



Bottom-up and top-down control of small pelagic forage fish: factors affecting age-0 herring in the Strait of Georgia, British Columbia

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ABSTRACT: Small pelagic fish are key planktivores and prey in marine ecosystems, and their population abundances undergo strong temporal and spatial variability. Top-down (predator controlled) and bottom-up (prey-driven) processes during early life history are important for determining forage fish survival and recruitment. We examined biological and environmental factors hypothesized to influence age-0 Pacific herring *Clupea pallasii* in the Strait of Georgia (SOG), British Columbia, Canada. Primarily bottom-up processes affected interannual variability in age-0 herring abundance and condition, with some evidence of top-down effects on condition. Age-0 herring abundance increased with increasing adult spawning biomass and peaked when most adults spawned about 20 d prior to the peak spring primary production bloom. This timeline would temporally align first-feeding herring larvae with their prey, such as small copepods. Age-0 herring abundance also increased with increasing juvenile salmon abundance, indicating that conditions favourable for herring were also favourable for their predators and competitors. Age-0 herring condition decreased with increasing spawning biomass, increased when most adults spawned closer to the peak spring bloom, increased with increasing temperatures above 8.2°C, and increased then stabilized with increasing prey zooplankton density. Age-0 herring condition had a dome-shaped relationship with predator abundance, indicating that high predator abundances negatively affected fish condition. Study results suggest that density-dependent processes, such as intraspecific competition, may be important in the SOG. A positive correlation between age-0 herring abundance and subsequent age-3 recruit abundance may provide a leading indicator of low recruitment years.

KEY WORDS: Age-0 herring · Abundance · Condition · Bottom-up · Top-down · Forage fish · Strait of Georgia · Density dependence

INTRODUCTION

Processes occurring during the early life history of fish have been hypothesized as being important for determining fish survival and recruitment (Cushing 1969, Lasker 1975, Parrish et al. 1981, Schweigert et al. 2013). Small pelagic forage fish have been studied

extensively, and numerous hypotheses have been proposed to explain recruitment variability (Hjort 1914, Cushing 1972, Sinclair & Iles 1989, Bakun 1993), each with varying amounts of evidentiary support (Leggett & Deblois 1994). For example, bottom-up (prey-driven) mechanisms are important in Hjort's (1914) critical period hypothesis, which states that

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the oceanographic environment affects larval survival, thereby affecting recruitment success. In Lasker's (1975) 'stability' hypothesis, a stable environment is needed to allow successful feeding by larvae. There are additional bottom-up hypotheses that link larval survival and recruitment to ocean transport (Parrish et al. 1981), mesoscale oceanographic events (Sinclair & Iles 1989), and enrichment, retention, and concentration (Bakun 1993). Cushing's (1969) match–mismatch hypothesis states that the temporal overlap of fish larvae and their prey determines year class strength. Fish that acquire enough energy stores and are in good condition can also survive periods of low food availability such as their first winter (Paul et al. 1998, Foy & Paul 1999, Frisk et al. 2015). Top-down (predator-driven) processes have been identified as important in other hypotheses. For example, fast growth in good feeding conditions has been hypothesized to shorten the duration of exposure to predators (Cushing & Harris 1973, Bailey & Houde 1989, Meekan & Fortier 1996). Forage fish in 'wasp-waist' ecosystems can be driven by both top-down and bottom-up processes (Cury et al. 2000). The importance of top-down and bottom-up processes on fish growth and recruitment varies among species, regions, and life history stage, but are likely of particular importance during the pre-juvenile phase (Houde 1987, Leggett & Deblois 1994).

Several studies have examined environmental and biological drivers of Pacific herring *Clupea pallasii* recruitment (e.g. Stocker et al. 1985, Schweigert et al. 2013). For example, environmental variables, along with adult herring spawning biomass, have been identified as drivers of herring recruitment, including sea surface temperature, salinity, sea level, river discharge, and Ekman transport (Stocker et al. 1985, Stocker & Noakes 1988, Schweigert & Noakes 1990, Zebdi & Collie 1995). Multiple environmental variables that are region- or stock-specific improve forecasts of Pacific herring recruitment (Williams & Quinn 2000, Dreyfus-León & Chen 2007, Dreyfus-León & Schweigert 2008). The effect of temperature and salinity on fish survival between the egg and first-feeding larval stages is a potential mechanism affecting recruitment (Alderdice & Hourston 1985). Reum et al. (2013) found that the size of age-0 Pacific herring in Puget Sound was related to temperature in the summer and to abundance in the fall—the latter suggesting density dependence. Pacific herring off the west coast of Vancouver Island (WCVI) may be driven by several processes, such as prey availability, competition, and predation (Schweigert et al. 2010). The abundance of Strait of Georgia (SOG) age-0

Pacific herring in the fall has been previously attributed to the match or mismatch (i.e. Cushing's 1969 match–mismatch hypothesis) in the timing between larval herring energy requirements and the spring plankton bloom (Schweigert et al. 2013).

