The potential impact of time-variation in vital rates on fisheries management targets for marine fishes

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ABSTRACT

Fisheries scientists are increasingly concerned about changes in vital rates caused by environmental change and fishing impacts. Demographic parameters representing individual growth, maturity, mortality, and recruitment have previously been documented to change over decadal time scales. However, there has been relatively little comparison regarding which vital rates cause relatively greater or lesser impacts on commonly used fisheries management targets. We therefore use a life table (based on age-structured assessment models) to explore the sensitivity of fishing mortality, spawning biomass, and catch targets to changes in parameters representing growth, mortality, recruitment, and maturation rates for three representative life histories representing long-, medium-, and short-lived species. The elasticity analysis indicates that demographic changes can result in substantial variation in fisheries management targets, but that changes in mortality rates are particularly important for spawning biomass and catch targets while maturity and recruitment compensation are also important for fishing mortality targets. We conclude by discussing the importance of improved data repositories to address covariation among maturity, growth, and mortality parameters.

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1. Introduction

For over a hundred years, marine ecologists and fisheries scientists have recognized that the ocean environment is highly variable on both fine and course spatial and temporal scales (Smith, 2007; Stommel, 1963). Ecologists also generally recognize that life history traits of populations emerge from optimizing fitness given environmental constraints (Stearns, 1976), where life history strategies emerge over evolutionary time (Charnov, 1993; Stearns, 1992) and life history tactics may change on smaller time scales (Rochet, 2000a,b) due to behavioral and inducible phenotypic changes (Clark and Mangel, 2000).

Environmental variability is well documented in marine systems, and is theorized to cause changes in a variety of vital rates, including individual growth, sexual maturation and investment, natural mortality, spatial distribution, and the strength of population regulation due to within- and among-species interactions. Ample evidence exists in the literature that vital rates for populations of fish vary over time, although it is often difficult to attribute a single cause to variation for a given population. For example,

natural mortality, recruitment, maturity, and growth have all been documented to vary significantly over decadal time scales in at least some populations (see Appendix A for representative examples). Variability in these demographic parameters has been documented in marine and freshwater systems in many different ecological systems and using a variety of measurement methods and models. Variability in these vital rates can have different effects on population dynamics, and depends on the life history strategy that a given species adopts (Heppell et al., 2000).

Due to the increasing evidence for time-varying vital rates, there has been recent research regarding the impact of variation in individual demographic rates (e.g., reproductive potential: Brooks, 2013; or adult survival rates: Gerber and Heppell, 2004), and the potential impact of individual causes of demographic variation (e.g., fishery-induced evolution: Rochet, 2000a,b; Heino et al., 2013) on fisheries management. However, there have been few studies quantifying and comparing the relative impact of variation of different vital rates on fisheries management targets of fishes (Frisk et al., 2005; Gerber and Heppell, 2004).

Perturbation analysis is a method to quantify the impact of variation in vital rates on demographic statistics, and is generally understood to have two basic approaches (Caswell, 2000). The first, termed "prospective" analysis, uses well-established demographic theory to answer "what would be the effect on a demographic

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statistic if a particular vital rate changed by X%?" Demographic models used in prospective analyses are generally based on theoretical assumptions about population dynamics and life history theory, so conclusions drawn from sensitivities of demographic statistics are true as long as the demographic model is correct. However, the demographic model used in a prospective analysis might provide a poor approximation to any real-world population, limiting the interpretability of results. Despite this limitation, prospective perturbation analyses are useful for quantifying the impacts of varying vital rates given a specified demographic model.

The second perturbation method, "retrospective" analysis, analyzes historical changes in demographic statistics and their empirical (co)variation with vital rates (Caswell, 2000). One example might be an empirical meta-analysis of changes in early life history and its covariation with observed changes in spawning biomass (Szuwalski et al., 2014). Retrospective analyses can identify historical variation in vital rates and their association with variation in demographic statistics, but are problematic when predicting future changes because future covariation of vital rates and population statistics may not resemble past covariation. Retrospective analysis therefore represents an empirical (meta-analytic) alternative to the theoretical approach used by prospective analysis. In this study, we have chosen to use prospective analysis (i.e., analyzing idealized types of marine fishes using population and life history theory) given that the empirical variation and covariation among demographic traits has not previously been well quantified.

