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Empirically based models of oceanographic and biological influences on Pacific Herring recruitment in Prince William Sound

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ABSTRACT

Abundances of small pelagic fish can change dramatically over time and are difficult to forecast, partially due to variable numbers of fish that annually mature and recruit to the spawning population. Recruitment strength of age-3 Pacific Herring (Clupea pallasii) in Prince William Sound, Alaska, is estimated in an age-structured model framework as a function of spawning stock biomass via a Ricker stock-recruitment model, and forecasted using the 10-year median recruitment estimates. However, stock size has little influence on subsequent numbers of recruits. This study evaluated the usefulness of herring recruitment models that incorporate oceanographic and biological variables. Results indicated herring recruitment estimates were significantly improved by modifying the standard Ricker model to include an index of young-of-the-year (YOY) Walleye Pollock (Gadus chalcogrammus) abundance. The positive relationship between herring recruits-per-spawner and YOY pollock abundance has persisted through three decades, including the herring stock crash of the early 1990s. Including sea surface temperature, primary productivity, and additional predator or competitor abundances singly or in combination did not improve model performance. We suggest that synchrony of juvenile herring and pollock survival may be caused by increased abundance of their zooplankton prey, or high juvenile pollock abundance may promote prey switching and satiation of predators. Regardless of the mechanism, the relationship has practical application to herring recruitment forecasting, and serves as an example of incorporating ecosystem components into a stock assessment model.

1. Introduction

Single-species population models commonly used in management of fished stocks have mixed success in predicting future stock size based on past stock size alone. One reason for the difficulty is unaccounted-for ecosystem effects on stock size, yet few examples exist of assessment models incorporating ecosystem variables (Skern-Mauritzen et al., 2016). Ecosystem effects on recruitment are of special interest for herring and other short-lived clupeoid fishes because changes in abundance can be driven largely by variability in the annual number of fish that recruit to the spawning stock (Blaxter and Hunter, 1982).

Pacific Herring (*Clupea pallasii*; hereafter herring), is a vital trophic link between plankton and upper-level predatory fish (Bishop and Powers, 2013), seabirds (Willson and Womble, 2006; Bishop et al., 2015), and mammals (Iverson et al., 1997). In addition to its ecological role, herring in Prince William Sound (PWS) supported an important commercial fishery prior to its population collapse in the early 1990s. The population size has fluctuated widely over time since 1980, when the modern stock assessment time series began (Quinn et al., 2001; Hulson et al., 2008). According to age-structured-assessment (ASA) model estimates, pre-fishery stock biomass has ranged from a peak of 139,298 t (126,369 metric tons [mt]) in 1989, to a low of 10,375 t (9412 mt) in 2001 (Wiese et al., 2015). Identifying the main factors controlling PWS herring recruitment is essential for modeling herring population dynamics and understanding the functioning of this ecosystem.

Recruitment strength for PWS herring, conventionally defined as the annual number of age-3 individuals joining the spawning population (Funk, 1994; Williams and Quinn, 2000), may be determined by multiple factors. Of particular importance are seasonal environmental and biological variables that affect herring survival during their first year (Norcross and Brown, 2001), which begins with spawning in April followed by a three- to four-week egg incubation period (Brown et al., 1996). Survival at the egg stage can be affected by predation pressure from seabirds (Bishop and Green, 2001), invertebrates (Haegele and Schweigert, 1991), other fish (Rooper and Haldorson, 2000), and physical factors such as wave and air exposure (Rooper, 1996). Larvae may be susceptible to high predation mortality (Purcell and Grover,

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1990), drifting to unsuitable habitat (Norcross et al., 2001), and starvation (McGurk et al., 1992). Favorable feeding and growing conditions for larval and early juvenile herring in PWS are compressed by the seasonal pattern of productivity typical of high latitude coastal areas. A large spring phytoplankton bloom in April is generally followed three to four weeks later by increased zooplankton abundance in May through June (McRoy et al., 1997; Eslinger et al., 2001). High spring phytoplankton biomass should support high abundances of summer zooplankton prey for juvenile herring (Eslinger et al., 2001; Ware and Thomson, 2005). With sufficient food, herring growth and survival should be promoted by high summer temperatures. Juvenile survival to the end of the first summer can portend relative recruitment strength (e.g., Schweigert et al., 2009), though high variability in the relationship may be due to mortality during the first winter (reviewed in Hurst et al., 2007). Zooplankton abundance declines to winter lows from October or November through March or April, accompanied by a higher proportion of empty stomachs among juvenile herring (Foy and Norcross, 2001). Juvenile herring, like other forage fishes, may experience increased predation risk as hunger and declining condition through winter (Paul and Paul, 1998) suppress predator avoidance behavior (e.g., Robinson and Pitcher, 1989; Sogard and Olla, 1997). Water temperature (Gay and Vaughan, 2001), food availability (Foy and Norcross, 1999), herring condition (Norcross et al., 2001), and predation pressure (Stokesbury et al., 2002) vary among bays in PWS and over time, and this variability likely contributes to differences in survival to recruitment at age 3. Demonstrations of ecosystem effects on herring recruitment are rare, but recruitment variability has been quantitatively linked to summer (July - August) temperature in the herring hatching year and zooplankton biomass in the following spring (April - May) as herring approach age 1 (Brown and Norcross, 2001). Winter sea surface temperature prior to and including spawning has also been shown to influence recruitment (Zebdi and Collie, 1995; Williams and Ouinn, 2000); the mechanism is unclear, but it may involve temperature effects on rates of egg and embryonic development and subsequent timing mismatch to the spring phytoplankton bloom.