Pacific herring in the SOG, which are an important species for First Nations and commercial fishers, undergo considerable variability in recruitment abundances due in large part to mortality during their first months of life (Schweigert et al. 2009). In late winter and spring, adult SOG herring (age-3 and older) migrate from summer feeding areas in coastal shelf waters off the WCVI to the SOG to spawn (Taylor 1964). Eggs are predominately deposited on shallow macrophytes, such as eelgrass, rockweed, kelps, and algae (Humphreys & Hourston 1978, Haegele et al. 1981). Herring egg hatching time is temperature dependent and can range from 9 to 33 d (Outram 1955, Alderdice & Velsen 1971, Taylor 1971, Alderdice & Hourston 1985). Larval yolk reserves are utilized in approximately 1 or 2 wk, depending on temperatures and salinities (Alderdice & Velsen 1971). After hatching and yolk absorption, age-0 herring spend their first summer in nearshore areas, close to the sea floor during daytime hours and dispersed in the upper portion of the water column during nighttime hours (Haegele & Armstrong 1997, Emmett et al. 2004).

Primary predators of age-0 herring in the SOG include juvenile coho salmon *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* that consume age-0 herring during the summer and fall (Beamish et al. 2004, Duffy et al. 2010, Preikshot et al. 2013, Kemp 2014). Other age-0 herring predators might include adult Chinook and coho salmon, Pacific hake *Merluccius productus*, spiny dogfish *Squalus suckleyi*, seabirds, and perhaps pinnipeds (Schweigert et al. 2010); however, in the SOG, there is either limited information on the specific age of herring that these predators consume and/or there is limited time series of the abundance of these predators. Potential competitors include juvenile chum *O. keta*, pink salmon *O. gorbuscha*, and sockeye salmon *O. nerka*, which all share common prey items (such as amphipods, copepods, and euphausiids) with age-0 herring (Haegele 1997, Beamish et al. 2004).

The objective of this study was to examine the influence of biological and environmental factors on the interannual variability of SOG age-0 herring abundance and condition. Factors included adult herring spawning biomass and timing of spawning, prey availability, predator abundance, competitor abundance, and ocean temperatures. It was pre-

dicted that age-0 herring abundance would be higher with fewer predators (Chinook, coho), fewer competitors (pink, chum, sockeye), more prey (zooplankton), higher adult herring spawning biomass, and if the date of peak adult herring spawning biomass temporally aligned hatched larvae with their prey. The same predictions applied for age-0 herring condition, except it was expected that condition would be higher when there were more predators (Chinook and coho) that would selectively remove fish in poorer condition (Tucker et al. 2016), fewer adult herring spawning (resulting in less intraspecific competition), and with warmer temperatures (resulting in higher productivity and food availability).

MATERIALS AND METHODS

Field and laboratory sampling

The SOG age-0 Pacific herring *Clupea pallasii* survey time series was used to estimate the relative abundance and condition of age-0 herring after their first summer, following methods described in Boldt et al. (2015). The survey was conducted annually during September and October from 1992 to 2016 (except 1995) using survey methodology and transect locations described in Thompson et al. (2003). There were 10 core transects, each with 3 to 5 core stations, distributed at approximately equal intervals around the perimeter of the SOG (Fig. 1, Table 1). Sampling was conducted after dusk when herring were near the surface, and generally one transect was sampled per night over the course of a 4 to 7 h period. A purse seine was used for all fishing events, and techniques (e.g. pursing speed and drumming of net) were kept as uniform as possible among years. During 1996 to 2016, the net used was 183 m long \times 27 m deep, resulting in an area fished of ~ 2660 m² (based on the geometric formula for the area of a circle). Prior to 1995, the net length was 220 m long \times 27 m deep, resulting in an area fished of 3852 m². Net mesh sizes remained the same throughout the time series. The 11.6 m Fisheries Research Vessel 'Keta' was used from 1992 to 1994 and the 12 m Fisheries Research Vessel 'Walker Rock' was used from 1996 to 2016.

Some exceptions in sampling occurred; for example, from 1997 to 1999, only 2 or 3 stations were sampled along core transects. In some cases the presence of large abundances of jellyfish inhibited the ability to acquire representative fish samples, and in some cases inclement weather prevented sampling. Over the 24 yr time series, there was a total possible sam-



Fig. 1. Purse seine set locations along the 10 core transects (1 to 6 and 8 to 11; there is no transect 7) of the Strait of Georgia juvenile Pacific herring survey. Grey and turquoise lines represent the 50, 100, 150, and 200 m isobaths. ▲: Chrome Island lighthouse

ple size of 1152 stations from the 10 core transects and 48 core stations. The realized sample size was 1056 stations because 96 stations were not sampled (Boldt et al. 2015, Thompson & Boldt in press, Thompson et al. in press).

