

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 \pm SE = $20 \pm 3.6\%$). 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

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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 (Haegerle 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-

ferences and accounts for their seasonal ability to restore energy reserves depleted during winter or migration (Anderson et al. 2009). However, the extent to which changes in population size by these species may depend on available herring remains unknown. High levels of consumption of herring spawn by many other waterbird species underscore herring's importance to wintering waterbirds (Bayer 1980, Haegele 1993a, Bishop & Green 2001, Willson & Womble 2006, Bishop et al. 2015).

Pacific herring enter estuaries along the Pacific Coast of North America to spawn each year, generally from early winter to early summer (Haegele & Schweigert 1985). In central California, USA, spawning activity occurs from late November to early March, with eggs deposited on blades of eelgrass *Zostera marina* and, to a lesser extent, on other vegetative substrates and rocks in subtidal and low-intertidal zones (Hardwick 1973, Haegele & Schweigert 1985). As a mid-level forage species in estuaries, herring and their deposited roe transfer energy and nutrients to higher trophic levels, providing seasonal food for numerous other species including pinnipeds, fishes, and crabs (Varpe et al. 2005, Willson & Womble 2006). Thus, the concentrated seasonal spawning activities of Pacific herring have broad ecosystem importance.

Foraging theory suggests that birds, including estuarine waterbirds, behave in ways that optimize energy intake and lead to distributional shifts in response to variation in the availability or quality of prey (Fretwell & Lucas 1970, Stephens & Krebs 1986, Lok et al. 2012). The enhanced availability of specific types of prey may lead to strong winter site fidelity, in particular areas that may be associated with winter philopatry (Robertson & Cooke 1999, Kirk et al. 2008). The potential benefits of such behavioral options, structured over extended periods of time may result in persistent, dynamic, or lagged numerical responses to changes in the availability of prey such as Pacific herring.

Numerous studies have documented the correlated responses of waterbirds to concurrent changes in herring spawning activity in Pacific Coast estuaries (e.g. Haegele 1993a, Sullivan et al. 2002, Rodway et al. 2003, Willson & Womble 2006, Lok et al. 2008, Anderson et al. 2009). These patterns suggest variance-sensitive foraging decisions in response to the ephemeral availability of Pacific herring or their roe (Stephens & Krebs 1986, Kacelnik & Bateson 1996). Specifically, opportunistic shifts in waterbird abundance and distribution among coastal wintering areas with annual changes in herring spawning activity

suggest potential fitness benefits related to variance-prone exploitation of prey, in which individuals adaptively seek out more variable foraging options with a greater chance of major rewards (classically measured as the expected gain divided by the expected foraging time). Such variance-prone behavior is most likely related to variation in the time delay of foraging rewards, or the unpredictable timing of herring spawn; in contrast, the foraging decisions of animals may be more variance-averse, seeking more constant foraging opportunities when rewards vary primarily in the amount of available food (Kacelnik & Bateson 1996, Buchkremer & Reinhold 2010). Such variance-averse behavior would suggest that predators respond to historical patterns of herring activity by returning to areas where herring roe is traditionally available, to avoid risks related to foraging over a more extensive wintering range. Because herring spawning activity varies in both its timing and amount, variation in waterbird numbers may reflect more complex responses over time. In addition, birds are more likely to exhibit variance-prone behaviors when faced with a negative energy budget (Caraco et al. 1980, Caraco 1981, Kacelnik & Bateson 1996). Despite considerable attention to waterbird–herring relationships, the numerical responses of waterbirds to variation in the frequency, intraseasonal timing, or extent of herring spawning activity have not been thoroughly investigated.

The aggregate responses of wintering waterbirds to incursions of spawning herring occur over a few to several days, and may involve waterbird movement over substantial distances within a wintering region (Rodway et al. 2003, Anderson et al. 2009). After spawning activity and the availability of deposited roe subsides (after 10 to 14 d incubation; Hardwick 1973, Haegele et al. 1981), some waterbird species apparently return rapidly to their main wintering sites, whereas other waterbird species numbers decline slowly over several weeks (Haegele 1993a, Rodway et al. 2003). However, previous studies have not investigated the extent to which the numerical responses of waterbirds to pulses of herring might persist over longer periods of time. Conditional variance-averse foraging behavior associated with the pulsed availability of food would be suggested if increased waterbird abundances are sustained after large pulses of available food from herring decline to previous levels. Under this hypothesis, waterbirds would exhibit site faithfulness for months or years after an unusually large spawning event, despite the return to the normal background levels of available

spawn. Such responses would further suggest an underlying expectation of potential fitness benefits related to future spawning events. Similarly, a persistent decrease in waterbird abundance after a steep crash in spawning biomass, despite a return to normal spawning levels, would suggest that the expected probability of future spawning activity is low.

If the numerical responses of foraging waterbirds to pulses of spawning activity persist beyond the subsequent return of normal levels of spawning, predictions of future waterbird abundances should be improved by information on unexpected increases (or decreases) in the availability of herring. Such predictions would substantiate inferences that winter waterbird abundances in areas where herring spawn depend at least partially on the temporal pattern and extent of food provided by spawning herring.

Pacific herring fisheries are driven primarily by the commercial value of herring roe, obtained from herring caught in gill nets as they approach their estuarine spawning beds (CDFW 2001). In November 2012, the California Fish and Game Commission adopted a policy recognizing the important role of forage fish, such as Pacific herring, in sustaining healthy marine ecosystems (CFGF 2012). This policy targets the sustainable management of forage fisheries by incorporating Essential Fishery Information that includes the 'effects on dependent predators.' Currently, information is lacking to determine whether food resources from spawning herring are essential in sustaining regional populations of wintering waterbirds or if herring merely provide a profitable alternative for waterbirds among other viable food resources (Anderson et al. 2009). Although Pacific Coast herring fisheries have cautiously limited commercial fishing pressure to minimize the potential impacts on herring stocks (CDFW 2001), information is lacking to evaluate the potential extent of competition between humans and waterbirds for herring or herring roe.

Tomales Bay, California, supports a spawning biomass of 2564 ± 586 (SE) metric tons (t) of Pacific herring annually (1989 to 2007; California Department of Fish and Wildlife fishery reports), providing potentially critical food for waterbirds which can number up to 50 000 during winter (Kelly & Tappen 1998, Audubon Canyon Ranch unpubl. data). Our study incorporates 3 components of investigation. First, we used time-series analyses based on 23 yr of winter waterbird abundances and 18 yr of herring spawning activity (CDFW 2007) in Tomales Bay to measure the potential dependence of winter waterbird abundances on variation in herring spawning activity. We hypothesized that the abundances of wintering

waterbirds in future years depend in part on the current extent of herring spawning activity. We predicted that waterbird responses would be consistent with conditional variance-averse exploitation of available herring or herring roe, marked by temporally distributed increases in waterbird numbers in response to unusually large pulses of spawning herring. Second, we evaluated the potential importance of food energy for waterbirds provided by herring by calculating the seasonal energy requirements of wintering waterbird species and the proportion of those requirements that could be met annually by available herring roe during the 90 d spawning season (December to February). Finally, we investigated the extent to which the foraging distributions of waterbird species shift within Tomales Bay in response to spawning herring by estimating the change in foraging density, by species, in the vicinity of individual spawning events relative to the expected density in the absence of spawning. We predicted that species known to forage on herring would shift their distributions toward individual spawning events and that species with stronger bay-wide numerical responses to pulses of herring activity would exhibit stronger distributional shifts within the bay.

