



The relative importance of subpopulation connectivity and the age distribution of mortality in exploited marine fish populations



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ABSTRACT

Exploited marine fish populations are known to exhibit complex spatial dynamics and display age-structured processes, yet many models of these populations do not account for within-population variability in age in conjunction with the spatial distribution of individuals within a stock management area. Our work presents a method of modeling, known as hybrid modeling, which incorporates both continuous-time and discrete-time processes into a single modeling framework. Using this model together with its parameterization, we show that assumptions about the age distribution of mortality affect predictions of spawning population attributes, namely abundance and the proportion of the stock that is mature. However, the precise nature of this effect on whole population scales depends on both the life history characteristics of the species and the level of connectivity between subpopulations. Long-lived and fast-maturing fish are shown to be most sensitive to the age distribution of mortality rates, but this sensitivity decreases as age at maturity increases. Additionally, when connectivity between subpopulations operates in a pseudo source-sink fashion, regardless of life history, abundance of large mature fish is higher and also the proportion of mature fish in the population is greater when the exploitation rate on the source population is higher than that on the pseudo sink population. Lastly, we show that spawning stock attributes are highly sensitive to age-dependence of the fishing mortality rates. This final result reinforces the need for reliable estimates of age-dependent fishing mortality rates in exploited stocks.

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1. Introduction

Fisheries stock assessment models, along with the estimates of survival rates which they produce, are used to determine population size and the level of mortality associated with the harvesting process. Assessment models that are age structured can also estimate the abundance of young fish (recruits) and spawners, thus providing a means to understand the relationship between spawning outputs and subsequent recruitment, the process by which new fish are added to the exploitable fish population. Population size, mortality, and reproduction are then used to predict future yields and help manage the fishery in a sustainable manner (Fournier et al., 1998; Methot and Wetzel, 2013).

Stock assessment scientists, however, face a clear trade-off between relying on either simple assessment models with minimal data requirements, or complex models with high and costly

data requirements. Given these trade-offs, and in light of the difficulty of acquiring robust data in wild fish populations, fishery scientists have generally opted to make simplifying assumptions about the spatial distribution and age structure of marine populations and the fleets that harvest them. Spatially explicit models are typically limited to a few, large areas that are often contiguous with the jurisdictions of the relevant management bodies, and it is assumed that abundance or fishing pressure within these areas is spatially homogeneous. These assumptions are often accompanied with simplifying assumptions about how survival depends on age or size (SEDAR, 2010; Walters and Martell, 2004). Fishing pressure, however, is rarely homogeneous across these large areas, reflecting heterogeneity in the spatial distribution of the targeted species and the socio-economic and regulatory environments that affect the distribution of fishing pressure (Kulka, 2002; Morato et al., 2010; Watson et al., 2007).

In most cases, subpopulation structure of fish and fishing fleets is greatly simplified within accepted management areas. Such compromise may improve management efficiency, but it can lead to a loss of explanatory power in the assessment of the dynamics of marine fish populations if it oversimplifies subpopulation structure. For example, few stock assessment models explicitly

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consider seasonal migration within a management area and thus poorly reflect one of the most obvious dynamics of fish populations. Such pressure to simplify model structure often extends to age-dependent mortality rates as well. Many models assume that natural mortality rates are age-invariant within the management area, most commonly because of the difficulty of estimating natural mortality rates within wild marine populations, let alone to get age or size specific estimates (Mace, 2001; Shepherd and Pope, 2002; Crone et al., 2013).

More complex, and increasingly used, statistical stock assessment models, like MULTIFAN-CL (Fournier et al., 1998) or SS3 (Methot and Wetzel, 2013), define natural mortality rates by age or length. These models are a representation of the belief that natural mortality rates at early ages and small sizes are high and quickly decline as the fish ages and grows (Lorenzen, 2006). These models can also accommodate finer spatial structure than that corresponding to the management area; however, the available data are often too limited to support the increased complexity and associated larger number of parameters that must be estimated. Both MULTIFAN CL and SS3 have hundreds of estimable parameters, and adding spatial complexity to them often multiplies the number of parameters and makes the estimation process considerably more difficult as well as increasing uncertainty around estimates.

Another compromise adopted by many stock assessment models is to assume that the pattern of fishing mortality at age can be modeled with a function known as a fishing selectivity function, often either dome-shaped or asymptotic (Crone et al., 2013). Asymptotic fishing selectivity assumes that fishing pressure is low in young age classes and increases rapidly as the fish ages approaching an asymptotic maximum in the older age classes of the population. A discrete step-function, in which fish are either fully selected or not selected, known as a knife-edge fishing selectivity function, is often substituted for a continuous asymptotic fishing selectivity function in fishery assessment models. Unlike asymptotic fishing selectivity, dome fishing selectivity assumes that fishing pressure has a distinct peak (or peaks) at intermediate age or sizes classes. Dome fishing selectivity is often used to model fish populations that are managed using recreational slot limits such as in the case of the Common Snook, *Centropomus undecimalis* recreational fishery in the Gulf of Mexico (Muller and Taylor, 2013). Dome fishing selectivity is also used in cases where size selective fishing gear, such as gillnets, are utilized or for species that are, for a variety of reasons, in some way unavailable to the fishery over certain age ranges (Crone et al., 2013).