For most purse seine sets, it was possible to land the entire catch for biological sampling. On occasion, it was not practical to land a large set in its entirety, so subsampling was necessary and total catch weight was visually estimated (see Boldt et al. 2015). Catch per unit effort (CPUE) was calculated as catch weight (g) divided by the area fished by the net. All fish (or a subsample of fish) were retained for sampling in the laboratory, with the exception of large predator species (e.g. adult salmon and flatfish), which were individually measured in the field. During 1992 to 2013, all fish were preserved in a 10% formalin and seawater solution, whereas from 2014 to 2016, fish were frozen. In the laboratory, herring from each station were measured to standard length (mm) and weighed (g). Herring were assigned to age-class by examining the length frequencies (e.g. Thompson et al. 2013). No corrections to fish lengths or weights were made to account for shrinkage due to preservation methods used (formalin from 1992 to 2013 vs. freezing from 2014 to 2016), because the difference in percent shrinkage between the 2 preservation methods has

Table 1. Core station and transect names and locations sampled as part of the Strait of Georgia age-0 Pacific herring survey during September and October 1992 to 2016 (no survey in 1995; there is no Transect 7)

Transect	Transect name	Stn	Latitude (°N)	Longitude (°W)
1	Clarke Rock	1	49.22	123.94
1	Clarke Rock	2	49.23	123.93
1	Clarke Rock	3	49.24	123.92
1	Clarke Rock	4	49.24	123.91
1	Clarke Rock	5	49.24	123.90
2	Yellow Point	1	49.04	123.75
2	Yellow Point	2	49.05	123.73
2	Yellow Point	3	49.06	123.72
2	Yellow Point	4	49.06	123.71
2	Yellow Point	5	49.07	123.70
3	Bowser	1	49.45	124.68
3	Bowser	2	49.46	124.67
3	Bowser	3	49.47	124.66
3	Bowser	4	49.48	124.66
3	Bowser	5	49.48	124.65
4	Henry Bay	1	49.59	124.87
4	Henry Bay	2	49.60	124.87
4	Henry Bay	3	49.60	124.86
4	Henry Bay	4	49.60	124.85
4	Henry Bay	5	49.60	124.84
5	French Creek	1	49.35	124.35
5	French Creek	2	49.35	124.34
5	French Creek	3	49.36	124.33
5	French Creek	4	49.36	124.32
5	French Creek	5	49.37	124.32
6	Trincomali Channel	1	48.85	123.43
6	Trincomali Channel	2	48.86	123.42
6	Trincomali Channel	3	48.87	123.42
6	Trincomali Channel	4	48.87	123.41
6	Trincomali Channel	5	48.88	123.41
8	Smelt Bay	1	50.04	125.00
8	Smelt Bay	2	50.05	125.02
8	Smelt Bay	3	50.05	125.03
9	Atrevida Reef	1	49.92	124.66
9	Atrevida Reef	2	49.91	124.67
9	Atrevida Reef	3	49.91	124.68
9	Atrevida Reef	4	49.91	124.69
9	Atrevida Reef	5	49.90	124.71
10	Cape Cockburn	1	49.67	124.20
10	Cape Cockburn	2	49.66	124.22
10	Cape Cockburn	3	49.65	124.24
10	Cape Cockburn	4	49.64	124.26
10	Cape Cockburn	5	49.63	124.28
11	Secret Cove	1	49.53	123.98
11	Secret Cove	2	49.53	124.00
11	Secret Cove	3	49.53	124.01
11	Secret Cove	4	49.53	124.04
11	Secret Cove	5	49.52	124.06

been shown to be small. If conversion formulae for *Gadus chalcogramma* of similar sizes (Buchheister & Wilson 2005) were used, preserving an average sized age-0 herring (87.6 mm and 8.6 g) would result in a difference of 1.4 mm (1.6%) in length and 0.3 g (3.7%) in weight between freezing fish and preserving fish in 10% formalin.

Relative abundance of age-0 herring

To calculate an index of the relative abundance of age-0 herring, 2-stage sampling formulae (Thompson 1992) were used to calculate the mean and variance of weight CPUE (see Boldt et al. 2015 for detailed methods). The first stage of sampling was transects, assumed to be selected quasi-randomly without replacement. The second stage was stations that were systematically selected without replacement so that they were evenly spaced along transects. In 2-stage sampling, mean weight CPUE and variance were calculated using the second stage (stations) for each transect. Next, the mean weight CPUE and variance were calculated across the first stage averages (transects) to compute an overall mean. The variances resulting from each of the 2-stages of sampling were then combined to calculate an overall variance estimate (Thompson 1992). We assumed for our analyses, as stated in Szarzi et al. (1995, p. 279): '(1) sample sizes at each stage were assumed to be small compared to the total number of possible samples, therefore finite population correction factors were ignored; (2) to simplify calculations of means and variances it was assumed that the total numbers of possible samples at each stage were equal; and (3) it was assumed that the systematic random sampling at the second stage could be treated as simple random sampling for the calculation of variances.' Analyses were performed using R version 3.1.0 (R Core Team 2014).