MATERIALS AND METHODS

Study area

Tomales Bay, on California's central coast approximately 45 km northwest of San Francisco (Fig. 1), differs from other, generally shallower Pacific Coast estuaries and lagoons in having a much greater area of open water at low tide. Because most of the waterbird habitat is available through the tidal cycle, the bay is structurally similar to California's San Francisco Bay and Humboldt Bay. Two primary sources of freshwater runoff enter the bay, one at Lagunitas Creek at the south end of the bay, and one at Walker Creek near the north end (Fig. 1). Spatial and temporal variations in salinity are substantial, influenced by variably high levels of freshwater inflow during the winter, low flows in the summer, and constraints on tidal exchange with the ocean imposed by the linear shape of the bay (Hollibaugh et al. 1988). Approximately 91 % of the bay's 28.5 km area is subtidal. Tomales Bay contains 37 eelgrass *Zostera marina* beds used as spawning areas by Pacific herring *Clupea pallasii*, covering a total area of 392 ha that extends across most of its 20 km length (Spratt 1989). Water depths average about 3 m below mean

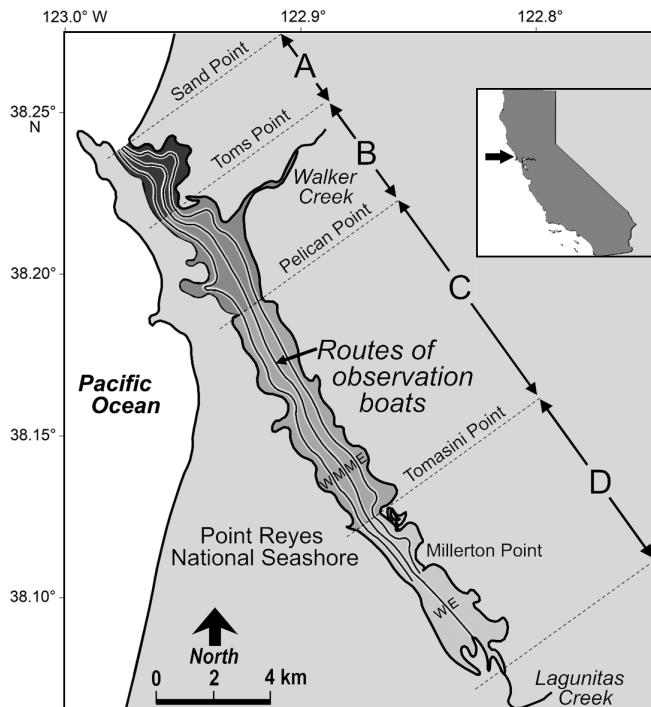


Fig. 1. Winter waterbird count areas (A, B, C, and D) in Tomales Bay, California, with sub-areas along the west shore (W), mid-bay (M), and east shore (E) marked by the routes of observation boats and by mid-bay markers observed from shoreline positions south of Millerton Point. Inset: California

lower-low water and vary from intertidal shoals along the east shore to areas up to 20 m deep in the main channel along the west shore.

Waterbirds

A total of 69 bay-wide waterbird surveys were conducted on Tomales Bay over 23 winters, from 1989–1990 through 2011–2012 (3.2 ± 0.15 [SE] yr^{-1}). All waterbird species in the bay were included in the study, with the exception of sandpipers (Scolopacidae), plovers (Charadriidae), oystercatchers (Haematopodidae), and gulls (Laridae). Each year, repeated counts were made at 2 to 3 wk intervals from mid-December to late February. Each bay-wide survey involved simultaneous counts conducted from three 6 m (or longer) motorized boats. The survey boats traveled in formation along 3 parallel 18 km transects, from Millerton Point near the south end of the bay north to the Sand Point Buoy (Fig. 1). During count periods, conditions on the bay were calm (Beaufort scale 0 to 2). Detailed survey methods are presented in Kelly & Tappen (1998).

Waterbird surveys were partitioned into 4 sections along the length of the bay (Fig. 1), distinguished by estuarine conditions that might influence the composition, distribution, or availability of food for waterbirds, including differences in water turbidity, substrate texture (Daetwyler 1966), water temperature, freshwater inflow, and ocean-water exchange (Hollibaugh et al. 1988), as well as the distribution of eelgrass used as spawning substrate by herring (Spratt 1989). Therefore, data from each bay-wide survey were partitioned into 12 sub-areas of the bay, delineated by 3 transects, each divided into 4 sections. The survey boats moved slowly (<3 knots), so waterbirds very rarely flushed into other sub-areas of the bay. Waterbirds in the shallows at the extreme south end of the bay (south of Millerton Point) were counted from shore and recorded as occurring in either east-shore or west-shore transects. To facilitate comparisons among count areas of different sizes, we transformed species abundances into densities (birds km^{-2}).

Pacific herring

We used annual herring-fishery reports from the California Department of Fish and Wildlife (CDFW) to compile available information on seasonal Pacific herring spawning biomass over 18 yr (December to February, 1989 to 2007) and the timing, size (roe count), and location of spawning events within Tomales Bay over 17 yr (from 1990–1991 until monitoring of herring activity was discontinued at the end of the 2006–2007 season; CDFW 2007). The waterbird time series extended to 2012 to consider the lagged effects of herring activity for an additional 5 yr. Spawning biomass estimates by CDFW were calculated using data from spawning deposition surveys, conducted continually (daily to several days per week) through each winter, combined with data from hydroacoustic surveys, catch sampling with commercial gill nets, and age-and-sex sampling with multi-panel variable-mesh gill nets (detailed in Trumble et al. 1982, Moore & Mello 1995). Roe counts from spawning deposition surveys were based on repeated samples of eggs taken from random locations in proportion to the areal extent and vegetation density (eelgrass and *Gracilaria* spp.) of each spawning area. In 7 of 17 years, roe counts for individual spawning runs were not available and were calculated using conversion factors provided by Watters et al. (2004): $1 / [F \times (p / P) \times 10^6]$, where F = fecundity (113 eggs g^{-1} body weight, males and females com-

bined; Spratt 1986, Reilly & Moore 1986), p = percent females in a given spawning run, obtained from CDFW midwater trawl samples for each year (assumed to be 50% during 3 of the study years when sex ratios were not available; Ryan Bartling CDFW pers. comm.), and P = percent females in the population (assumed to be 50%, based on local data; Moore & Mello 1995). A test of this conversion factor, over the 10 yr when roe counts for individual spawning runs were available, closely approximated the available roe counts with no significant difference ($t_{94} = 0.007$, $p = 0.99$).

