



Transient population dynamics and viable stage or age distributions for effective conservation and recovery

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ABSTRACT

Threshold population sizes are often used to determine the status of depleted populations. The thresholds are typically derived assuming the population is in a steady state. However, although a population may be at the threshold level, the stage or age distribution could be far from the steady state, which may induce transient dynamics. As a result, one may erroneously conclude the status of the population as 'safe' when it is not, or vice versa, using such a threshold population size. Here, we describe the metrics called extinction effective population (EEP) and scaled spawning age (SSA). These are used in addition to population sizes for assessing the population status, as they account for the deviations from the stable stage or age distribution. Using these metrics, we demonstrate the importance of incorporating the transient stage or age distributions in population management.

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1. Introduction

Conservation biologists and fisheries managers are tasked with the same goal: ensuring the recovery of depleted populations to some specified level. Under the Endangered Species Act of 1973 of the United States, organisms that experience a threat of extinction from human activities are categorized into threatened and endangered status. One of the population threshold criteria is the minimum viable population (MVP), which is the minimum size above which the risk of extinction within a specified timeframe is greatly reduced. Many conservation biologists have constructed demographic models for stage structured populations to determine which stages should be the focus of recovery efforts to increase the chance of a population reaching the MVP. This approach typically involves perturbing stage-specific parameters and measuring the resulting change in the long-term (asymptotic) growth rate (Caswell, 2001; Morris and Doak, 2002), and has been done for numerous species, including loggerhead sea turtles (*Caretta caretta*; Crouse et al., 1987), cheetahs, (*Acinonyx jubatus*; Crooks et al., 1998; Lubben et al., 2008), and various plant species (e.g. Oostermeijer et al., 1996; Jongejans et al., 2008).

For overfished populations in the US, managers are mandated by the Sustainable Fisheries Act of 1996 to rebuild the populations to a specified level as quickly as possible (Safina et al., 2005). While it is often debated whether the cause of the depletion was overfishing, other human activities, or natural environmental factors, the policy implications remain the same: to reduce harvest rates to allow for rebuilding (Rosenberg, 2003). Although the rebuilding threshold may vary slightly among fisheries management councils, the goal is to rebuild the population biomass to a size where the largest harvest can be sustainably removed (Swasey and Rosenberg, 2006). In both cases (MVP and the rebuilding threshold), the threshold is usually a population size, with little consideration of how that number may be distributed among stage or age classes.

Recently, the importance of transient dynamics in the study of populations has been recognized (Hastings, 2001, 2004; Haridas and Tuljapurkar, 2007; Wright, 2008). In the context of conservation biology or fisheries management, transients may lead us to misinterpret the dynamics of a system and conclude that a population has reached a size at which it can be considered safe when in fact it is not. More particularly, stage or age distributions that differ considerably from those in the steady state can induce transient behavior. Koons et al. (2005) modeled the impact that deviations from the stable stage distribution have on the short-term (transient) growth rates for different species, and found that growth rates either decreased or increased with larger deviations, depending on whether older life stages senesce or not,

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respectively. Thus, even if the size of a population is 'big enough', if the distribution across stages or ages is far from the steady state, one may draw the wrong conclusions about the status of the population. This point may seem obvious, but clearly begs the question: how does one know if the distribution is close enough so that one can consider the population relatively safe? How does one assess the implications of a deviation from the stable stage or age distribution?

Here, we illustrate the procedures that can be used to answer this question. As in other questions of conservation (e.g. Mangel, 1998, 2000a,b,c), we emphasize that the answer to the question 'is this population big enough?' is neither 'yes or no,' nor is it a particular size, but rather a procedure that if followed will provide insight concerning the question. We use two examples. The first concerns the extinction risk assessment of endangered populations. The classification of species as threatened or endangered requires consistent assessments of their extinction risks across sub-populations. This necessitates the consideration of differences in stage and age distributions and how these differences may induce transient dynamics. Although each individual in a population contributes to reducing the extinction risk, the contribution differs depending on the life stage and/or age of the individuals. For example, individuals in a mature stage can contribute to their population by reproducing immediately, while those in a juvenile stage must survive until they mature before they can start reproducing. Even within mature stages, there may be differences in reproductive success. Younger mothers may have lower reproductive success due to their inexperience, while older mothers may have less success due to senescence (e.g. Ramsay and Stirling, 1988; Huber et al., 1991). Thus, if the stage or age distribution differs from stable state, their extinction risk is also likely to be different from that for the stable state. Unfortunately, the risk assessments of endangered species usually ignore such deviations in stage and age distributions. For example, in the risk assessment of endangered Pacific salmon, the age distributions of mature individuals are often assumed to be stable (e.g. Allendorf et al., 1997; McClure et al., 2003; Good et al., 2005, 2007). To account for the transient stage or age distributions and to demonstrate its importance in extinction risk assessments, we use the extinction effective population (EEP) index. The EEP index was first introduced (Fujiwara, 2007) to account for the differences in life history strategies among populations when assessing their extinction risks from demographic stochasticity, but it can also be used to account for the deviations from the stable stage or age distribution. Here, the index is applied to Pacific salmonids (*Onchorhynchus* spp.) under various stage distributions. Many Pacific salmonid populations are currently considered threatened or endangered (Nehlsen, 1994).