Size and condition

Mean annual age-0 herring lengths and weights were calculated by averaging all measurements in each year. Individual herring weights were log transformed and regressed against log-transformed standard lengths for all years combined. Mean residuals from the log-transformed length-weight regression were calculated as an index of fish condition (hereafter referred to as length-weight residuals or condition); positive residuals indicate that fish were heavier for a given length than average and, hence, in better condition. An analysis of variance (ANOVA) was used to determine if the mean values of fish condition varied among years and a *k*-sample Anderson-Darling test was used to test if the distributions of condition values were similar among years. The R package 'kSamples' was used for this test (R Core Team 2014, Scholz & Zhu 2016).

Zooplankton

Zooplankton samples were collected using stepped oblique tows at 2 to 5 stations on each transect immediately prior to and at the same locations where herring were sampled (Haegele 1997, Thompson et al. 2003). The net was a dual 19 cm diameter bongo net with 350 μm mesh, equipped with a flowmeter to acquire the volume filtered. Samples were collected from 20 or 10 m (for shallow stations) depths using

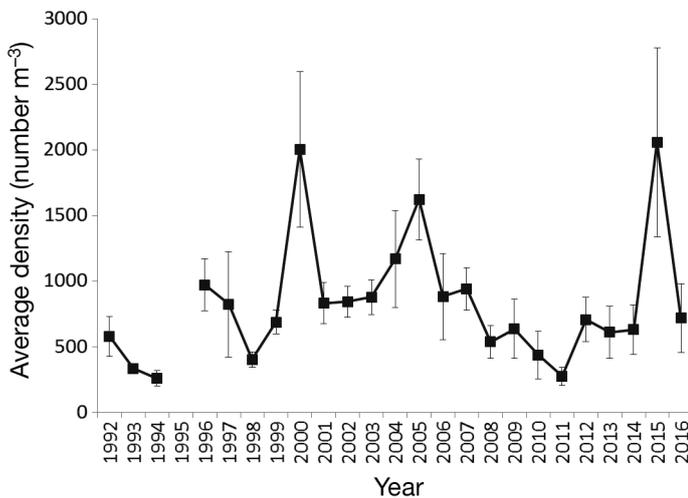


Fig. 2. Average (\pm SE) density of zooplankton animals that are prey for age-0 Pacific herring in the Strait of Georgia, September and October 1992 to 2016

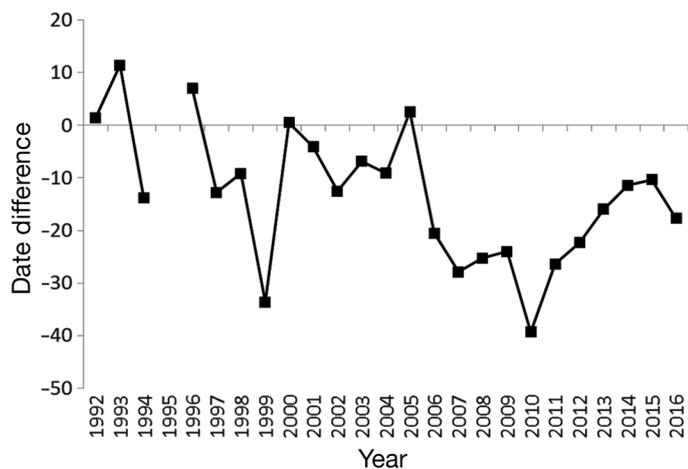


Fig. 3. Date difference (days) between when most adult Pacific herring spawned relative to the date of the peak spring primary production bloom during 1992 to 2016 (except 1995). Date difference is the mid-spawn date, weighted by spawn biomass, minus spring bloom date (peak spring bloom date from Allen & Wolfe 2013 and Allen et al. 2017). Values >0 indicate that most adult herring spawned after the peak spring bloom date; values <0 indicate that most adult herring spawned before the peak spring bloom date

methods outlined in Haegele (1997) and preserved in 10% formalin. In the lab, zooplankton species were enumerated to the lowest possible taxonomic group and densities calculated.

The density of age-0 herring prey in zooplankton samples was used as an indicator of prey availability. Previously published studies show that the main prey groups (percent number) of age-0 herring include copepods (58%; such as *Metridia pacifica*), barnacle cyprids and nauplii (10%), larvaceans (7%), *Euphausia pacifica* adults and larvae (2%), amphipods (2%), crab megalops and zoeae (2%), and other invertebrates (17%; e.g. cladocerans, ostracods, insects, chaetognaths, isopods, others; Haegele 1997, Haegele et al. 2005). To determine the availability of age-0 herring prey in the water column, densities of these prey groups (number m^{-3}) in each zooplankton sample were summed for each station and then averaged over all stations in each year (Fig. 2).