Statistical analyses

Time series

The bay-wide densities of each waterbird species and the cumulative annual (within-winter) spawning biomass of herring were expressed as time series structured by a generic sequence of six 15-d winter periods within each December through February spawning season. Thus, the last (February) time step each winter was followed by the first (December) time step in the subsequent winter, with the effects of herring spawning activity on wintering waterbirds assumed to be independent of processes operating in breeding areas to the north (Bautista et al. 1992, Torres-Reyna 2013, Kelly & Condeso 2017); the time-series models control for annual trends and other background dynamics in waterbirds and herring. We used cumulative annual herring spawning biomass to model waterbird responses to the total annual availability and intraseasonal timing of available herring, based on samples collected continually through each winter and summed within 6 consecutive intraseasonal periods per year. We \log_e transformed estimates of waterbird densities and cumulative tons of herring spawning biomass to facilitate the evaluation of proportional rates of change. Estimates of bay-wide waterbird density were structured to coincide with the endpoints of 6 intraseasonal time periods used to measure cumulative herring biomass, based on daily estimates modeled by best-fit linear or quadratic trends within years for each species ($R^2 = 0.61 \pm 0.02$).

The responses of wintering waterbirds to herring spawning activity depend not only on the annual extent of herring spawning biomass, but also on the intraseasonal timing of spawning. The intraseasonal rate of growth in (\log_e) waterbird abundance per unit of herring spawning biomass, weighted equally

among years, declined significantly as wintering birds arrived each year: for all waterbird species combined, the response rate declined by 5% with each successive intraseasonal period ($b = -0.05$, $SE = 0.006$, $t_{(77)} = 8.1$, $p < 0.001$). Thus, limiting the analysis to annual time series would mask the differential, intraseasonal effects of spawning activity on the impulse-response dynamics of winter waterbird abundances.

To investigate evidence for causative effects of changes in herring spawning biomass on winter waterbird abundances, we conducted separate vector autoregression (VAR) analyses for each species. VARs account for the co-integration of lagged relationships between herring spawning activity and winter waterbird densities to estimate, specifically, the influences of past values of herring activity on future waterbird densities (Bisgaard & Kulahci 2011, Delorme et al. 2011, Beckett 2013). The analyses control for underlying variation by modelling the autoregressive processes that generate the associated trends or other dynamics in both time series, then test whether current herring activity significantly improves predictions of future waterbird numbers (relative to the null condition of random residuals with a mean of zero and constant variation over time). Granger causality Wald tests were used to determine whether the lagged effects of changes in herring biomass significantly improved forecasts of waterbird density. The VAR analyses provide a more stringent criterion for causation than simple cross-correlations distributed over time, to determine the extent to which increases in herring biomass 'Granger cause' increases in the abundances of wintering waterbirds (Beckett 2013).

The analysis assumes that the observed changes in waterbird abundances are not driven by species interactions or by other (unknown) variables that might influence the system or covary with the modeled parameters. Thus, inferences from the analysis do not account for other potentially more complex pathways of causation.

To specify each model, we selected a preliminary model with optimum lag length based on minimized values of Schwarz's Bayesian information criterion (SBIC) or Hannan and Quinn information criterion (HQIC), which are generally considered to provide the most consistent and parsimonious estimates of the true lag order (Lütkepohl 1993, Beckett 2013). Because the maximum lag lengths selected by minimizing Akaike's information criterion (AIC) may generate more accurate impulse-response functions (Ventsislav & Kilian 2005), we used Wald exclusion

tests to cautiously select additional lags up to the length associated with the minimized AIC value (Lütkepohl 1993, Beckett 2013). We then iteratively eliminated nonsignificant lags with the lowest χ^2 value and, finally, added any remaining significant lags to the model. We then confirmed that the revised models further minimized SBIC or HQIC. Based on this process, we included at least the first 6 lags in the model for every species, fully incorporating the inter-annual and intraseasonal dynamics between herring spawning biomass and winter waterbird responses. This process allowed us build a more parsimonious model, while retaining important lags needed to generate accurate impulse-response functions.

After estimating the parameters, we confirmed the stationarity and stability of each model by checking the condition that all eigenvalues of the companion matrix lie inside the unit circle (Hamilton 1994). We used Portmanteau (Q) tests to further confirm that the residuals in each model were reduced to white noise, Bartlett's tests to confirm the absence of nonrandom periodicity in the residuals, and diagnostic plots and Shapiro-Wilk tests to ensure that the distributions of residuals were approximately normal.

Finally, orthogonal impulse-response functions (IRFs) were calculated from the model results for each wintering waterbird species, and the resulting confidence intervals were verified using bootstrap SEs with 500 replicates (Bisgaard & Kulahci 2011, Beckett 2013). Because the variables were \log_e transformed, the IRFs reflect the temporally distributed percent change in waterbird density for each percent increase of herring spawning biomass.

Energy calculations

We evaluated the potential importance of herring in the energy budget of waterbirds by estimating the seasonal energy demand by waterbirds and the energy available from herring eggs. We calculated the bay-wide winter abundance for each waterbird species known to consume herring roe, assuming that the estimated mean number of birds was present each day for 90 d (from 1 December through February; see Table 1). We then calculated the energy required by each roe-eating waterbird species in each winter season, using allometric equations that relate metabolic rate to mean body mass.

Field metabolic rate (FMR) of seabirds can be calculated from a plethora of allometric equations based on doubly labeled water measurements (for reviews see Birt-Friesen et al. 1989, Nagy et al. 1999, Nagy

2005, Shaffer 2011), but none of the equations differ statistically, most data are for breeding, not wintering birds, and penguin and procellariid species often dominate. For 'marine birds' (cormorants *Phalacrocorax* spp., loons *Gavia* spp., grebes [Podicipedidae], herons and egrets [Ardeidae], common murre *Uria aalge*, American coot *Fulica americana*), we used $FMR = 14.25 \times [\text{body mass (g)}]^{0.659}$, where FMR is in kJ d^{-1} (Nagy et al. 1999). For Anatidae, we calculated FMR from resting metabolic rate (RMR) using the factor $FMR / RMR = 3$ (Heitmeyer 1989, Nagy 2005) and Miller & Eadie's (2006) allometric relation for Anatidae, $RMR = (422 \times [\text{body mass (g)} / 1000]^{0.74}) \text{kJ d}^{-1}$. Finally, we compared these results to the estimated energy available from herring spawn within each winter season, based on available information on spawning event timing, size, and location in Tomales Bay (CDFW 2007).

