eqn 15, the low-frequency variability (Fig. 3) can be seen to be due to the way the stochastic forcing, α_1, is echoed through the life cycle by the intercohort interaction, γ. The stochastic forcing is echoed further in a distributed fashion across the stock, to induce additional red-shifting (cf. Fig. 2d).

Discussion

COHORT RESONANT EFFECTS

Our analysis of two models explores the interplay between stochastic reproduction and density-dependent survival and fecundity as mediated by intra- and inter-cohort interactions. We show that apparent trends can arise when the stochastic recruitment is echoed by the life cycle either through being distributed across multiple adult cohorts or through being echoed through intercohort interactions. In both cases, this phenomenon emerges because at least one age-class is interacting with more than one other age-class. In analyses of numerous other life cycles, we have found that cohort resonant effects can induce low-frequency fluctuations in groups of cohorts and/or individual cohorts in any life cycle except for the simplest non-interactive and semelparous one (unpublished results). Such low-frequency fluctuations correspond to apparent trends that can potentially mimic critical variation in abundance linked to environmental change, over-exploitation or other types of anthropogenic forcing. We stress

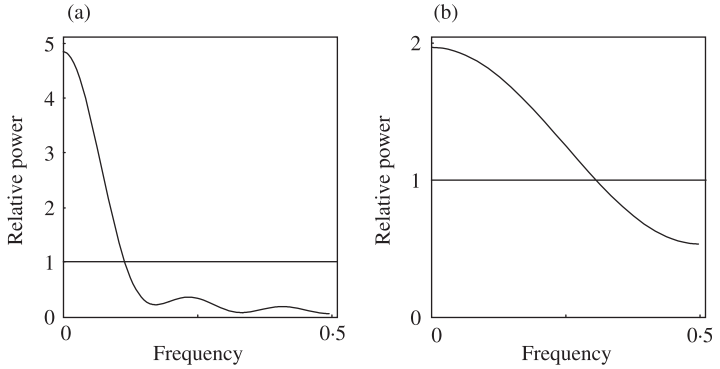

Fig. 4. The relative influence of 'cohort resonance' on amplifying/reducing variation at various frequency. Because cohort resonance induces distributed stochastic forcing, low-frequency variation tends to be enhanced at the expense of high-frequency variation (and thus the induction of apparent 'trends'). The graphs quantify the relative amplification (response > 1) or reduction (< 1) in variation at different frequencies in (a) the long-lived model (with five adult cohorts), and (b) the short-lived model. The *y*-axis represents the spectral power relative to the naive theory ignoring cohort resonance (i.e. assuming density-dependent population growth, but ignoring the echoing of the stochasticity). Parameters are (a) $\lambda_S = 0{\cdot}9$ and (b) $\gamma = 0{\cdot}4$. Relative amplifications are independent of all other parameters (cf. eqn 10 vs. eqn 11 and eqn 16 vs. eqn 15). In both cases the age-structured echoing of the stochastic recruitment greatly enhance the importance of low-frequency relative to high-frequency variability.

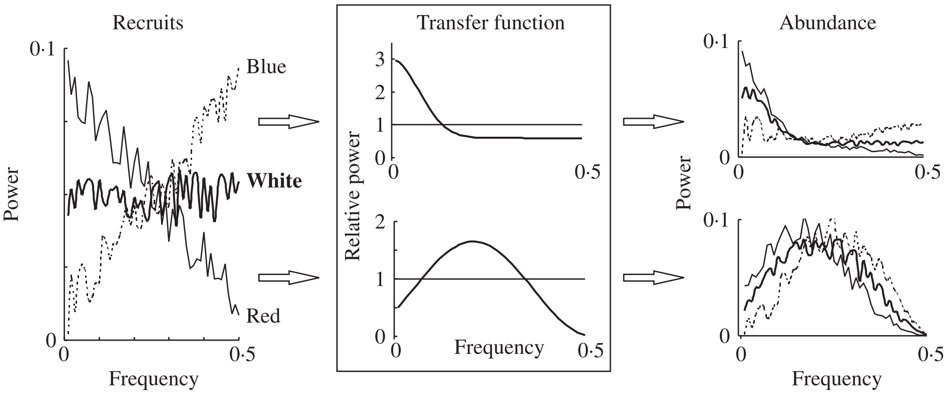

Fig. 5. Environmental stochasticity can rarely be approximated as white noise. The figure depicts how two sample transfer functions filter other types of stochastic forcing. In this case, noise with reddened and blued spectra are used for illustration. With white-noise stochastic forcing, the spectra of abundances takes the shape of the transfer function, for other types of stochastic forcing the amplitudes for the spectra of abundances are enhanced/reduced in proportion to the amplitude of the transfer function at the different frequencies.

that cohort resonance is unrelated to, and should not be confused with, drift in weakly regulated systems with long return times (e.g. Yodzis 1989: ch. 2·4).

