Vol. 597: 243–257, 2018
https://doi.org/10.3354/meps12594

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 11

Echoes of numerical dependence: responses of wintering waterbirds to Pacific herring spawns

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ABSTRACT: We investigated the ecological importance of Pacific herring *Clupea pallasii* spawning activity to wintering waterbird numbers in Tomales Bay, California, USA. Time-series analyses were used to assess the potential dependence of future waterbird abundances on current changes in herring spawning biomass, independent of underlying trends or other dynamics in waterbird numbers or herring activity. Forecasts of winter waterbird abundance were significantly improved by considering the lagged effects of changes in herring spawning biomass. Impulse-response functions provided strong evidence that the dynamics of winter waterbird abundances include 'echoes' of response over time to any unusual pulse of herring activity, with carryover effects leading to sustained increases in waterbird species' abundances over multiple years, and increases in the abundance of all waterbird species (combined) over the subsequent 3 winters. Increases in waterbird abundance consistent with variance-prone responses to the pulsed availability of prey were sustained by periods of conditional variance-aversion associated with subsequent declines in herring spawning biomass to expected long-term levels. Annual spawning activity was highly variable, and when the availability of roe was relatively high, the potential consumption of herring eggs could account for up to 64 % of the collective energy needs of waterbirds (all species combined) over the 90 d herring season (mean ± SE = 20 ± 3.6 %). Several waterbird species shifted their bay distributions in response to herring spawning events within 2 d; however, some species that did not concentrate in spawning areas exhibited sustained annual increases in bay-wide winter abundance in response to increased herring spawning biomass.

KEY WORDS: Forage fish · Predation · Pulsed resource · Time series · Estuaries · Variance sensitivity

INTRODUCTION

Environmental conditions encountered by migratory birds during the nonbreeding portion of their annual cycle have increasingly important implications for conservation as birds face progressively greater rates of anthropogenic environmental change (Robbins et al. 1989, Baker et al. 2004, Sherry et al. 2005, Calvert et al. 2009). In addition to the effects of winter conditions on annual survival, physiological condition generated during the nonbreeding season can impact subsequent reproductive fitness in waterbirds, and consequently, influence overall population dynamics (Baldassarre & Bolen 2006, Drent et al. 2006, Calvert et al. 2009). In areas where Pacific herring *Clupea pallasii* spawn, the distributions of waterbirds in the winter and spring are correlated with the concurrent size and distribution of herring spawning events (Haegele 1993a, Sullivan et al. 2002, Lok et al. 2008). In British Columbia, Canada, the importance of herring spawn (roe) to energy balance in waterbirds has been demonstrated for surf scoter *Melanitta perspicillata* and white-winged scoter *M. fusca* — 2 species of sea ducks that are well known consumers of herring spawn. In these species, the availability of herring spawn drives dietary pref-

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