We calculated the energy available from herring roe, assuming birds obtained 2.53 MJ kg^{-1} wet weight of roe consumed, based on a roe energy content of 3.08 MJ kg^{-1} wet weight (USDA 2016) and an assimilation efficiency of 82%, calculated assuming 60% of the metabolizable energy contained in herring eggs is derived from protein and 40% is derived from fats and carbohydrates (USDA 2016), with 70% of the protein energy and 100% of the fat and carbohydrate energy available to birds (Blaxter 1989). We then calculated, for all Tomales Bay waterbird species known to consume herring roe (see Table 1), the usable energy ingested per day per kilogram of eggs consumed and used the results to estimate the annual number of 'winter survival days', defined here as the number of days roe-eating birds could survive on herring roe alone. These calculations assumed that (1) birds fed entirely from herring roe, whenever available, and maximized their energy intake at 1.65 times their average daily requirement (Kirkwood 1983), thereby increasing their endogenous energy reserves (primarily fat) to capitalize on the ephemeral, unpredictable energy resources, (2) roe were available to the birds for 10 d after each spawning event (Miller & Schmidtke 1956, Hardwick 1973), and (3) birds consumed the oldest (earliest deposited) roe first, when roe from more than one spawning event was available (for consistency with assumed maximum daily consumption; multiple spawning events with concurrently available roe never occurred at the same location). The results estimate the maximum overall benefit waterbirds were likely to obtain from spawning activity in Tomales Bay, in terms of the percent winter survival days within the 90 d herring season. The relative annual

consumption of energy by individual species is reflected in their percent of the annual bay-wide field metabolic rate of all species (see Table 1).

Distributional responses to spawning events

To determine whether waterbird species alter their distributions in response to herring spawning events, the density of each species in each sub-area within 2 d of active spawns was compared to the density when no spawning activity occurred. We limited the measurement of waterbird responses to short, 2 d time periods after active spawning events to avoid potentially confounding differential responses of waterbird species over time, relative to the availability of herring eggs in large versus small events. Sub-areas of the bay were classified as having no active spawning on any given date if spawning had not occurred within the previous 10 d. Waterbird responses were measured as \log_e densities, so that model coefficients measured proportional changes in waterbird abundance. The models were run using the R package 'nlme' (Pinheiro et al. 2017) and included an ANOVA (run first, to generate model comparisons), a generalized least squares model (GLS; when a significant [$p < 0.05$] random categorical effect for year was not indicated), and a linear mixed-effects model (LME). The LME included a random, categorical covariate for year to control for variation among annual waterbird seasons (winters). Initially, a random interaction term was included, between year and the occurrence of a spawning event within the sub-area of the bay, but was determined to be nonsignificant ($p > 0.05$) in all models and subsequently dropped. Whenever the effect of spawning was significant ($p < 0.05$) or marginally significant ($p < 0.07$) in any of the fitted models, a post hoc GLS was run, using size of the spawning event (number of eggs) to determine if birds responded more strongly to larger spawning events.

RESULTS

Waterbird abundance and herring spawning activity

A daily average of $24\,664 \pm 1050$ (SE) waterbirds (min. = 14 257; max. = 38 189) was recorded annually during the 23 yr of censuses (Fig. 2). Among these, $20\,470 \pm 890$ (min. = 12 239; max. = 34 152) individuals of 26 species assumed to consume Pacific herring

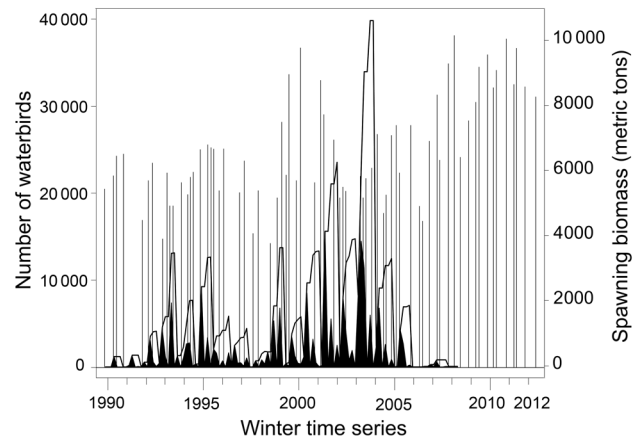


Fig. 2. Bay-wide abundance of wintering waterbirds, excluding gulls and shorebirds (Charadriiformes), known to consume herring or herring roe in Tomales Bay, California, December to February, 1989 to 2012 (thin bars, all species combined). Biomass of Pacific herring 1989 to 2007 is indicated by spawning event (filled spikes) and cumulative spawning biomass within years (thick lines)

Clupea pallasii roe were recorded on each survey day (species known to consume and readily forage on herring roe and non-piscivorous waterbirds assumed to consume herring roe because they actively select spawn areas for foraging; Table 1). The annual spawning biomass of herring was 2564 ± 586 t, December through February, 1989 to 2007, with an annual deposition of 335 ± 77 t of herring roe.

Time-series analysis

In 32 of 36 waterbird species measured (species known to consume herring roe and piscivorous species likely to consume herring), forecasts of bay-wide abundance given the prior dynamics and trends were significantly improved by considering the lagged effects of changes in herring biomass (Granger causality Wald tests: $p < 0.001$ in 24 species, $p < 0.01$ in 8 species; Table 2); forecasts of surf scoter abundance were marginally improved ($F_{7,89} = 2.0$, $p = 0.06$). Forecasts for 3 species (Pacific loon *Gavia pacifica*, red-breasted merganser *Mergus serrator*, and eared grebe *Podiceps nigricollis*) were not significantly improved by considering changes in herring biomass ($p > 0.35$; Table 2).

Significant IRFs provided evidence that, for most species, any single increase in herring biomass exceeding normal levels of variation results in a sustained increase in waterbird abundance over multiple years (Figs. 3 & 4, Table 2). The impulse responses of waterbirds at each time lag are aver-

Table 1. Mean (\pm SE, $n = 69$) annual abundance, individual body mass (Dunning 1993), bay-wide biomass, bay-wide field metabolic rate (FMR), and (sorted by) percent bay-wide FMR waterbird species in Tomales Bay, California, 1990 to 2007. These species include those known to consume and readily forage on herring roe and non-piscivorous waterbirds assumed to consume herring roe because they are known to actively select spawn areas for foraging; gulls and shorebirds (Charadriiformes) are excluded (Hardwick 1973, Bayer 1980, Vermeer 1981, Haegele 1993a, Vermeer et al. 1997, Sullivan et al. 2002, Lewis et al. 2007, Lok et al. 2008, Bishop & Green 2001). See Table 2 for species' scientific names