Models

To test whether top-down or bottom-up factors affect age-0 herring, general additive models (GAMs) were used to explore the relationships between age-0 herring abundance and condition, as response variables, and biotic and abiotic predictor variables. The first predictor variable was an index of adult herring spawning biomass that would have spawned the age-0 progeny. The index was calculated from a dive survey of egg deposition conducted annually in the SOG that provided an index of eggs, from which adult spawning biomass was back calculated (see Schweigert 1993 for methods). In addition, the dates and adult spawning biomass were recorded for individual spawning events, so the date when most herring spawning occurred was known. The second predictor variable was the difference between the mean date of spawning (weighted by spawning biomass) and the spring bloom date. Negative values indicated that most herring spawned prior to the spring bloom and positive values indicated that most herring spawned after the spring bloom (Fig. 3). Model-based estimates of the peak spring bloom timing were provided by Allen et al. (2017), as calculated in Allen & Wolfe (2013). Shortly after the spring bloom date, it would be expected that zooplankton, such as small copepods (Mackas et al. 2013), would be available as prey for larval herring that have exhausted their yolk sac. The spring bloom date is therefore used as an indicator of subsequent zooplankton prey availability to age-0 herring. A third predictor variable in

the GAMs was the annual estimate of average density of age-0 herring prey in zooplankton samples collected during the age-0 herring survey as an indicator of prey availability. Temperature has been linked to processes at multiple herring life history stages, such as hatch rates, survival, metabolism, recruitment, and maturation (Alderdice & Hourston 1985, Hay 1985, Winters et al. 1986, Zebdi & Collie 1995, Toresen & Ostvedt 2000). A fourth predictor variable was sea surface temperatures (SST), as measured at the Chrome Island lighthouse in the SOG (www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html; accessed 23 September 2016). Monthly averages in December to March were used to estimate the winter SST.

To examine top-down and competitive factors, we included indices of predators and competitors as the final 2 predictor variables. Juvenile Chinook and coho salmon are predators of age-0 herring in the SOG during July to September (Beamish et al. 2004, Duffy et al. 2010, Kemp 2014), whereas juvenile chum, pink, and sockeye salmon are potential competitors because they consume similar prey items as age-0 herring (Beamish et al. 2004). Predators may reduce the abundance of age-0 herring or they may affect age-0 herring condition. For example, predators may only select prey that are in poor condition relative to those that are available (Tucker et al. 2016); therefore, the fish that survived would be larger and in better condition. SOG surface trawl surveys conducted by Fisheries and Oceans Canada (DFO) in July and September each year provide an index of relative abundance (CPUE; no. of fish caught h^{-1}) of each juvenile salmon species (Beamish et al. 2012, C. Neville, DFO unpubl. data). The sum of species-specific average CPUEs provided indices of relative predator (juvenile Chinook and coho salmon) and competitor (juvenile chum, pink, and sockeye salmon) abundances.

Age-0 herring abundance was log transformed to achieve normality (log-transformed weight CPUE) and modeled as a smooth spline function of herring spawning biomass, the difference between mid-spawn date weighted by herring spawning biomass and the spring bloom date, prey zooplankton density, predator CPUE, and competitor CPUE. Age-0 herring condition (log-transformed length–weight residuals) was modeled as a function of the same factors but also with Chrome Island lighthouse SST (winter average during December to March).

To ensure predictor variables included in the models were not overly correlated, multicollinearity among variables was examined. Variance inflation

factors were also examined to check for collinearity among predictor variables using the method of Zuur et al. (2009). All hypothesized variables were included in initial GAMs and knots were constrained to 3 to reduce overfitting. Non-significant variables were removed one at a time, starting with the highest p-value, if 2 of 3 conditions were met (Wood & Augustin 2002, Weinberg & Kotwicki 2008): (1) $p > 0.05$; (2) generalized cross validation (GCV) score was reduced when the variable was eliminated; and (3) effective degrees of freedom were close to 1.0. The 'mgcv' (Wood 2004, 2006) library in R was used to run the GAM models.

RESULTS

Age-0 herring abundance, size, and condition

Of the 1056 seine net samples collected between 1992 and 2016, 836 samples contained age-0 Pacific herring *Clupea pallasii*; 220 samples had none. Three years had high proportions of samples with no age-0 herring: 1993 (0.46; 22 of the 48 samples); 2005 (0.74; 34 of the 46 samples); and 2007 (0.87; 40 of the 46 samples). Together, the zero-catches in these 3 years comprised almost half of all zero-catches in the time series.