In our analyses we made the heuristic assumption that environmental forcing on recruitment constitutes a white-noise (i.e. uncorrelated) process. However, all calculations apply in the case of non-white forcing in that the transfer functions still provide the proportionate amplification/reduction of fluctuations at the various frequencies irrespective of the shape of the spectrum of the environmental forcing (Fig. 5).

Much recent work focuses on the interplay between density-dependent/regulatory and density independent/stochastic processes on shaping the dynamics of populations. The overall consensus is that both regulatory and stochastic forces must be considered to understand the dynamics of real populations (e.g. Turchin 1995; Bjørnstad & Grenfell 2001). Several different facets of this interplay have been described. First, highly nonlinear density dependence may lead to chaotic dynamics that result in rapid amplification of stochasticities (e.g. Ellner & Turchin 1995). Secondly, stochastic disturbance can shift populations from one attractor to another in systems with alternative stable states (e.g. Nisbet & Onyiah 1994). Thirdly, complex noise–determinism interactions can arise in the presence of unstable equilibria ('saddle nodes') or unstable manifolds ('repellors') (Rand & Wilson 1991; Cushing *et al.* 1998). A fourth important effect is that stochastic forcing can induce periodic trajectories in a range of asymptotically stable systems (Nisbet & Gurney 1976, 1982; Stenseth, Bjørnstad & Saitoh 1996; Higgins *et al.* 1997). Most of these effects predict short-term cycles and/or other types of high frequency fluctuations as a result of the noise–determinism interaction.

Cohort resonance in age-structured populations provides a fifth way in which regulatory and stochastic processes interact to shape population dynamics. In contrast to the above effects, cohort resonance leads to low frequency variability. The resultant fluctuations in abundance may appear as apparent trends in all but the longest time series. Intriguingly, in the case of strong intercohort interactions, one mechanism (asymmetric competition/cannibalism between cohorts) results in dual scales of variability – both single-generation cycles and trends – in the presence of stochastic recruitment (Fig. 3; see also Bjørnstad *et al*. 1999a).

Cohort resonance may be of particular interest in fisheries ecology, as aggregate cohorts – the spawning stock biomass (SSB) – are a key variable when assessing the status of a stock (e.g. Hilborn & Walters 1992). Our current theorizing may provide a new method to help distinguishing between mechanisms causing long-term fluctuations in population size. For instance, the literature on long-term fluctuations in bluefin tuna suggests two possible scenarios: (1) variations in recruitment, or (2) changes in migration patterns (Ravier & Fromentin *et al*. 2001). Our models indicate that climatic variability affecting recruitment should provide a delayed and distributed signal between climate and stock size (Fig. 2d). Any synchronous (lag-zero) covariation between climatic forcing and stock size would suggest that behavioural shifts are the more probable cause. In addition, correlational studies between abundance and climate have been fraught previously with complications relating to multiple testing and data dredging. The combination of transfer functions and delay-coordinate models provides a mechanistic way to predict what the relation should look like for a given life cycle. In particular, the delayed and distributed signal may provide an explanation for – and eventually a solution to – the problems of discerning environmental signatures in age-structured dynamics that is discussed by Kaitala & Ranta (2001).

The likelihood of obtaining resonant effects within a natural population imply sufficient stochasticity within the reproduction/recruitment together with intercohort interactions and/or a long adult life span. While the combination of stochastic recruitment and density-dependent demography is documented most fully in marine populations, it will be interesting to see whether other animals that exhibit stochastic age-structured dynamics, such as large mammals (Gaillard, Festa-Bianchet & Yoccoz 1998; Coulson *et al*. 2001), exhibit cohort resonant effects. A critical challenge that arises from our study is to separate apparent trends that are intrinsic to age-structured dynamics from externally driven trends that are of key concern to management and conservation.