Species	Abundance	Body mass (g)	Bay-wide biomass (kg)	Bay-wide FMR (MJ d ⁻¹)	Percent FMR of all species
Surf scoter	5377 \pm 422.9	1098	5904 \pm 464.4	7294.9 \pm 573.74	36.0 \pm 2.84
Greater scaup	5102 \pm 559.4	1007	5138 \pm 563.3	6492.6 \pm 711.87	29.4 \pm 3.23
Brant	1373 \pm 92.6	1300	1785 \pm 120.4	4033.8 \pm 242.57	12.3 \pm 0.83
Bufflehead	6231 \pm 374.7	404	2517 \pm 151.4	2110.7 \pm 142.35	7.3 \pm 0.44
Ruddy duck	972 \pm 101.9	545	530 \pm 55.5	785.3 \pm 82.33	1.9 \pm 0.20
American coot	598 \pm 74.5	642	384 \pm 47.8	603.5 \pm 75.19	1.6 \pm 0.20
American wigeon	295 \pm 36.2	756	223 \pm 27.4	303.6 \pm 37.26	1.0 \pm 0.13
Northern pintail	149 \pm 26.4	947	141 \pm 25.0	181.2 \pm 32.10	0.8 \pm 0.14
Canada goose	11 \pm 3.2	3727	41 \pm 12.0	124.6 \pm 9.61	0.6 \pm 0.18
Common goldeneye	105 \pm 8.1	916	96 \pm 7.4	111.9 \pm 8.49	0.5 \pm 0.04
Red-breasted merganser	87 \pm 6.6	1022	89 \pm 6.8	76.5 \pm 15.85	0.5 \pm 0.04
Lesser scaup	70 \pm 14.5	820	58 \pm 11.9	57.8 \pm 11.96	0.3 \pm 0.06
Black scoter	44 \pm 9.1	1052	46 \pm 9.5	36.9 \pm 10.72	0.3 \pm 0.06
Mallard	20 \pm 4.4	1171	23 \pm 5.2	28.5 \pm 6.26	0.1 \pm 0.03
White-winged scoter	14 \pm 3.6	1757	24 \pm 6.3	26.9 \pm 6.92	0.2 \pm 0.05
Canvasback	9 \pm 4.3	1203	11 \pm 5.1	13.1 \pm 6.24	0.1 \pm 0.03
Common merganser	6 \pm 1.5	1471	8 \pm 2.2	10.1 \pm 2.53	0.1 \pm 0.02
Other species assumed to consume roe ^a	8.3 \pm 1.1	843 ^b	7 \pm 1.0	9.3 \pm 1.23	0.0 \pm 0.01
All roe-eating species combined	20470 \pm 890.1		17025 \pm 760.1	22301.1 \pm 964.73	100.0

^aRedhead *Aythya americana*, ring-necked duck *Aythya collaris*, long-tailed duck *Clangula hyemalis*, Barrow's goldeneye *Bucephala islandica*, cinnamon teal *Anas cyanoptera*, common murre *Uria aalge*, hooded merganser *Lophodytes cucullatus*, harlequin duck *Histrionicus histrionicus*, Ross's goose *Chen rossii*; ^bMean body mass among species

aged over all steps in the time series. Therefore, the modelled results reflect the lagged responses of waterbirds to a single impulse of herring at any time during the winter. Consequently, on average, 17, 33, 50, 67, 83, and 100% of waterbird responses 1 to 6 lags, respectively, after an impulse of herring at any intraseasonal point in time, occur in winter of the subsequent year (Figs. 3 & 4). All responses at lags of 6 or more time steps occur least 1 yr after the corresponding impulse. Therefore, significant multi-year responses to impulses of herring are most clearly revealed at IRF lags of 6 or more time steps. The cyclic annual and intraseasonal responses to any single impulse in herring biomass subside eventually to zero, consistent with the underlying, long-term dynamics of wintering waterbirds and herring.

Declining IRF values above zero represent declining rates of increasing waterbird abundance (not declining abundance), relative to underlying trends. These values reflect the declining influence of herring activity over intraseasonal time lags, as number of arriving waterbirds declines and the annual abundance of waterbirds is established each winter. Negative impulse-response values occurred at intra-

seasonal lags (repeated annually), reflecting rates of declining waterbird abundance in (1) mid-to-late-winter that overpower any influxes of additional wintering birds and (2) early winter, relative to the previous year, before annual abundances are re-established by arriving, wintering birds.

The sustained growth of winter waterbird abundances over multiple years is revealed by significant, temporally distributed increases, at repeated (annual) intervals of approximately 6 lags, in response to any single impulse of herring (Figs. 3 & 4, Table 2). A few species, such as Brandt's cormorant *Phalacrocorax penicillatus*, great blue heron *Ardea herodias*, and brown pelican *Pelecanus occidentalis*, exhibited relatively small or delayed responses to impulses of herring activity in the current year, followed by stronger increases in abundance in subsequent years (Fig. 4). Other species, such as western grebe *Aechmophorus occidentalis*, horned grebe *Podiceps auritus*, and ruddy duck *Oxyura jamaicensis*, exhibited strong initial responses to increased herring spawning biomass in the current year, but relatively little if any continuing response in future years (Fig. 4).

Table 2. Lagged increases in winter waterbird density, December to February, 1989 to 2012, estimated by impulse-response functions (lagged responses: orthogonal impulse-response function lags with the lower 95% confidence limit greater than zero) after any unusual, one-time impulse of Pacific herring biomass, December to February, 1989 to 2007, in Tomales Bay, California. Vector autoregression (VAR) models with associated lags and coefficients showing significant or marginally significant increases in waterbird density with increased herring biomass ($p < 0.07$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$). Granger causality Wald tests, and Portmanteau (Q) tests for white noise in residuals are indicated. Lagged responses at ≥ 6 lags indicate increases in subsequent years; intervals of approximately 6 lags reflect repeated annual increases in winter waterbird density