The second example concerns the declaration that an overfished population has been rebuilt. A population is considered rebuilt or recovered when the biomass (or spawning biomass) crosses some specified threshold (usually associated with the spawning biomass that generates maximum sustainable yield, see Mangel (2006)). In general, recruitment fluctuates greatly in many fish populations due to environmental stochasticity, and strong recruitment events in particular years will likely result in an increase in population biomass as the recruited cohorts grow and mature (the magnitude of the increase will depend on a variety of density-dependent factors such as food and habitat availability, and also fishing pressure; Jennings et al., 2001). The population may cross the rebuilding threshold as the result of a single or a few strong year classes, and thus the recovered population will have an age distribution that is skewed relative to the stable age distribution (SAD). However, the cohorts will ultimately move out of the population, depending on the longevity of the species, and if no additional strong recruitment events occur during this time period, the biomass of the population will decline. We introduce the metric of

scaled spawning age (SSA) to demonstrate the impact that a skewed age distribution may have on the long-term recovery of a population, and provide examples of populations that were overfished but then recovered with a skewed age distribution.

2. Methods

2.1. The extinction effective population index in stage structured populations

The EEP index is used to evaluate the among-stage differences in individual contributions toward reducing the population extinction risk. Here, a synopsis of the index is described; a more detailed description of the EEP index can be found in Fujiwara (2007).

The EEP index uses the concept of lineage extinction probability $q_{i,\tau}$, which is the probability that all of the descendants from individual i (including itself) alive at time 0 die by time τ . This quantity is the same for all individuals in the same stage at time 0, but usually differs among stages. The lineage extinction probability can be estimated using various methods, but in the present analysis, we used branching process methods (Harris, 1989; Caswell, 2001; Fujiwara, 2007; Haccou et al., 2005), which permits us to calculate $q_{i,\tau}$ analytically.

The individual contribution toward reducing the extinction risk of the population is given by $-\ln(q_{i,\tau})$ (Fujiwara, 2007). By summing over all of the individuals of interest at the initial state, we obtain the EEP index φ_τ :

$$\varphi_\tau = - \sum_k \ln(q_{i,\tau}) \quad (1)$$

When the sum is taken over all individuals in a population, the EEP index is a measure of population viability (Fujiwara, 2007). However, in Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) populations, we can often observe only mature adults; furthermore, the Endangered Species Act focuses on adult numbers (Shea and Mangel, 2001; Shea et al., 2006). Hence, we calculate the EEP index associated with mature individuals only and the resulting index measures the contributions of mature individuals toward reducing the extinction risk of their population.

For Chinook and steelhead, we use the stage structures shown in Fig. 1 (also see Fujiwara, 2007). Both species are similar in that they spawn in freshwater, and migrate to the ocean to grow and mature (i.e. they are anadromous). However, Chinook die after spawning, while steelhead may survive to spawn multiple times (Fig. 1). We model fecundity as a Poisson process, and survival processes as multinomial distributions. For each species, we consider eight scenarios that differ in the distributions of individuals among stages, but with the same total number of mature individuals (100). For illustrative calculations, we assume that 100 mature individuals distributed according to the stable stage distribution is the MVP threshold.

2.2. Transient age distributions and rebuilding fisheries

To consider the impact that a skewed age distribution may have on the long-term recovery of a population (defined as remaining above the specified recovery threshold) we use a standard age-structured model (Quinn and Deriso, 1999; Haddon, 2001; Ralston and O'Farrell, 2008). We use a generic model for the population characterized by the parameters shown in Table 1; with appropriate changes in parameter values, the model can be applied to a wide range of species. The number of individuals reaching a given age a at time $t + 1$, $N_a(t + 1)$, is a function of recruitment (assumed to occur at age 1) at time $t + 1$, $R(t + 1)$, instantaneous rates of natural and fishing mortality, M and F , respectively, and age-specific

