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Detecting the effects of management regime shifts in dynamic environments using multi-population state-space models



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ABSTRACT

Keywords: Coho salmon Management effectiveness Non-stationary Population dynamics Relative reproductive success Detecting the effectiveness of management actions intended to increase the abundance of threatened or exploited species can help resolve uncertainties about cost-effective management tactics. However, the complexity of ecological systems can make it difficult to identify important factors causing change in population abundance. This difficulty extends from detecting naturally-caused ecosystem regime shifts to managementinduced regime shifts and the attendant change in population dynamics parameters. The adult abundance of naturally-produced coho salmon (Oncorhynchus kisutch) on the Oregon Coast generally declined until these fish were listed as threatened under the Endangered Species Act in 1998. The subsequent rebuilding of Oregon coastal coho adult abundance is coincident with increased habitat restoration, reduced hatchery production, and reduced harvest. Importantly, ocean survival also improved, thereby complicating the assessment of management effectiveness at the adult life stage. Our objective was to assess change in the freshwater production of juveniles (smolts) through time in order to determine if recent increases in adult abundance could be related to management affecting the freshwater juvenile production. We combined 46 years of data associated with 18 populations of Oregon coastal coho. Spawner-to-smolt relationships were modeled with Bayesian hierarchical state-space implementations of the logistic hockey stick recruitment function. We also develop a method of estimating the relative reproductive success of hatchery spawners. We found more evidence for decline than increase in productivity in the spawner-to-smolt life stage, suggesting that changes in physical oceanographic conditions are responsible for recent increases in adult abundance. The reproductive success of hatchery-origin fish relative to natural-origin fish was 0.51 with a 95% credible interval from 0.19 to 0.89. While some management effects may unfold on longer time-scales than we observed, we nonetheless contend that carefully tailored models of non-stationary population dynamics are needed to understand and the effectiveness of management actions intended to recover populations.

1. Introduction

The status of fish populations and associated fisheries is a paramount concern that extends from hearty academic debate to uncertainty in management actions affecting the fate of species, local economies, and food security (Szuwalski, 2016). The perceived decline in abundance of fishes around the world has induced change in management actions intended to enhance sustainability (Worm et al., 2009; King et al., 2015). The ability to detect the effects of these management actions on population dynamics is constrained by the simultaneous changes in complex ecological systems, and the models and data used to understand those systems (Lonergan, 2014).

The common assumption that intrinsic population growth rate and the density-dependent crowding effects that give rise to "carrying capacity" (Mallet, 2012) are fixed, stationary values may be useful to parsimoniously describe a time series of observed abundances, but cannot be true over relevant ecological time scales because of change in the abiotic (Kilduff et al., 2015) and biotic (Pinsky et al., 2013) components of nature (Szuwalski et al., 2015). Thus there is a great deal of interest in detecting nonstationary population dynamics caused by these natural "regime shifts" (Vert-pre et al., 2013). We contend that both natural regime shifts and the large-scale management efforts intended to enhance sustainability- "management regime shifts"- can be studied with similar analytical methods. Detecting management regime shifts has received relatively little attention, but is nonetheless an important component of resolving uncertainty in management strategies (Punt et al., 2016).

Oregon coastal coho salmon (*Oncorhynchus kisutch*) provide a good opportunity to apply methods of detecting regime shifts on population dynamics. The adult abundance of naturally produced Oregon coastal

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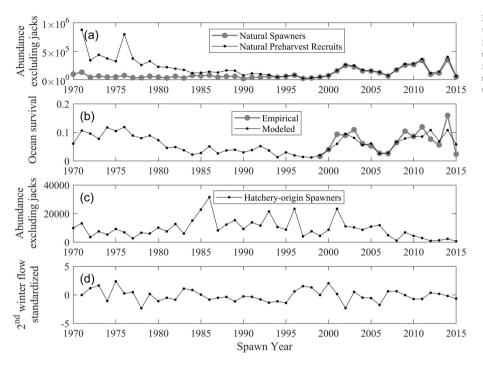