Species	Impulse-response function: — VAR model —		Granger causality		Portmanteau test (df = 40)	
	Lagged responses	Model lags	Coefficients	F (df1,df2)	p	Q
All species combined	5, 11, 12, 18	1-6, 12	1*, 5***, 6*, 12***	9.7 (8, 87)	<0.001	18.4 >0.99
Greater scaup <i>Aythya marila</i>	1, 7, 13, 19	1-7	1***, 7**	15.0 (7, 94)	<0.001	20.4 >0.99
Lesser scaup <i>Aythya affinis</i>	1, 7, 13, 19	1-7	1***, 7***	7.0 (7, 89)	<0.001	15.5 >0.99
Surf scoter <i>Melanitta perspicillata</i>	12	1-6, 12	1*, 12*	2.0 (7, 89)	0.06	24.9 >0.97
White-winged scoter <i>Melanitta fusca</i>	1, 13, 25, 37	1-6, 12, 13	1***, 6*, 12**	3.4 (8, 86)	<0.01	51.2 0.11
Double-crested cormorant <i>Phalacrocorax auritus</i>	11, 18, 23, 30, 35	1-6, 11-13	6*, 11*, 13**	3.8 (9, 84)	<0.001	37.1 0.60
Bufflehead <i>Bucephala albeola</i>	5, 12, 24, 30, 36, 42, 48, 54	1-7, 12, 13	5*, 12***, 13**	3.8 (9, 84)	<0.01	47.0 0.21
Brant <i>Branta bernicla</i>	1, 7, 13, 19	1-6	1***	6.1 (6, 97)	<0.001	30.6 0.86
Common loon <i>Gavia immer</i>	2	1-6, 12	2*, 3, 12**	43.0 (7, 89)	<0.01	42.1 0.37
Red-throated loon <i>Gavia stellata</i>	11, 19, 29	1-6, 11, 12	11***, 12**	4.7 (8, 87)	<0.001	19.9 >0.99
Pacific loon <i>Gavia pacifica</i>		1-6		1.1 (6, 97)	0.35	47.8 0.19
Ruddy duck <i>Oxyura jamaicensis</i>	1, 5	1-6	1***, 5***, 6**	4.8 (6, 97)	<0.001	17.9 >0.99
Black scoter <i>Melanitta americana</i>	1, 13	1-6	1***	17.6 (6, 97)	<0.001	17.5 >0.99
Red-breasted merganser <i>Mergus serrator</i>		1-6		0.7 (6, 97)	0.69	36.4 0.63
Common merganser <i>Mergus merganser</i>	6, 12, 18	1-6	6***	4.7 (6, 97)	<0.001	36.0 0.07
American coot <i>Fulica americana</i>	5	1-6	5**, 6*	20.7 (1, 112)	<0.001	16.7 >0.99
American wigeon <i>Mareca americana</i>	2, 18	1-6, 12, 13	2***, 3*	8.7 (8, 86)	<0.001	26.2 0.95
Northern pintail <i>Anas acuta</i>		1-6		6.2 (6, 97)	<0.001	41.3 0.41
Common goldeneye <i>Bucephala clangula</i>	12	1-7, 12	12	2.9 (8, 87)	<0.01	32.2 0.80
Canvasback <i>Aythya valisineria</i>	12	1-6, 12	12*	8.3 (8, 87)	<0.001	26.5 0.95
Mallard <i>Anas platyrhynchos</i>	5, 12, 24, 30, 36	1-6, 12	12***	7.9 (7, 89)	<0.001	44.0 0.30
Western grebe <i>Aechmophorus occidentalis</i>	1, 13	1-6	1***	7.3 (6, 97)	<0.001	42.9 0.35
Clark's grebe <i>Aechmophorus clarkii</i>	1, 7, 13	1-6	1***	45.7 (1, 112)	<0.001	28.4 0.91
Red-necked grebe <i>Podiceps griseogena</i>	1, 7, 14	1-6, 13	1**	4.0 (7, 88)	<0.001	46.6 0.22
Horned grebe <i>Podiceps auritus</i>	1	1-6	1**	3.6 (6, 97)	<0.01	26.0 0.96
Eared grebe <i>Podiceps nigricollis</i>		1-6		0.5 (6, 97)	0.80	8.7 >0.99
Pied-billed grebe <i>Podilymbus podiceps</i>	1, 11	1-7, 11-13	3*, 7***, 11**, 13**	11.7 (10, 82)	<0.001	42.1 0.38
American white pelican <i>Podilymbus podiceps</i>	6, 12, 18	1-6	1*, 6**	2.8 (6, 97)	0.01	50.5 0.12
Brown pelican <i>Pelecanus occidentalis</i>	5	1-6	1**, 5**, 6**	4.7 (6, 97)	<0.001	41.8 0.39
Brandt's cormorant <i>Phalacrocorax penicillatus</i>	5, 12, 24	1-6, 12	5*, 6*, 12*	10.0 (6, 97)	<0.001	47.8 0.19
Pelagic cormorant <i>Phalacrocorax pelagicus</i>	11, 17, 23, 28, 35, 41	1-6, 11	11***	2.9 (6, 97)	0.01	34.4 0.71
Great blue heron <i>Ardea herodias</i>	11, 18, 23, 30, 35, 42	1-12	1*, 3*, 4*, 5***, 6**, 12*	3.5 (12, 79)	<0.001	41.9 0.38
Great egret <i>Ardea alba</i>	1, 13	1-6, 12	1*, 6, 12**	3.4 (7, 89)	<0.01	25.0 0.97
Snowy egret <i>Egretta thula</i>	2, 8	1-7, 12	2*, 3, 6**, 7***, 12**	8.0 (8, 87)	<0.001	16.7 >0.99
Canada goose <i>Branta canadensis</i>	1, 7, 13, 19, 25	1-13	1***, 2*, 3, 4*	5.8 (6, 97)	<0.001	33.2 0.77
Gadwall <i>Mareca strepera</i>	1, 7, 13, 19, 25, 31	1-12	1**	1.6 (12, 79)	0.10	51.0 0.12
Green-winged teal <i>Anas crecca</i>	1, 7	1-6	1**, 6***	5.9 (6, 97)	<0.001	29.8 0.88
Northern shoveler <i>Spatula clypeata</i>		1-6	6*	2.1 (6, 97)	0.06	21.2 >0.99

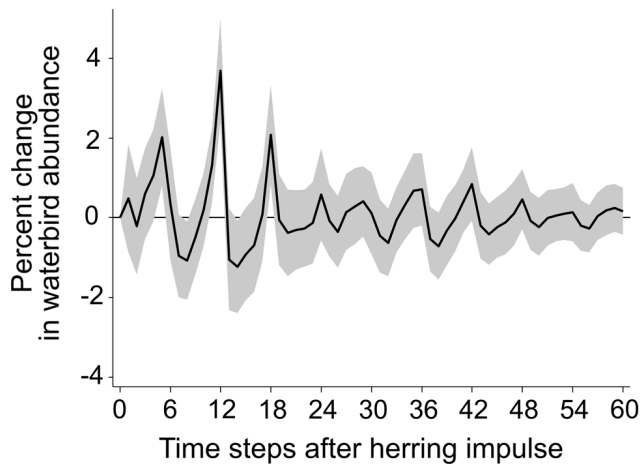


Fig. 3. Orthogonal impulse-response function of the percent change in winter waterbird abundance in Tomales Bay (all species combined, December to February, 1989 to 2012), for each percent increase in the spawning biomass of Pacific herring associated with any unexpected, one-time impulse of herring biomass in year zero ($x = 0$), based on 6 time steps yr^{-1} . Shaded area: 95% confidence intervals

Consumption of herring roe

Roe-eating waterbirds in Tomales Bay were capable of collectively consuming an annual average of 14.1 ± 3.7 t of herring roe d^{-1} (min. = 11.2; max. = 19.1) over the 90 d (December to February) herring season, assuming that birds consumed only herring roe when available, at their energetic maximum rate. The most abundant roe-eaters with the greatest collective energy demand were surf scoter *Melanitta perspicillata*, greater scaup *Aythya marila*, brant *Branta bernicla*, and bufflehead *Bucephala albeola* (Table 1). Based on variation in annual waterbird abundances and the intraseasonal availability of herring roe, wintering waterbirds were collectively capable of consuming an average of $89 \pm 3.7\%$ of the available roe each year if storing energy maximally; the actual amount of roe consumed would be considerably less because substantial amounts of roe may be lost to tidal and wave action and some is consumed by fishes and invertebrates. Given maximal consumption rates to hedge against periods of reduced foraging efficiency with an abundant yet ephemeral food supply, waterbirds may have been capable of consuming all of the available herring roe in 9 of 17 years (although a declining functional response and competition would likely limit consumption at low roe densities). On average, among years, the potential consumption of available herring roe in Tomales Bay accounted for $20 \pm 3.6\%$ of the collective energy needs of waterbirds during the 90 d