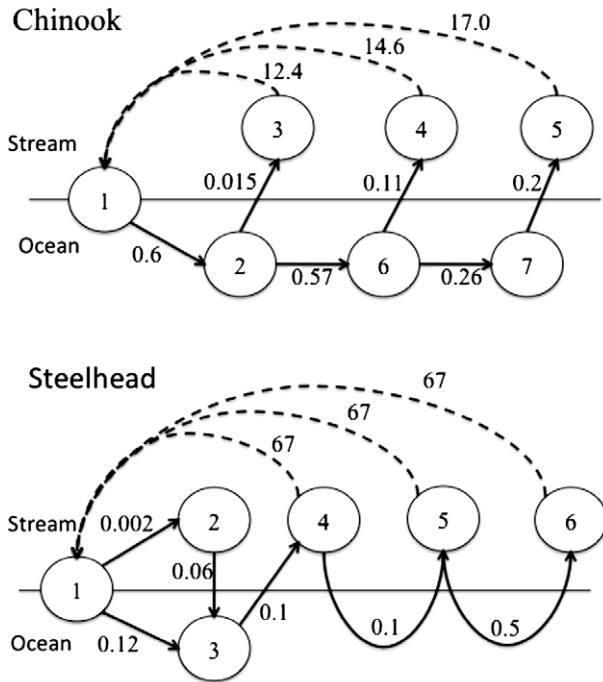


Fig. 1. Stage structures of Chinook salmon and Steelhead. The horizontal line represents the boundary between the stream and ocean habitats. The numbers inside the circles indicate different stages, solid arrows indicate potential transitions of individuals among stages from 1 year to the next, and dashed arrows indicate reproduction and survival of offspring until stage 1. Survival probabilities and expected number of offspring (eggs produced × survival to stage 1) are also shown. Chinook salmon parameters are taken from Greene and Beechie (2004). Steelhead parameters are taken from Shapovalov and Taft (1954) and Quinn (2005). The survival probabilities of juveniles were adjusted so that the asymptotic population growth rate, λ , is 1.0. Juvenile Chinook (stage 1) migrate to the ocean in the year they were spawned where they may remain as immature individuals for one, two, or three years (stages 2, 6, 7, respectively) before returning to freshwater to spawn (stages 3, 4, and 5). Note that after spawning, Chinook salmon die. Steelhead juveniles in freshwater may migrate to the ocean the year they were spawned (stage 1), or may remain in freshwater for another year (stage 2) before migrating to the ocean (stage 3). Steelhead then return to freshwater to spawn (stage 4), but unlike Chinook, they may survive the spawning and reproduce again (stages 5 and 6).

Table 1
Age-dependent population parameters, where s_a , m_a , and w_a , are fishery selectivity, proportion mature and weight-at-age, respectively. With appropriate modification of life history parameters, this model can be applied to a wide variety of species.

| Age (year) | s_a | m_a | w_a (kg) |
|------------|-------|-------|------------|
| 1 | 0 | 0.04 | 0.26 |
| 2 | 0.01 | 0.38 | 0.86 |
| 3 | 0.29 | 0.89 | 1.81 |
| 4 | 0.99 | 0.99 | 2.34 |
| 5 | 1 | 1 | 3.31 |
| 6 | 1 | 1 | 4.66 |
| 7 | 1 | 1 | 7.92 |
| 8 | 1 | 1 | 10.89 |
| 9 | 1 | 1 | 14.25 |
| 10 | 1 | 1 | 16.2 |
| 11 | 1 | 1 | 17.47 |

selectivity, s_a (the fraction of individuals in an age class that are subject to harvesting):

$$N_a(t+1) = \begin{cases} R(t+1) & a = 1 \\ N_{a-1}(t)e^{-(M+s_a F)} & 1 < a < 11 \\ N_{11}(t)e^{-(M+s_{11} F)} + N_{10}(t)e^{-(M+s_{10} F)} & a = 11+ \end{cases} \quad (2)$$

where $a = 11+$ corresponds to all individuals age 11 or older.

Recruitment (individuals per year) is assumed to depend on spawner biomass (S), and is density-dependent. We use the Beverton–Holt spawner–recruit relationship (Beverton and Holt, 1957; Mangel, 2006):

$$R(t+1) = \frac{\alpha S(t)}{\beta + S(t)} e^{\epsilon - 0.5\sigma^2} \quad (3)$$

where α/β is the maximum reproductive output per unit spawning biomass in the absence of recruitment fluctuations, β is the spawning biomass at which half of this value is reached, again assuming no fluctuations, and $\epsilon \sim N(0, \sigma)$. We examine the impact that recruitment variability may have by exploring three values of σ (0.2, 0.5, and 0.8).

If m_a denotes the probability that an individual is mature at age a and w_a its weight at age a , then

$$S(t) = \sum_{a=1}^{11} N_a m_a w_a \quad (4)$$

In the absence of fluctuations in recruitment, the solution of Eqs. (2) and (3) leads to a stable age distribution (SAD) in which the fraction of individuals in each age class is constant in time.

The standard management reference points for this population are the fishing mortality F_{MSY} that generates maximum sustainable yield (MSY) and the spawning biomass that produces MSY, S_{MSY} , when $F = F_{MSY}$. We estimate them deterministically using the methods outlined in NEFSC (2003). A population is classified as overfished when $S(t)$ falls below some threshold, but the threshold is somewhat arbitrary, and can vary among the different fisheries management councils. Some example overfished thresholds are 50% S_{MSY} , and 25% of the unfished spawner biomass (Swasey and Rosenberg, 2006). We define a population as overfished (and therefore in need of rebuilding under the law; Safina et al., 2005) if $S(t) < 50\% S_{MSY}$, and the stock is rebuilt or recovered if $S(t)$ subsequently exceeds S_{MSY} .

We start the solution of Eq. (2) with a recovered population that has a skewed age distribution. That is, we start the population at $S(0) > S_{MSY}$ ($S(0) = 1.1 \cdot S_{MSY}$), but the fraction of the total spawning biomass that falls into each age class differs from the SAD. There are many ways to estimate how skewed an age distribution is from the SAD (Menning et al., 2007), but it can be easily understood with the metric of scaled spawning age (SSA), χ ,

$$\chi = \sum_{a=1}^{11} a p_a \quad (5)$$

where p_a is the fraction of the total population spawning biomass in age class a . For a population with characteristics shown in Tables 1 and 2, at the SAD, $\chi = 6.5$, so $\chi < 6.5$ means that the age distribution is left-skewed with more young spawners, and $\chi > 6.5$ means that it is right-skewed with more old spawners, even though the population is considered recovered on the basis of biomass alone (Table 2). We project the population for 10 years (estimating χ in year 1) with stochasticity in the spawner–recruit relationship (Eq. (3)), under three levels of annual harvest ($\leq MSY$) and we determine if $S(t)$ falls below S_{MSY} and 50% S_{MSY} within this timeframe. We re-