The question of how sensitive population dynamics are to variability in life history traits is particularly relevant to fishery managers. Population models are routinely used to determine biological reference points, which are in turn used in fisheries management control rules to increase or decrease fishery catches (Hilborn and Walters, 1992). Given the role of population models in fisheries management, there is increasing concern about how fish populations may change due to natural and human-caused climate, habitat, and evolutionary changes and how that may affect harvest (Hilborn et al., 2003). Evolutionary changes may be important for some populations (Conover and Munch, 2002; Pinsky and Palumbi, 2014; Ricker, 1981), although the generality of evolutionary impacts remain contested (Hilborn and Minte-Vera, 2008). Environmental changes in the marine environment, whether cyclic or directional, have also been hypothesized to cause changes in productivity for many populations (Dorner et al., 2008). Finally, the impact of habitat alteration can most easily been seen for diadramous species (e.g., Raymond, 1988), but may also exist for marine species, affecting vital rates and hence demographic statistics.

In this study we provide a prospective analysis of demographic changes using a generic life-table model, as is commonly used in fisheries stock assessment, to determine the relative sensitivity of management targets to changes in different vital rates. Elasticities are used to quantify the effect that changes in vital rates would have on fisheries management targets. We also provide a preliminary literature review of model estimates of changes in basic vital rates, including maturity, individual growth, natural mortality, and density-dependent recruitment. In doing so, we seek to determine the relative magnitude of changes in these vital rates over decadal time scales. We therefore identify which vital rates have the greatest potential impact on fisheries management targets, and which are likely to undergo the greatest changes over time.

2. Methods

2.1. Building a demographic model using life history theory

In order to conduct a prospective analysis, we first need to develop a demographic model for fishes that is representative of different life history strategies. The model depends on only three parameters (vital rates): the natural mortality rate occurring at the age at maturity, the asymptotic maximum length, and the degree of recruitment compensation, and all other vital-rate parameters are derived using established life history theory. Given these parameters, the model produces equilibrium behavior under a given fishing pressure, from which management targets are calculated.

We start developing the model by using the following identities to develop a set of life history relationships that are biologically plausible:

1. Growth follows the 'specialized' von Bertalanffy growth function:

$$\frac{dW}{dt} = A \cdot W^{2/3} - B \cdot W \tag{1}$$

where W is weight, A is the rate of energy acquisition (anabolism) and B is the rate of energy expenditure (catabolism). This implies that asymptotic maximum weight W_∞ is:

$$W_\infty^{1/3} = \frac{A}{B} \tag{2}$$

and where the Brody growth coefficient $k = B/3$ and asymptotic maximum length $L_\infty \propto A/B$ (see Charnov et al., 2013; Essington et al., 2001) for details of the derivation).

2. The instantaneous rate of natural mortality $M(w)$ varies as a function of individual weight w:

$$M(w) = \left(\frac{w}{W_\infty}\right)^{-1/2} \cdot \left(\frac{A}{3}\right) \cdot W_\infty^{-1/3} \tag{3}$$

This equation is derived from an empirical meta-analysis of growth and mortality parameters (Gislason et al., 2010) as re-analyzed by Charnov et al. (2013).

3. Age at maturity a_{mat} is a function of individual growth and natural mortality rates:

$$a_{mat} = \frac{1}{k} \log\left(\frac{3k + M}{M}\right) \tag{4}$$

(Williams and Shertzer, 2003 after correcting their Eq. (15)). This expression is obtained from combining two separate derivations for a_{mat} (Beverton, 1992), and results in a similar estimate of length at maturity L_{mat} (calculated from a_{mat} using the von Bertalanffy length-at-age curve; see Table 1 for details) to that derived from the expression $L_{mat} = (2/3)L_\infty$ (Charnov et al., 2013).

4. Weight at age is a function of individual length:

$$W = \theta_1 L^{\theta_2} \tag{5}$$

where $\theta_1 = 0.01$ on average for Fusiform-shaped fishes and we assume $\theta_2 = 3$ (this is a common mathematical convenience, despite Fusiform-shaped fishes having on average $\theta_2 = 3.04$; Froese et al., 2014).

In addition, we make two pragmatic assumptions. First, we assume that:

$$Pr[Mature|a] = \Phi\left(\frac{a - a_{mat}}{0.25 a_{mat}} \times 1.96\right), \tag{6}$$

where $Pr[Mature|a]$ is the probability of maturity for an individual of age a, and Φ is a normal cumulative distribution function. This ad hoc assumption implies that 95% of individuals are mature within ±25% of a_{mat}, and is necessary to ensure that MSY-based targets are relatively smooth (i.e., differentiable) with respect to changes in a_{mat} (as is necessary for subsequent perturbation analysis). Second, we assume that fishes are "born" at a weight $W_0 = 0.1$ g. This assumption replaces any detailed consideration of early life history (i.e., larval survival and growth, Mangel et al., 2010), and