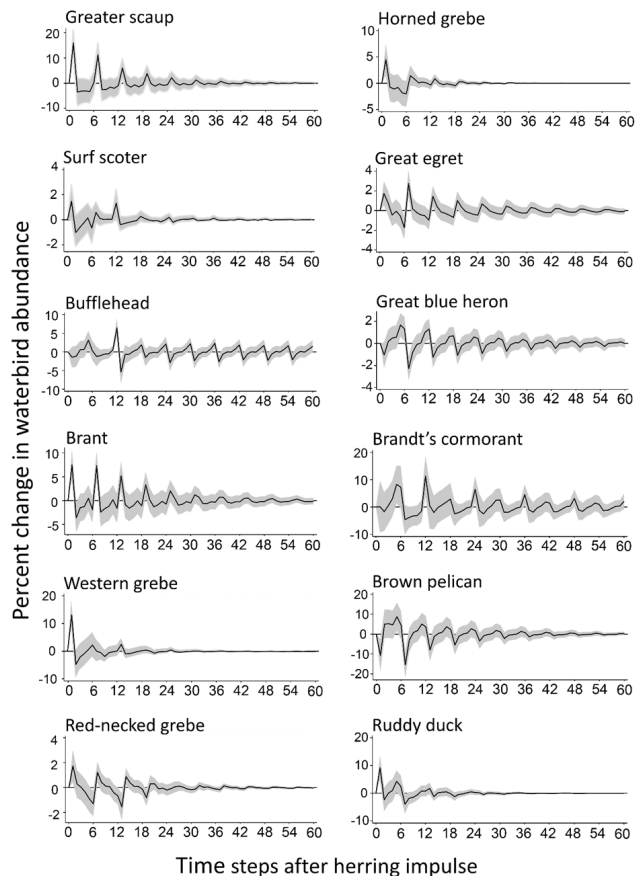


Fig. 4. Orthogonal impulse-response functions of the percent change in different waterbird species' abundance in Tomales Bay (December to February, 1989 to 2012), for each percent increase in the spawning biomass of Pacific herring associated with any unexpected, one-time impulse of herring biomass in year zero ($x = 0$), based on 6 time steps yr^{-1} . Shaded area: 95% confidence intervals

herring season (max. = 64.1%; min. <1% [deposition of only 219 kg roe in 2006–2007]).

Distributional responses to spawning events

Several waterbird species in Tomales Bay significantly shifted their distributions in the bay within 2 d of herring spawning events (Table 3). These shifts were associated with average increases in the vicinity of herring spawning events of nearly 200% in the densities of double-crested cormorants *Phalacrocorax auritus* and surf scoters and of over 150% in greater scaup. Other species, such as bufflehead and brant, exhibited sustained bay-wide increases in winter abundance in response to impulses of herring spawning activity (Table 2, Fig. 4) but did not significantly shift their distributions toward individual spawning

Table 3. Distributional responses of waterbirds to herring spawning events in Tomales Bay, California, 1990 to 2007, within 12 sub-areas of the bay (Fig. 1), are indicated as significant ($p < 0.05$) or marginally significant ($p < 0.07$) percent increase in waterbird density and 95 % confidence intervals (CI), associated with a herring spawning event within the previous 2 days, relative to the expected density without a spawning event ($n = 828$). Estimates for percent increase are based on back-transformed coefficients for change in \log_e density from linear mixed-effects models (year as a random effect)

Species	Percent increase	95 % CI	p
Double-crested cormorant	198	73.7–412.2	<0.001
Surf scoter	191	86.9–352.4	<0.001
Greater scaup	153	30.1–391.3	0.006
Common goldeneye	92	29.6–185.0	0.001
Red-throated loon	86	12.2–208.0	0.016
Brown pelican	79	6.7–201.9	0.028
Black scoter	49	-3.2–128.7	0.070
Horned grebe	47	-1.7–119.3	0.061

events (Table 3). Conversely, some species, such as horned grebe and brown pelican, significantly altered their within-bay distributions to exploit herring spawning events (Table 3), but their longer term, bay-wide responses to impulses of herring spawning biomass were relatively limited, declining to expected background levels after the second year (Table 2, Fig. 4). None of the distributional responses of waterbird species were significantly related to the size of spawning events ($p > 0.05$).

DISCUSSION

Our results provide evidence that waterbird numbers in Tomales Bay are functionally related to the availability of Pacific herring *Clupea pallasii*. Specifically, increases and decreases in the herring spawning biomass lead, respectively, to temporally distributed increases and decreases in waterbird abundances relative to underlying trends. Unusual increases in herring spawning biomass increase the growth rates of waterbird abundances in Tomales Bay and, for most species, those increases persist over multiple years.

The observed increases in waterbird numbers in response to pulses of herring spawning activity suggest 'variance-prone' foraging. After the initial response, however, most waterbirds exhibit an aversion to subsequent declines in herring activity, consistent with the likely enhancement of their average nutritional state (Kacelnik & Bateson 1996), marked

by a continuing pattern of enhanced annual growth that falls off gradually over multiple years. Given the sustained numerical responses of most waterbirds, any repeated pulses of herring activity before enhanced waterbird numbers decline to previous levels would lead to compounded rates of increasing waterbird abundance relative to underlying trends.

The persistent annual increases in waterbird abundances observed in this study, for up to 4 or 5 yr in response to pulses of increased herring biomass suggest continuing benefits in terms of potential fitness. Such benefits may involve (1) enhanced winter philopatry, (2) increased recruitment of wintering adults or juveniles, (3) an expectation of profitable 'aftershocks' of increased herring spawning activity, or (4) lagged trophic effects of increased herring biomass on the future availability of herring or other prey. However, we did not directly investigate these possible explanations. Strong patterns of winter philopatry are considered to reflect potential fitness benefits based on prior knowledge of profitable habitats and available food in familiar wintering areas (Robertson & Cooke 1999), which might drive site faithfulness in juvenile or adult waterbirds that choose to winter in the bay during good herring years. Benefits to philopatric or newly recruited individuals may include not only improved physical condition and increased overwinter survival, but also enhanced reproductive success if they obtain advantages in finding previous mates or mates that are also in good condition (Robertson & Cooke 1999).

Although herring spawning activity varies dramatically among years (CDFW 2001, Schweigert et al. 2010), the possible expectation of profitable 'aftershocks' of repeated spawning activity is supported by significant autocorrelation of spawning biomass (Portmanteau tests, $p < 0.0001$) and by significant, positive serial correlation of spawning activity at lags of 1 and 2 yr (respectively, $r = 0.37$, $p < 0.0001$ and $r = 0.23$, $p < 0.03$). The potential for lagged trophic enhancement on future prey abundances for waterbirds is unknown but suggested by substantial consumption of herring spawn by numerous other estuarine taxa, especially crabs and other epibenthic invertebrates and fishes (Haegle & Schweigert 1990, Haegle 1993b, Schweigert et al. 2010).