Acknowledgements

This work was supported partially by the National Center for Ecological Analysis and Synthesis (a Center funded by NSF grant no. DEB-94–21535, the University of California Santa Barbara, and the State of California) (O.N.B. and R.M.N.), from the European Union (project EU-DGXIV 99/022) (J.M.F.) and from the National Science Foundation (R.M.N.).

References

Akaike, H. (1974) Markovian representation of stochastic processes and its application to the analysis of autoregressive moving average processes. *Annals of the Institute of Statistical Mathematics*, **26**, 363–387.

Aoki, M. & Havenner, A. (1991) State space modeling of multiple time series. *Econometric Reviews*, **10**, 1–59.

Bjørnstad, O.N., Falck, W. & Stenseth, N.C. (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proceedings of the Royal Society of London B*, **262**, 127–133.

Bjørnstad, O.N., Fromentin, J.-M., Stenseth, N.C. & Gjøsæter, J. (1999a) Cycles and trends in cod population. *Proceedings of the National Academy of Sciences USA*, **96**, 5066–5071.

Bjørnstad, O.N., Fromentin, J.-M., Stenseth, N.C. & Gjøsæter, J. (1999b) A new test for density-dependent survival: the case of coastal cod populations. *Ecology*, **80**, 1278–1288.

Bjørnstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–643.

Bjørnstad, O.N., Sait, S.M., Stenseth, N.C., Thompson, D.J. & Begon, M. (2001) Coupling and the impact of specialised enemies on the dimensionality of prey dynamics. *Nature*, **409**, 1001–1006.

Caswell, H. (2000) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA.

Cohen, J.E. (1995) Unexpected dominance of high frequencies in chaotic nonlinear population models. *Nature*, **378**, 610–612.

Costantino, R.F., Cushing, J.M., Dennis, B. & Desharnais, R.A. (1995) Experimentally induced transitions in the dynamic behaviour of insect populations. *Nature*, **375**, 227–230.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather and population crashes in Soay sheep. *Science*, **292**, 1528–1531.

Cushing, D.H. (1990) Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, **26**, 249–293.

Cushing, D.H. (1995) *Population Production and Regulation in the Sea: A Fisheries Perspective*. Cambridge University Press, Cambridge.

Cushing, J.M., Dennis, B., Desharnais, R.A. & Costantino, R.F. (1998) Moving towards an unstable equilibrium: saddle nodes in population systems. *Journal of Animal Ecology*, **67**, 298–306.

Diekmann, O., Nisbet, R.M., Gurney, W.S.C. & Van den Bosch, F. (1986) Simple models of cannibalism: a critique and a new approach. *Mathematical Biosciences*, **78**, 21–46.

Eckert, G.L. (2003) Effects of the planktonic period on marine population fluctuations. *Ecology*, **84**, 372–383.

Ellner, S. & Turchin, P. (1995) Chaos in a noisy world: new methods and evidence from time series analysis. *American Naturalist*, **145**, 343–375.

Fromentin, J.M. & Fonteneau, A. (2001) Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fisheries Research*, **53**, 133–150.

Fromentin, J.-M., Stenseth, N.C., Gjøsæter, J., Bjørnstad, O.N., Falck, W. & Johannesen, T. (1997) Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. *Marine Ecological Progress Series*, **155**, 209–222.

Fromentin, J.-M., Myers, R.A., Bjørnstad, O.N., Stenseth, N.C., Gjøsæter, J. & Christie, H. (2001) Effects of density-dependent and stochastic processes on the regulation of cod populations. *Ecology*, **82**, 567–579.

Fromentin, J.-M., Stenseth, N.C., Gjøsæter, J., Johannesen, T. & Planque, B. (1998) Long-term fluctuations in cod and pollack along the Norwegian Skagerrak coast. *Marine Ecological Progress Series*, **162**, 265–278.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Gurney, W.S.C. & Nisbet, R.M. (1980) Age-dependent population dynamics in static and variable environments. *Theoretical Population Biology*, **17**, 321–344.

Gurney, W.S.C., Nisbet, R.M. & Lawton, J.H. (1983) The systematic formulation of tractable single-species population models incorporating age structure. *Journal of Animal Ecology*, **52**, 479–495.