Changes in the abundances of the main natural predators of herring, including piscivorous fishes, seabirds, and humpback whales (Megaptera novaeangliae), likely cause changes in predation mortality and may impact herring abundance and recruitment. For example, herring recruitment in Hecate Strait, British Columbia tended to be low when Pacific Cod (Gadus macrocephalus) abundance was high (Walters et al., 1986), though the persistence of that relationship is uncertain (Ahrens et al., 2012). Biomass of predatory Pacific Hake (Merluccius productus) during the first year for herring negatively affects recruitment of West Coast Vancouver Island herring (Tanasichuk, 2017). Pacific Cod and Walleye Pollock (G. chalcogrammus; hereafter pollock) are likely the primary fish consumers of juvenile herring in PWS, as indicated by their abundance and diet composition (Bishop and Powers, 2013). Predation effects may differ with fish predator age, but their relative importance is often unclear. For example, predation pressure or competition may be greater from juvenile than adult pollock (Sturdevant et al., 2001; Bishop and Powers, 2013) due to greater spatial overlap among juvenile pollock and herring, but adult pollock diets can contain higher proportions of herring (Willette et al., 1999). Hatchery-reared Pink Salmon (Oncorhynchus gorbuscha) fry, released in the hundreds of millions annually since the late 1980s, may negatively influence herring recruitment through competition for zooplankton prey or predation (Deriso et al., 2008; Pearson et al., 2012). Adult pink salmon returning to PWS to spawn have also been suggested as important herring predators (Deriso et al., 2008). Seabird predation, predominantly by murres (Uria spp.), can remove as much as 10% of the adult herring biomass and even greater biomass of juveniles (Bishop et al., 2015). The abundance of another major herring predator, humpback whales, has increased five-fold since 1978 in PWS (Teerlink et al., 2015), and bioenergetic models indicate they may remove large portions of the herring stock biomass annually (11 - 77%, Rice et al., 2011; 26%, Pearson et al., 2012). It is unclear how much these sources of predation and competition influence herring stock size through reductions in juvenile survival and recruitment.

Some ecosystem factors influencing herring recruitment may also affect other species with similar early life history traits in the same region. Regional synchrony of strong year classes (Hollowed et al., 1987; Hollowed and Wooster, 1995) or recruitment (Mueter et al., 2007) can occur among some North Pacific fish stocks, especially within species groups that are subject to shared forcing factors. Associations between different species have recently been described for the Bering Sea, where age-4 Chum Salmon (Oncorhynchus keta) growth, a proxy for ocean conditions, predicts age-1 pollock recruitment the following year (Yasumiishi et al., 2015). Such connectivity has led to expectations that strong herring year classes in PWS may be portended by high juvenile survival of other species, for example, age-0 gadids in PWS (S. Moffitt, ADFG, USA, pers. comm.), PWS pink salmon in their first ocean year (Pegau, 2014), and juvenile pollock in Shelikof Strait (Pegau, 2014). Quantifying linkages among species for PWS or the broader Gulf of Alaska (GOA) could aid in understanding and predicting herring recruitment.

The numbers of age-3 recruits and other year classes of PWS herring are estimated by managers using an ASA model (described in Hulson et al., 2008). Herring year-class sizes are estimated using a weighted least squares approach that minimizes differences between model estimates and observations of egg densities, mile-days of milt, age composition from commercial seine catches, age composition from fisheries-independent sampling of spawners, hydroacoustic survey biomass, and Ricker stock-recruitment model estimates of age-3 recruits. The Ricker model (Ricker, 1975) is commonly used to estimate recruitment based on stock size and has a number of desirable model attributes: relative simplicity, ease of linearization for parameter estimation, and the ability to account for productivity and density-dependent effects of stock size on recruitment. Density-dependent effects on recruitment may occur in herring through cannibalism on early life stages (Holst, 1992) or mortality of eggs under high density spawning conditions (Taylor, 1971; Hourston et al., 1984). Including stock size in the recruitment models sets boundaries on recruitment at high or low spawning stock sizes (Quinn and Deriso, 1999); for the PWS herring model, it prevents the ASA model from estimating zero or negative recruits (Hulson et al., 2008). Although a Ricker-type relationship is often used in analyses of herring stocks (e.g., Zheng, 1996; Williams and Quinn, 2000), previous work has shown no obvious stock-recruitment relationship for PWS herring over the observed range of stock sizes (Zheng, 1996). Ricker model estimates of recruitment and the observed abundances of age-3 herring in PWS differ widely. The discrepancy reflects the weak relationship between spawning stock biomass and recruitment for PWS herring (Fig. 1), and limits the usefulness of stock size for projecting recruitment. Therefore, median recruitment

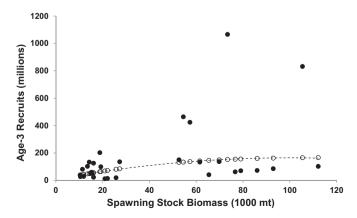


Fig. 1. PWS Pacific Herring age-3 recruits (millions) vs. spawning stock biomass (1000 metric tons), observed (•) and estimated by Ricker stock-recruit model (O, dashed line).

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