Although moderate-to-strong winter philopatry has been found in many species of waterfowl (Robertson & Cooke 1999, Eadie & Savard 2015), our results suggest considerable variation in the long-term responses to spawning herring among those species (e.g. greater scaup *Aythya marila*, surf scoter *Melanitta perspicillata*, bufflehead *Bucephala albe-*

ola). Waterbird species that consume primarily fish also vary considerably in their responses to pulses of herring. For example, the responses by red-necked grebes *Podiceps grisegena* and great egrets *Ardea alba* suggest significant conditional variance aversion over multiple years, whereas the responses of western grebes *Aechmophorus occidentalis*, horned grebes *Podiceps auritus*, and common loons *Gavia immer* exhibit short-term responses consistent with variance-prone behavior and a quick return to previous bay-wide abundances after increases in herring activity subside to normal levels. We are unable to explain the absence of significant responses by some piscivorous species (Pacific loon *Gavia pacifica*, red-breasted merganser *Mergus serrator*, and eared grebe *Podiceps nigricollis*), which could involve the exploitation of other prey or the use of other foraging areas, including coastal waters outside the bay. Available data on winter survival and lifespan among waterbird species are too limited to account for the differences observed in this study. A few species, such as Brandt's cormorant *Phalacrocorax penicillatus*, great blue heron *Ardea herodias*, and brown pelican *Pelecanus occidentalis*, exhibited minimal or delayed intraseasonal responses to impulses of herring activity, suggesting the possible late-winter movements, delayed detection of herring activity by birds wintering elsewhere in the region, or enhanced recruitment in subsequent years, but data are lacking to evaluate these possibilities. Many great blue herons may remain close to nesting areas in mid-to-late winter (Kelly et al. 2008), potentially limiting their ability to detect incursions of herring in other wetland systems. Further investigation is needed to understand the variation among waterbird species responses to herring spawning activity over time, which may involve complex differences related to philopatry, juvenile recruitment, midwinter movements, foraging habitat, energy balance, alternative prey populations, competition, or other aspects of their winter ecology (Robertson & Cooke 1999).

The relatively limited response by surf scoter, a species known to heavily exploit herring spawning events (Bayer 1980, Bishop & Green 2001, Anderson et al. 2009), is consistent with limited intraseasonal movements by wintering surf scoters in similar soft-bottom habitat in British Columbia, where habitat conditions and available prey are relatively stable (Kirk et al. 2008). The limited persistence of the surf scoter response might reflect frequent shifts to forage in nearby waters of the outer coast when herring biomass is low. However, we did not investigate waterbird movements or behaviors that might account for

the responses observed in this study. In addition, our results for surf scoter may be confounded by difficulties in modelling background variation related to their complex patterns of population change along the Pacific Coast of North America (Crewe et al. 2012, Anderson et al. 2015, Olson 2017).

The numerical responses of wintering waterbird species to large influxes of herring may represent a form of ecological release, resulting from the removal of constraints related to prey availability, foraging habitat selection, or energy balance (MacArthur & Wilson 1967, Bolnick et al. 2010). The capacity of waterbirds to consume, on average, 89% of the available herring spawn (100% in 9 of the 17 years of study), suggests that an increase in the number or size of spawning events could increase the extent to which waterbird energy requirements are met by available herring roe. If so, increases in the availability of herring may increase the carrying capacity of Tomales Bay for wintering waterbirds. Similarly, declines in waterbird abundance are predicted in response to any unusual decline in herring spawning biomass (as mirror images of responses to increased spawning biomass of the same magnitude), suggesting an associated decline in the carrying capacity of the bay. Anderson et al. (2009) found that the numerical responses of surf scoters and white-winged scoters *Melanitta fusca* in Puget Sound, Washington, increased with increasing biomass of spawning herring. Other studies have also demonstrated that the abundances of marine birds and other predators are limited by the availability of herring or other forage fish (Cury et al. 2000, Fauchald et al. 2011).

Gulls *Larus* spp. were excluded from our waterbird surveys and calculations of potential energy consumption from herring eggs. Gulls are potentially important consumers of herring roe (Bishop & Green 2001), but the number of eggs harvested by gulls is variable and may be much smaller than the numbers consumed by scoters, scaup, and other diving birds (Bayer 1980, Haegele 1993a). In Tomales Bay, herring roe is generally not available to gulls, except by pirating eggs from diving birds or picking up eggs that may drift in the water. In addition, wintering gulls in Tomales Bay typically commute daily to regional landfills to feed on garbage (Kelly et al. 1996, Kelly 2001). Gulls may join feeding flocks above active spawns, but local conditions strongly limit their access to herring eggs, which they can reach directly only if the eggs are deposited in a few particular areas that are both suitable for spawning (Haegele et al. 1981) and exposed by extremely low tides.

A relatively small number of waterbird species within Tomales Bay exhibited significant distributional shifts toward individual spawning events. Interestingly, many waterbird species showed numerical responses to the enhanced availability of herring or herring roe but did not exhibit significant movements toward spawning events. This suggests that many species that exploit herring spawn may not pursue spawning schools of herring or may avoid intense competition in feeding flocks associated with spawning events. Alternatively, our analyses may not have been intensive enough to detect the movements of many species. Significant shifts toward herring spawning events by double-crested cormorants *Phalacrocorax auritus*, red-throated loons *Gavia stellata*, and brown pelicans were consistent with the consumption of adult herring (Haegele 1993a, Bishop et al. 2015). Previous work in Tomales Bay identified an array of differences in waterbird species' habitat preferences and distributions in the bay (Kelly & Tappen 1998). Such differences, along with the distribution of eelgrass *Zostera marina*, might facilitate or limit the movements of waterbirds toward spawning events.

Given our results showing persistent responses to herring spawning activity by many waterbird species and the potential importance of energy from herring or herring roe in supporting the seasonal energy requirements of waterbirds, the maintenance of strong herring stocks may be a fundamental factor in sustaining concentrations of estuarine waterbirds along the Pacific Coast of California. The size and dynamics of Pacific herring stocks are limited by complex combinations of environmental processes, each influenced by the changing climate, including effects on spawning grounds or early life history stages, oceanic conditions such as upwelling, changes in the availability of suitable spawning habitat (eelgrass), variation in food supply (zooplankton), competition (e.g. Pacific sardine *Sardinops sagax* abundance), predation by marine mammals and fish, and intensive fishing (Schweigert et al. 2010, Siple & Francis 2016). The multiyear dependence of waterbirds on spawning herring in Tomales Bay suggests that any further limits on herring stocks imposed by these processes are likely to impact the abundances of wintering waterbirds. The incorporation of commercial fisheries data into analyses similar to the study presented here may be useful in evaluating the extent to which potential competition between humans and waterbirds for herring or herring roe might limit the abundances of estuarine waterbirds. Our results provide evidence that improvements in the size of herring

stocks are likely to enhance local waterbird numbers. Therefore, effective ecosystem-based management of the Pacific herring fishery may be important in managing the abundances of estuarine waterbirds.

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