Estimates of age-0 herring CPUE (catch weight) varied annually, with no overall trend during 1992 to 2016 (Fig. 4). Age-0 herring CPUE peaked every 2 or 3 yr, with peaks occurring in even years from 2004 to 2012. The index was relatively low and stable during 2013 to 2016 compared to the peaks within the time

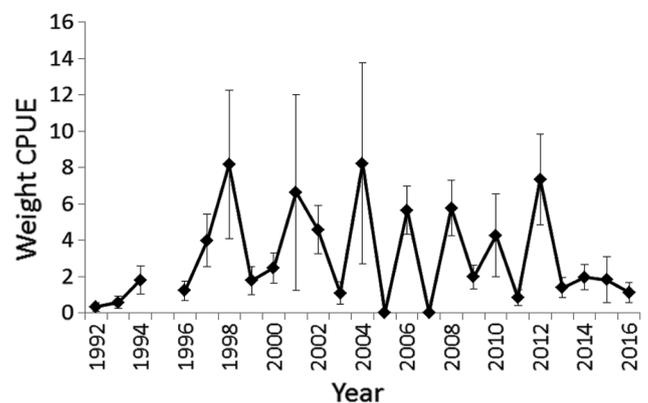


Fig. 4. Estimates of catch weight per unit effort (Weight CPUE; g m^{-2}) of age-0 Pacific herring caught in the Strait of Georgia age-0 herring survey at core transects and stations during September and October 1992 to 2016 (no survey in 1995). Standard error bars (using the Thompson 1992 variance estimator) are shown

series. High estimates of variability were associated with peak estimates; the survey CV was 0.47 averaged across all years.

Average age-0 herring lengths and weights ranged from 75 to 99 mm and 5 to 13 g, respectively (Fig. 5). During the time series, there was no significant linear temporal trend in mean lengths or weights of age-0 herring (Fig. 5). There was, however, a temporal shift in length–weight residuals (condition) of age-0 herring that was negative from 1992 to 2004 and 2006, and positive during 2005 and 2007 to 2016 (Fig. 6). The mean condition of age-0 herring differed significantly among years ($p < 0.001$) and increased during 1997 to about 2011 (Fig. 6). The distributions of condition values differed significantly among years ($p < 0.001$), with a broader range of values in years prior to 2005 compared to years after 2007.

Models

Variables retained in the final age-0 herring abundance model were herring spawning biomass, the timing of when most herring spawned relative to the

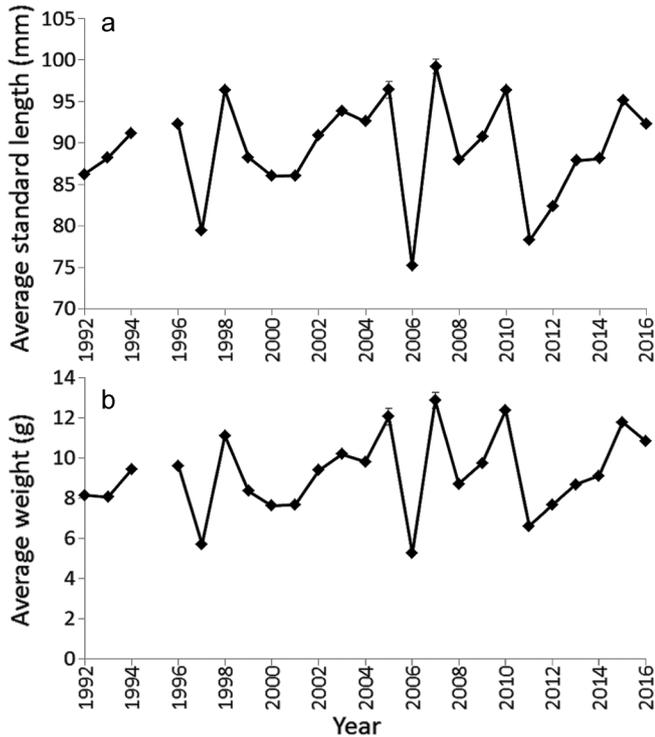


Fig. 5. Age-0 Pacific herring mean (a) standard lengths and (b) weights measured during the fall age-0 herring survey, September and October 1992 to 2016 (no survey in 1995). Standard error bars are shown, but are small: 0.1 to 3.5% of the mean values

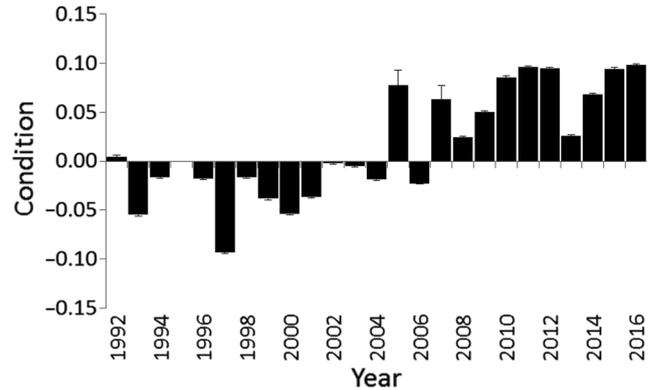


Fig. 6. Age-0 Pacific herring condition (length–weight residuals from a double log-transformed length–weight relationship) in the Strait of Georgia, during September and October 1992 to 2016 (except 1995). Standard error bars are shown

spring bloom, predator abundance, and competitor abundance (Fig. 7). Prey zooplankton density was not included in the final model. Total deviance explained by this model was 54%. Age-0 herring abundance (1) increased with increasing herring spawning biomass, (2) was highest when the peak herring spawn occurred about 20 d prior to the spring bloom, (3) increased with increasing predator abundance, and (4) increased with increasing competitors and then leveled off (with high variability and few data points; Fig. 7).