Hastings, A. & Costantino, R.F. (1991) Oscillations in population numbers – age-dependent cannibalism. *Journal of Animal Ecology*, **60**, 471–482.

Higgins, K., Hastings, A., Sarvela, J.N. & Botsford, L.W. (1997) Stochastic dynamics and deterministic skeletons: population behaviour of Dungeness crab. *Science*, **276**, 1431–1435.

Hilborn, R. & Walters, C. (1992) *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*. Chapman & Hall, London.

Hjort, J. (1926) Fluctuations in the year classes of important food fishes. *Journal du Conseil International Pour l'Exploration de la Mer*, **1**, 5–38.

Horwood, J.W. (1983) A general linear-theory for the variance of the yield from fish stocks. *Mathematical Biosciences*, **64**, 203–225.

ICCAT (1997) 1996 SCRS detailed report on bluefin tuna. *ICCAT Scientific Papers*, **46**, 1–301.

Ives, A.R., Gross, K. & Klug, J.L. (1999) Stability and variability in competitive communities. *Science*, **286**, 542–544.

Julliard, R., Stenseth, N.C., Gjøsaeter, J., Lekve, K., Fromentin, J.-M. & Danielssen, D.K. (2001) Age-specific survival of Atlantic cod (*Gadus morhua* L.) along the Norwegian Skagerrak coast: natural and fishing mortality. *Ecological Applications*, **11**, 540–558.

Kaitala, V. & Ranta, E. (2001) Is the impact of environmental noise visible in the dynamics of age-structured populations? *Proceedings of the Royal Society of London Series B*, **268**, 1769–1774.

Kooperberg, C., Stone, C.J. & Truong, Y.K. (1995) Logspline estimation of a possibly mixed spectral distribution. *Journal of Time Series Analysis*, **16**, 359–388.

Lande, R. (1998) Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos*, **83**, 353–358.

Lomb, N.R. (1976) Least-squares frequency analysis of unequally spaced data. *Astrophysics and Space Science*, **39**, 447–462.

Mather, F.J., Mason, J.M. Jr & Jones, A. (1995) *Historical Document: Life History and Fisheries of Atlantic Bluefin Tuna*. NOAA Tech Memorandum. NMFS, Miami, FL.

Mertz, C. & Myers, R.A. (1996) An augumented Clark model for stability of populations. *Mathematical Biosciences*, **131**, 157–171.

Nisbet, R.M. & Gurney, W.S.C. (1976) A simple mechanism for population cycles. *Nature*, **263**, 319–320.

Nisbet, R.M. & Gurney, W.S.C. (1982) *Modelling Fluctuating Populations*. Wiley, Chichester.

Nisbet, R.M. & Onyiah, L.C. (1994) Population dynamic consequences of competition within and between age classes. *Journal of Mathematical Biology*, **32**, 329–344.

Nisbet, R.M., Gurney, W.S.C. & Pettipher, M.A. (1977) An evaluation of linear models of population fluctuations. *Journal of Theoretical Biology*, **68**, 143–160.

Oster, G. & Takahash, Y. (1974) Models for age-specific interactions in a periodic environment. *Ecological Monographs*, **44**, 483–501.

Pascual, M. & Mazzega, P. (2003) Quasicycles revisited: apparent sensitivity to initial conditions. *Theoretical Population Biology*, **64**, 385–395.

Priestley, M.B. (1981) Spectral analysis and time series. Academic Press, London.

Rand, D.A. & Wilson, H.B. (1991) Chaotic stochasticity: a ubiquitous source of unpredictability in epidemics. *Proceedings of the Royal Society of London Series B*, **246**, 179–184.

Ravier, C. & Fromentin, J.-M. (2001) Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. *ICES Journal of Marine Science*, **58**, 1299–1317.

Ricker, W.E. (1954) Stock and recruitment. *Journal of Fishery Research Board Canada*, **11**, 559–623.

Ripa, J., Lundberg, P. & Kaitala, V. (1998) A general theory of environmental noise in ecological food webs. *American Naturalist*, **151**, 256–263.

Ripa, J. & Ives, A.R. (2003) Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology*, **64**, 369–384.

Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London.