Table 2
Age-independent population parameters and management reference points, where, M is the rate of natural mortality, and α and β are parameters from the Beverton–Holt stock–recruitment relationship, and S_{MSY} and F_{MSY} are the spawning biomass (mt) and fishing mortality rate that produce maximum sustainable yield (MSY; mt).

| Parameter | Value | Reference point | Value |
|-----------|--------|-----------------|---------|
| M | 0.2 | MSY | 12630.1 |
| α | 10,000 | S_{MSY} | 94008.6 |
| β | 22,000 | F_{MSY} | 0.176 |

peat the process 250,000 times to ensure that a sufficient number of samples result for the range of skewed age distributions, and calculate the probability of dropping below the recovery threshold (S_{MSY}) and overfished threshold ($50\%S_{MSY}$) within 10 years.

3. Results

3.1. The extinction effective population index

The EEP index can be considered as one measure of population size. However, it departs from a standard population size in that the EEP index is the weighted sum of the number of individuals. The weights are specific to each stage class and determined according to individuals' expected contributions toward reducing the population extinction risk. Consequently, even if the numbers of individuals are identical among two or more populations, the EEP indices can be different (Table 3) unless their stage distributions are also identical. In the case of Chinook salmon, fecundity is lowest for individuals in stage 3 and highest for those in stage 5. As a result, stage 3 individuals contribute the least towards the EEP index, while stage 5 individuals contribute the most. In contrast, for steelhead, the expected fecundity of the mature individuals is the same among the three mature stages but the probability of future reproduction and thus the expected number of offspring is different among them. Stage 6 steelhead contribute the least to the EEP index because they have no chance of future reproduction. On the other hand, the individuals in stage 5 contribute more than those in stage 4 because the survival probability from stage 5 to 6 is higher than the survival probability from stage 4 to 5.

The EEP index is proportional to the initial number of individuals. Thus, for example, the EEP can be doubled by doubling the initial number while keeping the same stage distribution (Fujiwara, 2007). Among the eight scenarios for Chinook salmon (Table 3), the EEP index ranges from 26.29 (scenario C1, where 80% of the spawners are stage 3) to 32.76 (C3, where 80% of the spawners are stage 5), with a value of 30.02 for the stable stage distribution (C^*). This range of values for Chinook salmon suggests that we need to have about 17% more in the initial population size under scenario C1 than C^* to have the same viability status under the two scenarios. On the other hand, there can be 6% fewer individuals under scenario C3 than C^* . Similarly, for the steelhead population (Ta-

ble 3), the EEP index ranges from 17.56 (scenario S3; 80% are stage 6) to 23.35 (S2, where 80% are stage 5) with the intermediate value of 20.22 under the stable stage distribution (S^*), suggesting we need to have as much as 33% difference in the initial population size among the eight scenarios. Clearly, the number of individuals alone is not sufficient information to assess the status of a population.

3.2. Transient age distributions and rebuilding fisheries

The impact that a skewed age distribution can have on the long-term recovery of a population is shown in Fig. 2. We show the probability that the population will drop below the recovery threshold and the overfished threshold within a 10-year period for different values of χ . For all levels of annual harvest we explored, the probability of dropping below the recovery target or overfished target was highest for populations that are heavily skewed towards older age classes (Fig. 2A). Furthermore, the greater the harvest allowed post-recovery, the higher the probability of dropping below either the rebuilding or overfished threshold. Changing recruitment variability (σ) also affects the probability of long-term recovery. As recruitment gets more variable, the probability of dropping below the threshold increases for a given value of χ . Changing the selectivity (s_a in Table 1) of the fishery also influences the curves shown in Fig. 2. Increasing s_a (harvesting fish at an

Table 3

The EEP index (φ_{25}) associated with 100 mature Chinook salmon and steelhead. The projection was done over 25 years ($\tau = 25$) and the distributions of individuals among the mature stages (stages 3–5 for Chinook salmon and stages 4–6 for steelhead) were varied among the scenarios. C^* and S^* represent stable stage distributions expected by the deterministic projection matrix and associated EEP indices correspond to the MVP. Note that the EEP can be greater than or less than that of the stable stage distribution.

| Species | Scenarios | Stage distribution | φ_{25} |
|----------------|-----------|--------------------|----------------|
| Chinook salmon | C^* | 0.14, 0.59, 0.27 | 30.02 |
| | C1 | 0.80, 0.10, 0.10 | 26.29 |
| | C2 | 0.10, 0.80, 0.10 | 29.38 |
| | C3 | 0.10, 0.10, 0.80 | 32.76 |
| | C4 | 0.33, 0.33, 0.34 | 29.52 |
| | C5 | 0.45, 0.45, 0.10 | 27.83 |
| | C6 | 0.45, 0.10, 0.45 | 29.52 |
| | C7 | 0.10, 0.45, 0.45 | 31.07 |
| Steelhead | S^* | 0.82, 0.12, 0.06 | 20.22 |
| | S1 | 0.80, 0.10, 0.10 | 19.98 |
| | S2 | 0.10, 0.80, 0.10 | 23.35 |
| | S3 | 0.10, 0.10, 0.80 | 17.56 |
| | S4 | 0.33, 0.33, 0.34 | 20.26 |
| | S5 | 0.45, 0.45, 0.10 | 21.67 |
| | S6 | 0.45, 0.10, 0.45 | 18.77 |
| | S7 | 0.10, 0.45, 0.45 | 20.45 |