In the final age-0 herring condition GAM, variables retained were herring spawning biomass, the timing of when most herring spawned relative to the spring bloom, predator abundance, SST, and prey zooplankton density (Fig. 8). The variable excluded from the final model was competitor abundance. Total deviance explained by this model was 87%. Age-0 herring condition (1) decreased with increasing spawning biomass, (2) increased when most herring spawned closer to spring bloom, (3) increased with increasing temperatures above 8.2°C, (4) followed a dome-shaped relationship with predator abundance, and (5) increased to level with increasing prey zooplankton density (with high variability and few data points at high prey zooplankton densities; Fig. 8).

DISCUSSION

In this study we identified important drivers of age-0 Pacific herring *Clupea pallasii* abundance and condition. Age-0 herring abundance and condition were linked to the date when most herring spawned relative to spring bloom date. We did not detect any negative impacts of salmon competitors (*Oncorhynchus*

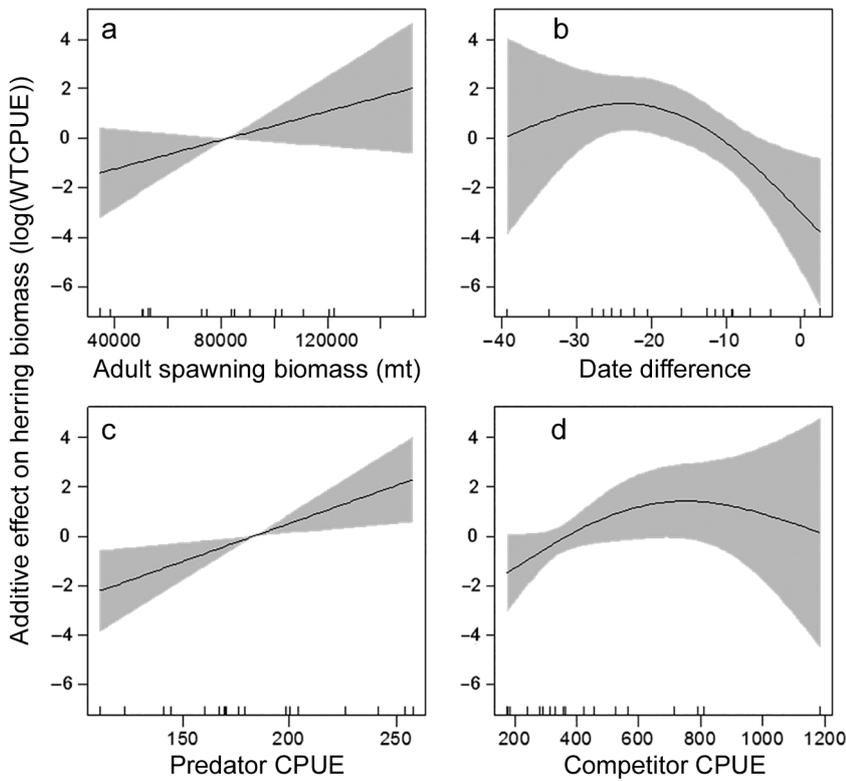


Fig. 7. General additive model results showing the additive effect of predictor variables on the relative index of age-0 Pacific herring biomass (log catch weight per unit effort [WTCPUE]). Predictor variables that were included in the final model were (a) adult herring spawn biomass, (b) date difference between the date when most adult herring spawned and the peak spring bloom (days), (c) juvenile salmon predator catch per unit effort (CPUE), and (d) juvenile salmon competitor CPUE