Stenseth, N.C., Bjørnstad, O.N., Falck, W., Fromentin, J.-M., Gjøsæter, J. & Gray, J.S. (1999) Dynamics of coastal cod populations: intra- and intercohort density-dependence and stochastic processes. *Proceedings of the Royal Society of London Series B*, **266**, 1645–1654.

Stenseth, N.C., Bjørnstad, O.N. & Saitoh, T. (1996) A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of the Royal Society of London Series B*, **263**, 1117–1126.

Tuljapurkar, S. (1990) *Population Dynamics in Variable Environments*. Springer, New York.

Turchin, P. (1995) Population regulation: old arguments and a new synthesis. *Population Dynamics* (eds N. Cappuccino & P. Price), pp. 19–39. Academic Press, New York.

Wooster, W.S. & Bailey, K.M. (1989) Recruitment of marine fishes revisited. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **108**, 153–159.

Wootton, R.J. (1990) *Ecology of Teleost Fishes*. Chapman & Hall, London.

Yodzis, P. (1989) *Introduction to Theoretical Ecology*. Harper & Row, New York.

Received 23 November 2003; accepted 22 April 2004

Appendix A

LINEARIZING IN LOG-ABUNDANCES

Consider a seasonally reproducing fish governed by age-structured dynamics (such as illustrated by our two case studies) and stochastic per capita reproductive rates. Let the vector $\mathbf{N}_t = (N_{0,t}, \ldots, N_{d,t})^T$ denote the abundances of the 0*th* through to the d*th* age class, ^{T} denotes matrix transpose. Reproduction and survival may depend on density (of all or some of the cohorts) and the stochastic forces, ζ. Thus, the age-structured system can generally be written as:

$$N_{j,t} = \Phi_j(\mathbf{N}_{t-1}, \zeta_t), \qquad \text{eqn A1}$$

where Φ_j is the function summarizing the density-dependent and density-independent influences on age-class j. On a logarithmic scale, eqn Al is:

$$\log \Phi_j(\mathbf{N_{t-1}}, \zeta_t) = \theta_j(\log \mathbf{N_{t-1}}, \log \zeta_t), \qquad \text{eqn A2}$$

where θ_j are the functions $\log \Phi_j$ recast in terms of log-abundances and log-stochasticity. To develop the transfer functions (eqn 4), we linearize (e.g. Nisbet & Gurney 1982) the log-system (eqn A2) around the equilibrium $\log \mathbf{N}^* = (\log N_0^*, \dots, \log N_d^*)$, taken at the expected value of $\log \zeta$. The linearized system is then:

$$\mathbf{x}_t = \mathbf{J}\mathbf{x}_{t-1} + \mathbf{A}\alpha_t \qquad \text{eqn A3}$$

where $\mathbf{x_t} = \log \mathbf{N_t} - \log \mathbf{N}^*$ and $\alpha_t = \log \zeta_t - \log \zeta^*$. Assuming log-normal recruitment, α_t will be a sequence of zero-mean normal variates (that need not necessarily be independent). The matrix $\mathbf{J}$ is the Jacobian matrix with elements:

$$J_{jk} = \frac{\partial \theta_j(\log \mathbf{N}^*, \log \zeta^*)}{\partial \log N_k}, \qquad \text{eqn A4}$$

and the vector $\mathbf{A}$ is the partial derivative with respect to the stochasticity. The vector elements are thus:

$$A_j = \frac{\partial \theta_j(\log \mathbf{N}^*, \log \zeta^*)}{\partial \log \zeta}, \qquad \text{eqn A5}$$

Appendix B

TRANSFER FUNCTIONS

We obtain the general transfer function eqns 4 and 5 through Fourier transforming and rearranging eqn A3. Denoting Fourier transforms with tilde, the transformed equation is:

$$\tilde{x}(f) = \mathbf{J}\tilde{x}(f)e^{-2\pi\iota f} + \mathbf{A}\tilde{\alpha}(f), \qquad \text{eqn B1}$$

which upon rearranging becomes:

$$\tilde{x}(f) = (\mathbf{I} - e^{-2\pi\iota f}\mathbf{J})^{-1}\mathbf{A}\tilde{\alpha}(f), \qquad \text{eqn B2}$$

where $\mathbf{I}$ is the identity matrix, and ι is the complex constant.