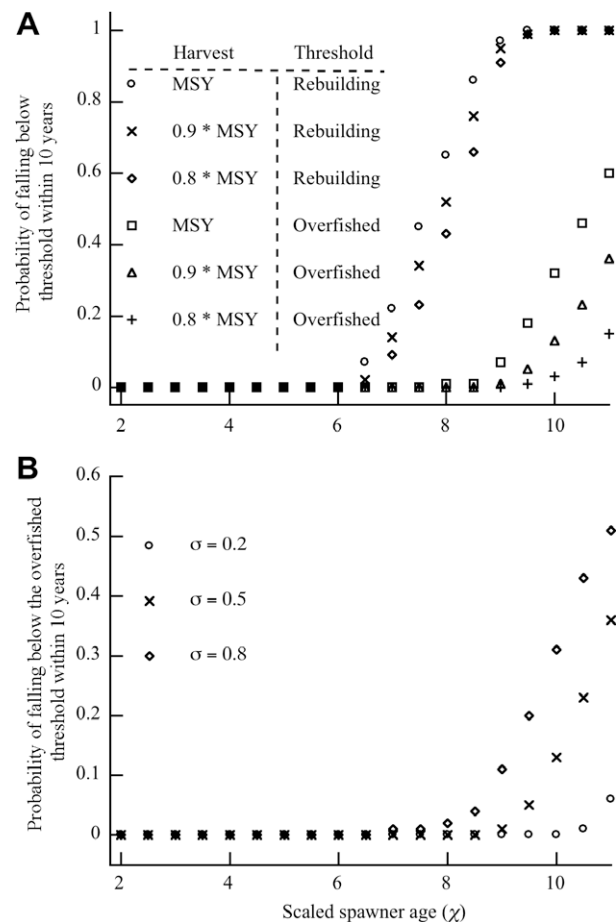


Fig. 2. The effect of different skewed age distributions (χ) on (A) the probability of dropping below the rebuilding threshold and the overfished threshold in a 10-year period for three annual harvest levels (with $\sigma = 0.5$), and (B) how altering recruitment variability (σ) changes the relationship (with 90% MSY removed annually).

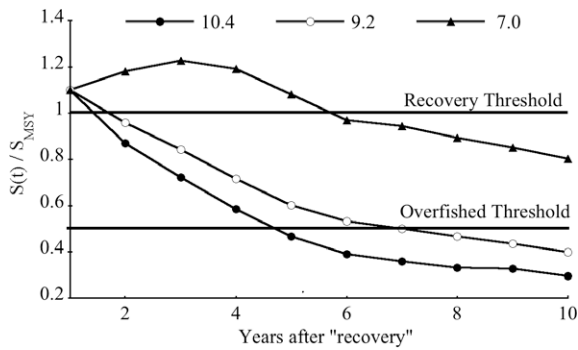


Fig. 3. Sample stock trajectories showing how rapidly a stock that is recovered as a result of a strong year class can decline once that year class moves out of the fishery. These trajectories are all for stocks that are heavily skewed towards older fish ($\chi \geq 7$) at the onset of recovery, with 90% of MSY removed each year for 10 years.

earlier age) will cause the curves to shift to the left, while decreasing s_a will shift the curves to the right.

In many management situations, population status is assessed every 4–5 years, but the trajectories shown in Fig. 3 suggest that things can still go wrong even in a shorter timeframe. These trajectories assume initial age distributions skewed towards older age classes and an annual harvest of 90% of MSY; they show both that a stock can be overfished again within 5 years, and that it may take longer than 5 years for the effects to be apparent (one trajectory does not drop below the rebuilding threshold until after year 5).

4. Discussion

The message of our work is twofold. The first might be considered obvious, once it is clearly stated; for populations that have stage or age differences (that is, for nearly all populations), we must account for the stage or age distribution when determining a recovery threshold. In particular, for populations that are far from the stable stage or age distributions, transient population dynamics are important and may drive total population size below the specified threshold, sometimes very rapidly.

The question is then, what can be done about this observation? The second part of our message is an answer to that question. We have shown that much insight can be gained by using the extinction effective population (EEP) index and augmenting total population biomass by the scaled spawning age (SSA). These metrics allow us to summarize the information content of the size or age distribution into a single value to give a better sense of the short-term consequences of having a population far from its stable distribution.

Currently, most endangered Pacific salmonid populations are managed without considering changes in their stage or age distributions. If the MVP size were estimated for Chinook salmon assuming a stable stage distribution (e.g. scenario C' in Table 3) and a census revealed that the abundance surpassed the MVP level, one might immediately conclude that the population is 'safe'. However, if scenario C1 represented the true distribution for Chinook, then the viability of the population is overestimated. When we overestimate or underestimate the viability status in this way, we can potentially observe a rapid decline or increase, respectively, in population abundance without changing their actual viability status. For example, if mature Chinook salmon abundance is inflated by less-fecund individuals, the population abundance can potentially decline rapidly as the population stabilizes toward the stable stage/age distribution because some of those individuals may be replaced by a smaller number of more-fecund individuals. On the other hand, if the population consists of more-fecund indi-

viduals, then the population abundance can potentially increase rapidly. Therefore, not only population abundance, but also the changes in the abundance can be misleading unless we account for the changes in the stage or age distribution of the population.