Only a handful of theoretical models have been developed to address the impacts of the presence of subpopulations on population-wide age structure. Most of these models have been applied only to specific species, including South Australian abalone (*Haliotis* sp.) (Sluczanowski, 1984), Atlantic herring (*Clupea harengus*) (Guan et al., 2013), California halibut (*Paralichthys californicus*), kelp bass (*Paralabrax clathratus*), kelp rockfish (*Sebastes atrovirens*), opaleye (*Girella nigricans*), ocean whitefish (*Caulolatilus princeps*), sheephead (*Semicossyphus pulcher*), and red sea urchin (*Strongylocentrotus franciscanus*) (Rassweiler et al., 2012), and each of these studies use a fully discretized approach in which both age and time varying dynamics are considered discrete annual processes. We contend that considerably more work is needed in this field as fish populations continue to decline worldwide, and our understanding of their within-population dynamics remains limited.

The model derived for this work combines a continuous intra-year time-dependent process simulating both movement and mortality with a discrete aging process simulating aging and recruitment, which, for the purposes of our work, is considered to be the process by which age-one fish are added to the population each year. This modeling framework is a pulsed hybrid dynamical systems model (Webb, 1985; Bainov and Simeonov, 1989).

Hybrid models have recently gained traction in mathematical biology and mathematical ecology due to their ability to simulate complex ecological or biological dynamical systems in which there are both discrete and continuous processes acting simultaneously. Recent examples of hybrid model usage include modeling erythropoiesis, the process by which red blood cells are made, (Kurbatova et al., 2011, 2013); neuroelectrical processes (Bressloff and Newby, 2014); cell cycle regulation (Singhanian et al., 2011); and forecasting changes in vegetation distribution (Bartlett, 2012). The model is derived for a system consisting of two subpopulations connected by movement and subject to total mortality, expressed as a combination of both naturally-occurring and fishing-induced mortality rates. A parameterization method follows which allows the model to differentiate between fishing and natural mortality rates and asymptotic and dome fishing selectivity. This parameterization also includes methods of controlling total fishing pressure across simulations, which allows us to test assumptions about the distribution of the fishing pressure across age classes without the introduction or removal of total fishing effort. Lastly, simulations are run for two forms of natural mortality functions, one constant in time and another age-dependent; three movement rates; and two fishing selectivity functions. These sets of simulations are run for four different spawning strategies.

The model utilized for this work is a pulsed hybrid dynamical systems model (also known as a semi-discrete or a semi-continuous model) (Bainov and Simeonov, 1989). These models belong to a class of dynamical systems models in which both discrete-time and continuous-time processes are incorporated into a single modeling framework, with the output from the discrete process “pulsed” into the system at specified times. Hybrid models have recently been used in numerous biological and ecological modeling applications since their original introduction to fishery science by Beverton and Holt (1957), Zhang et al. (2003), Ghosh and Pugliese (2004), Singh and Nisbet (2007) and Pachevsky et al. (2008). Readers interested in better acquainting themselves with this class of models and their applications in biology should consult Mailleret and Lemesle (2009), and those interested in a more rigorous mathematical treatment of hybrid models should consult Webb (1985) and Bainov and Simeonov (1989). The primary benefit of constructing a hybrid model in lieu of a discrete-time model, as is more commonly used in fisheries literature, comes from the hybrid model’s unique ability to incorporate continuous-time within-year movement processes while preserving a discrete year-to-year process. Since we preserve discrete annual time structure, results from our model are more readily comparable to previous work that utilizes a fully discrete modeling frameworks with annual time steps including stock assessment models (Fournier et al., 1998; Methot and Wetzel, 2013).

2. Methods

The model is a composition of a continuous intra-year process expressed by a system of ordinary differential equations composed within a discrete aging and recruitment process. The continuous system simulates mortality and movement processes within the year. The discrete process simulates the aging and recruitment processes among years. The simulated system is composed of two subpopulations of the same species with the same growth parameters, longevity, and maturity schedules. For our purposes, we assume that each parameter has no associated error, thereby, we assume that all processes are deterministic, not stochastic. The subpopulations are denoted by subpopulation *A* and subpopulation *B*, with $N_i(a, t, \tau)$, indexed by $i = A, B$, denoting the abundance of fish in subpopulations *A* and *B*, respectively at age *a* which ranges between 1 and ω (terminal age); within-year time *t*, which ranges between

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