Fig. 1. The abundance of natural-origin adult coho declined until the late 1990s (a), which is coincident with the pattern in ocean survival rate (b), but multiple biologically conservative actions also began in the late 1990s, including reduction in hatchery production (c). Mean second winter stream flow from Nov-March in four sites were standardized (*z*-score) over 1961–2015 and averaged together (d).

coho (O. kisutch) salmon generally declined until they were listed as threatened under the United States federal Endangered Species Act (ESA) in the late 1990s. Following the ESA listing, adult abundance began to increase (Fig. 1a) and reached a 30-year high in 2013. This increase is coincident with two fundamentally different processes. First, fishery-independent survival in the ocean improved (Fig. 1b). Second, several large-scale management changes were implemented leading up to and following the ESA listing. These management changes include: (i) reduction in ocean and freshwater harvest that caused the harvest rate to decline from a maximum of 91% in 1976 to a minimum of 3% in 2008 (Fig. 1a), (ii) reduction in hatchery production that caused the abundance of hatchery-origin fish spawning in the wild to decline from a maximum of 31,530 in 1986 (when the average spawning population had 27% hatchery fish) to just 662 in 2015 (when the average spawning population had 0.7% hatchery fish; Fig. 1b), and (iii) freshwater restoration investments that totaled over 100 million US dollars between 1997 and 2003 (Nicholas et al., 2005), and over 106 million US dollars of state and federal funding for projects begun between 2000 and 2013 (OWEB, 2017).

Separating how much of the increase in adult abundance is attributable to improvement in natural ocean conditions versus a shift in the management regime will improve understanding of management effectiveness and long-term population viability. For example, ocean conditions are largely beyond management control, so if ocean survival rates return to the low values observed in the late 1990s (Fig. 1c), then the direction and rate of change in adult abundance will depend, in part, on how well management actions have improved spawner-tosmolt production. If management actions have improved smolt production, then populations will be more likely to persist through periods of low ocean survival.

Here, we use 46 years of monitoring data from 18 populations of Oregon coastal coho (Fig. 2) to determine whether a change in spawner-to-smolt recruitment parameters (hereafter "smolt recruitment", which occurs in freshwater) coincides with a biologically conservative shift in the management regime. If ocean conditions, not management, are responsible for changes in adult abundance, then we expect to find no change in smolt recruitment across two periods roughly corresponding to pre- and post-biological conservation management. In contrast, if management actions have meaningfully improved smolt recruitment, then this should be detectable in the abundance time-series data after controlling for changing ocean conditions and changing proportions of hatchery-origin spawners, which may exhibit lower reproductive success than natural-origin fish. We evaluated the evidence in data for these contrasting hypotheses by reconstructing historical ocean survival and then fitting a density-dependent life-cycle model using a hierarchical, state-space approach.

2. Methods

2.1. Abundance time-series

The abundance of coho salmon spawning in multiple populations on the Oregon Coast has been monitored by the Oregon Department of Fish and Wildlife for many decades using many methods. We use annual spawner abundance estimates from 1970 through 2015. Although earlier estimates exist, we chose 1970 as the beginning of the time series for consistency with other authors who noted that earlier estimates are relatively unreliable (Rupp et al., 2012a; Rupp et al., 2012b). Improvements to the abundance sampling design were made after 1970 (Jacobs and Nickelson, 1998, Lewis et al., 2009), so we created statistical models that permit change in the magnitude of sampling error that correspond with three different periods of sampling design: 1970 to 1990, 1991 to 1998, and 1999 to 2015. These three periods correspond to the use of index site sampling, stratified random sampling, and generalized random tessellation sampling, respectively.

The time series for the Beaver Creek population contains missing values from 1975 to 1979 so we began that population's time series 1980. There are 15 missing values of spawner abundance scattered throughout the remaining populations and years, which do not pose a problem in our subsequent Bayesian analysis because these values can be treated as unknown parameters to be estimated (Gelman and Hill, 2006). The proportion of hatchery-origin and naturally-produced spawners is also known for each population and year through analysis of carcass scales and visual inspection for adipose fin removal.

2.2. Harvest time-series

Ocean harvest rates of coho in the Oregon Production Index (OPI)

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