The above problem is not limited to the management of Pacific salmonids. For example, Oostermeijer et al. (1994) noted that census surveys for the rare perennial *Gentiana pneumonanthe* typically focused only on flowering adults. However, they found large differences in the population stage structure across sites, with some areas containing mostly seedlings and juveniles (termed an "invasive" population), and other areas containing mostly adult plants with almost no seedling recruitment (termed a "regressive" population; Oostermeijer et al., 1994). Regressive populations had low mortality rates and could persist for decades, so a census ignoring the seedling and juvenile stages (the invasive populations) would likely result in the conclusion that the population is stable, when seedling recruitment may be changing dramatically (either increasing or decreasing). Thus, ignoring the stage structure of a population may increase the chance of erroneous estimations of population status.

Regardless of the species being managed, once corresponding lifecycle models are constructed and associated parameters are estimated (as in Fig. 1), stage abundance data (the number of individuals in different stages) can be converted into the EEP index using Eq. (1). The procedure includes estimating lineage extinction probability either by simulating or using branching process calculation (see Fujiwara (2007) for more detail). The estimated EEP index can be compared to the index under the stable stage assumption to evaluate the importance deviations population stage structure. When the estimated parameters have large uncertainties, sensitivity analysis can be used to assess their implication on the estimated viability status.

A review of rebuilding plans for overfished species in the US shows that after a decade since the passing of Sustainable Fisheries Act, only three out of 67 populations have been rebuilt (Rosenberg et al., 2006). One of the populations considered 'rebuilt' by Rosenberg et al. (2006) was Pacific hake (*Merluccius productus*), a valuable species found off the western US and Canada (Helsler, 2002). The population was assessed in 2002, and it was determined to be overfished and in need of rebuilding (Helsler, 2002). In 1999 there was a very strong recruitment event, and as this year class grew and matured, the spawning biomass increased and surpassed the recovery threshold in 2003 with an age distribution far from the SAD. The spawning biomass has since declined, the result of the 1999 cohort dying out of the population and no further strong recruitment events (Fig. 4). The population is estimated to be at 32% of virgin biomass (95% confidence intervals between 15% and 49%), and may become overfished again (less than 25% of virgin biomass) in the near future if catch limits are not reduced by as much as 50% over the next few years (Hamel and Stewart, 2009). It is important to note that the hake population is declining despite the fact that annual catches have been below the catch limits. Failure to reach the catch limits has been the result of strict limits on the amount of incidental catch of overfished species allowed (Hamel and Stewart, 2009). Had catches reached the levels set in recent years, the Pacific hake population would be lower than it currently is, perhaps even below the overfished threshold.

More recently another commercially important population, Georges Bank haddock (*Melanogrammus aeglefinus*, found in the northwest Atlantic), has recovered. Rebuilding for Georges Bank haddock began in 1994, resulting in a gradual increase in biomass (Swasey and Rosenberg, 2006). Biomass has increased rapidly in recent years, largely the results of the 2003 year-class (estimated to be the largest in the time-series going back to 1931; NEFSC, 2008). Many years later, the 2003 year-class still comprises the majority of the population (Fig. 5). Projections by stock assessment

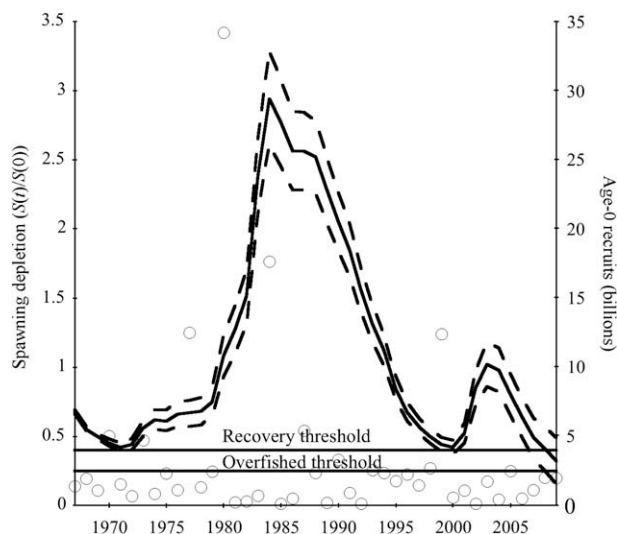


Fig. 4. Depletion (black line) with 95% confidence intervals (CI; dashed lines) and recruitment (circles) with 95% CI of Pacific hake from 1966 to 2007. Depletion is the ratio of spawning biomass at time t ($S(t)$) to the spawning biomass at $t = 0$ ($S(0)$), which in this case is the biomass estimate from 1966. For this particular stock, a depletion level of 0.4 is considered the recovery threshold, and a depletion of 0.25 is the overfished threshold.

scientists take into account the current age-structure when determining sustainable harvest rates for the near future (e.g. MacCall, 2007; NEFSC, 2008), but the politics of fisheries management typically results in catch restrictions being implemented slowly and eased quickly. This phenomenon is known as 'managing to the margins', and is widespread in fisheries management (Rosenberg, 2003). As a result, if catch limits are increased dramatically for Georges Bank haddock, and there are no more large recruitments in the near future, the stock biomass will likely decline as the 2003 year-class moves out of the population.

The model results for the fishery example (Fig. 2) are specific to the model inputs (Eqs. (2)–(4), Tables 1 and 2), and may vary substantially for different populations. For example, we assumed that mortality was constant across all ages, but mortality may be higher for younger fish (Lorenzen and Engberg, 2002), resulting in the curves in Fig. 2 becoming more U-shaped. We also assume that the age composition of the spawning biomass does not impact the resulting recruitment, but this may not be the case for many species. There is evidence that suggests that for some species, maternal effects such as the size or age at spawning may greatly impact recruitment (Murawski et al., 2001; Berkeley et al., 2004; Walsh et al., 2006). Older and larger members of a stock may produce more viable eggs and larvae, potentially resulting in strong recruitment events. Alternatively, smaller, younger fish may produce much less viable eggs and larvae, such that a population that contains mostly young spawners may experience successive recruitment failures. Thus, the results shown may not be applicable to other species, and the approach outlined must be done for individual species to determine the impact that a skewed age distribution will have on the long-term recovery of that species.

In summary, the implication for those interested in effective conservation and management is that when a population is reported to have achieved sustainable size or an exploited population is reported to have recovered, one must ask probing questions about the stage or age distribution of the population, not just about its total size. From those distributions and the metrics we have described, one will be able to assess whether transient population dynamics may be obscuring the true status of managed populations.

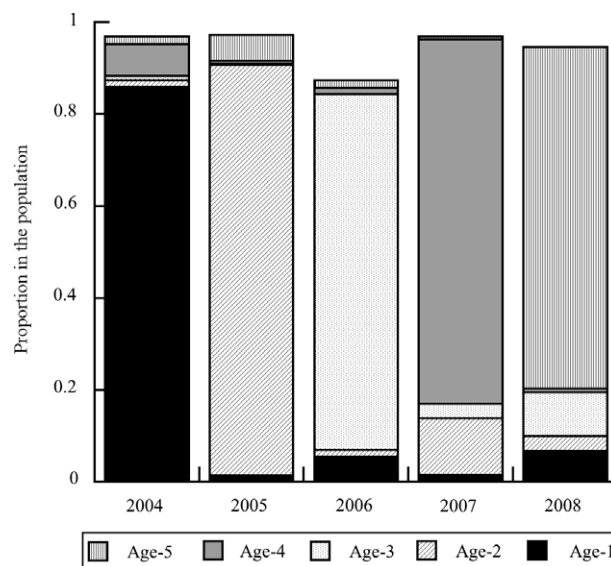


Fig. 5. Proportion of age classes 1–5 in the population of Georges Bank haddock from 2004 to 2008 determined from the numerical estimates of the Northeast Fisheries Science Center annual spring survey (NEFSC, 2008). Values do not sum to 1 because there are other age classes in the population that are not shown for clarity.

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References

- Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatoich, J.A., Nehlsen, W., Trotter, P.C., Williams, T.H., 1997. Prioritizing Pacific salmon stocks for conservation. *Conservation Biology* 11, 140–152.
- Berkeley, S., Chapman, C., Sogard, S., 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85, 1258–1264.
- Beverton, R., Holt, S., 1957. *On the Dynamics of Exploited Fish Populations*. Chapman and Hall, New York.
- Caswell, H., 2001. *Matrix Population Models: Construction Analysis and Interpretation*, second ed. Sinauer, Sunderland.
- Crooks, K.R., Sanjayan, M.A., Doak, D.F., 1998. New insights on cheetah conservation through demographic modeling. *Conservation Biology* 12, 889–895.
- Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68, 1412–1423.
- Fujiwara, M., 2007. Extinction-effective population index: incorporating life-history variations in population viability analysis. *Ecology* 88, 2345–2353.
- Good, T.P., Waples, R.M., Adams, P. (Eds.), 2005. Updated Status of Federally Listed ESUs of West Coast salmon and Steelhead. US Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-66.
- Good, T.P., Beechie, T.J., McElhany, P., McClure, M.M., Ruckelshaus, M.H., 2007. Recovery planning for Endangered Species Act-listed Pacific salmon: using science to inform goals and strategies. *Fisheries* 32, 426–440.
- Greene, C.M., Beechie, T.J., 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 61, 590–602.
- Haccou, P., Jagers, P., Vatutin, V.A., 2005. *Branching Processes Variation Growth and Extinction of Populations*. Cambridge University Press, Cambridge.
- Haddon, M., 2001. *Modeling and Quantitative Methods in Fisheries*. Chapman and Hall, CRC, Boca Raton.
- Hamel, O.S., Stewart, I.J., 2009. Stock Assessment of Pacific Hake, *Merluccius productus* (a.k.a. Whiting) in US and Canadian Waters. Pacific Fishery Management Council, 246 p.

- Haridas, C.V., Tuljapurkar, S., 2007. Time, transients and elasticity. *Ecology Letters* 10, 1143–1153.
- Harris, T.E., 1989. *The Theory of Branching Processes*. Dover Publications, New York.
- Hastings, A., 2001. Transient dynamics and persistence of ecological systems. *Ecology Letters* 4, 215–220.
- Hastings, A., 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* 19, 39–45.
- Helser, T., 2002. A Rebuilding Analysis of the West Coast Pacific Whiting (Hake) Stock. Pacific Fishery Management Council, 14 p.
- Huber, H.R., Rovetta, A.C., Fry, L.A., Johnston, S., 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. *Journal of Mammalogy* 72, 525–534.
- Jennings, S., Kaiser, M.J., Reynolds, J.D., 2001. *Marine Fisheries Ecology*. Blackwell Science, Oxford.
- Jongejans, E., de Vere, N., de Kroon, H., 2008. Demographic vulnerability of the clonal and endangered meadow thistle. *Plant Ecology* 198, 225–240.
- Koons, D.N., Grand, J.B., Zinner, B., Rockwell, R.F., 2005. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling* 185, 283–297.
- Lorenzen, K., Engberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society of London B* 269, 49–54.
- Lubben, J., Tenhumberg, B., Tyre, A., Rebarber, R., 2008. Management recommendations based on projection models: the importance of considering biological limits. *Biological Conservation* 141, 517–523.
- MacCall, A.D., 2007. Bocaccio Rebuilding Analysis for 2007. Pacific Fishery Management Council, 13 p.
- Mangel, M., 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1, 87–90.
- Mangel, M., 2000a. On the fraction of habitat allocated to marine reserves. *Ecology Letters* 3, 15–22.
- Mangel, M., 2000b. Irreducible uncertainties, sustainable fisheries and marine reserves. *Evolutionary Ecology Research* 2, 547–557.
- Mangel, M., 2000c. Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bulletin of Marine Science* 66, 663–674.
- Mangel, M., 2006. *The Theoretical Biologist's Toolbox*. Cambridge University Press, Cambridge and New York.
- McClure, M.M., Holmes, E.E., Sanderson, B.L., Jordan, C.Y., 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. *Ecological Applications* 13, 964–989.
- Menning, K.M., Battles, J.J., Benning, T.L., 2007. Quantifying change in distributions: a new departure index that detects, measures and describes change in distributions from population structures, size-classes and other ordered data. *Oecologia* 154, 75–84. doi:10.1007/s00442-007-0810-3.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Inc., Sunderland, MA.
- Murawski, S., Rago, P., Trippel, E., 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science* 58, 1002–1014.
- Northeast Fisheries Science Center (NEFSC), 2003. Final Report of the Working Group on Re-evaluation of Biological Reference Points for New England Groundfish. NEFSC Reference Document 02-04, 417 p.
- Northeast Fisheries Science Center (NEFSC), 2008. Assessment of 19 Northeast Groundfish Stocks through 2007: Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts, August 4–8, 2008. US Dep Commer, NOAA Fisheries, NEFSC Reference Document 08-15, 884 p.
- Nehlsen, W., 1994. Salmon stocks at risk: beyond 214. *Conservation Biology* 8, 867–869.
- Oostermeijer, J.G.B., Van't Veer, R., Den Nijs, J.C.M., 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in Netherlands. *Journal of Applied Ecology* 31, 428–438.
- Oostermeijer, J.G.B., Brugman, M.L., De Boer, E.R., Den Nijs, H.C.M., 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology* 84, 153–166.
- Quinn, T., 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle.
- Quinn, T., Deriso, R., 1999. *Quantitative Fish Dynamics*. Oxford University Press, Oxford, UK.
- Ralston, S., O'Farrell, M.R., 2008. Spatial variation in fishing intensity and its effect on yield. *Canadian Journal of Fisheries and Aquatic Science* 65, 588–599.
- Ramsay, M.A., Stirling, I., 1988. Reproductive biology of female polar bears (*Ursus maritimus*). *Journal of Zoology* 214, 601–634.
- Rosenberg, A.A., 2003. Managing to the margins: the overexploitation of fisheries. *Frontiers in Ecology and the Environment* 1, 102–106.
- Rosenberg, A.A., Swasey, J.H., Bowman, M., 2006. Rebuilding US fisheries: progress and problems. *Frontiers in Ecology and the Environment* 4, 303–308.
- Safina, C., Rosenberg, A.A., Myers, R.A., Quinn II, T.J., Collie, J.S., 2005. US ocean fish recovery: staying the course. *Science* 309, 707–708.
- Shapovalov, L., Taft, A., 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fish Bulletin 98, 1–373.
- Shea, K., Mangel, M., 2001. Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 58, 375–385.
- Shea, K., Wolf, N., Mangel, M., 2006. Influence of density dependence on the detection of trends in unobserved life-history stages. *Journal of Zoology* 269, 442–450.
- Swasey, J., Rosenberg, A.A., 2006. Phase I Report: An Evaluation of Rebuilding Plans for US Fisheries. Marine Resource Assessment Group. Report Presented to the Lenfest Ocean Program. <<http://www.mragamericas.com/pdf/sr/Rebuilding%20Report%20Phase%20I%20Final.pdf>>.
- Walsh, M.R., Munch, S.B., Chiba, S., Conover, D.O., 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology Letters* 9, 142–148.
- Wright, R.W., 2008. The geometry of transient crashes and their dependence on demographic rates. *Theoretical Population Biology* 73, 300–306.