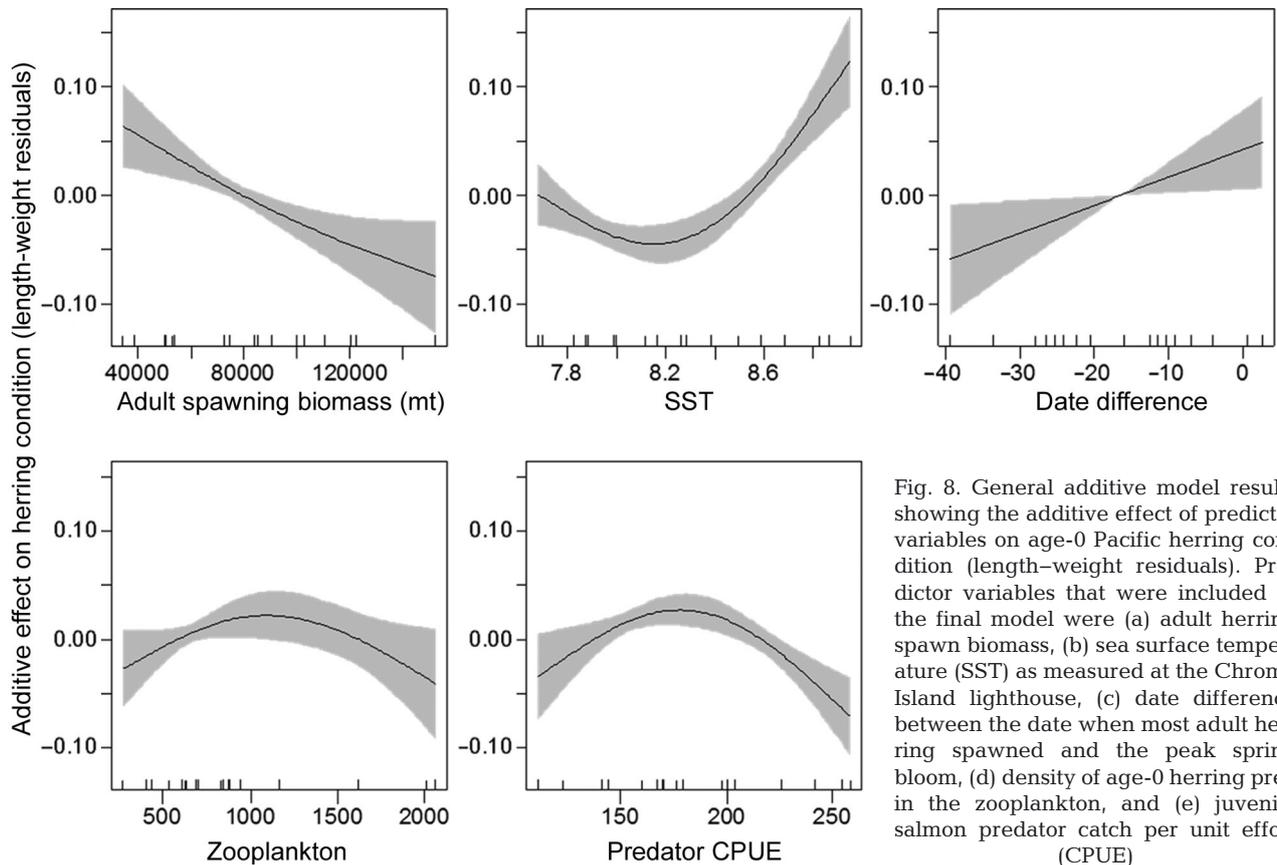


Fig. 8. General additive model results showing the additive effect of predictor variables on age-0 Pacific herring condition (length-weight residuals). Predictor variables that were included in the final model were (a) adult herring spawn biomass, (b) sea surface temperature (SST) as measured at the Chrome Island lighthouse, (c) date difference between the date when most adult herring spawned and the peak spring bloom, (d) density of age-0 herring prey in the zooplankton, and (e) juvenile salmon predator catch per unit effort (CPUE)

gorbuscha, *O. keta*, and *O. nerka*) on herring abundance or condition. Salmon predators (*O. kisutch* and *O. tshawytscha*) negatively influenced age-0 herring condition (not abundance) at high predator abundances. With this evidence, we conclude that primarily bottom-up processes affect the abundance and condition of SOG age-0 herring, with some evidence of additional top-down effects on herring condition. Previous basin-scale studies also showed that primarily bottom-up processes affected herring (Ware & Thomson 2005, Perry & Schweigert 2008), and similar results were evident for adult herring in an adjacent geographic area on the WCVI (Schweigert et al. 2010).

Our herring abundance GAM is consistent with Cushing's (1969) match–mismatch hypothesis and results of Schweigert et al. (2013) because the temporal match or mismatch between prey and first feeding larvae determines, in part, age-0 herring abundance. Schweigert et al. (2013) found that age-0 herring recruitment increased when mean annual spawning occurred 1 to 2 wk prior to the spring bloom. In our study, age-0 herring abundance peaked when more adult herring spawned (i.e. spawning biomass) about 20 d prior to the peak spring bloom. The intervening period (20 d) between the peak adult herring spawning and the spring bloom could potentially encompass hatching of herring eggs (Outram 1955, Alderdice & Velsen 1971, Taylor 1971, Alderdice & Hourston 1985) and larval yolk-sac absorption (Alderdice & Velsen 1971). First feeding larvae would, therefore, occur shortly after the peak phytoplankton bloom when zooplankton prey, such as small copepods, became abundant in May (Mackas et al. 2013). Matching first-feeding larval fish with their prey items would improve fish survival to the fall when the age-0 fish were sampled in our survey.

Fish growth, indicated by condition (Smith et al. 1986, Froese 2006), can be affected by changes in the physical and biological environment, such as temperature, salinity, prey abundance, interspecific competition, and/or predation (Flinkman et al. 1998, Casini et al. 2006, Brunel & Dickey-Collas 2010, Frisk et al. 2015). In this study, model results were contrary to some of our predictions; for example, age-0 herring condition increased when most adult herring spawned closer to the peak spring phytoplankton bloom date (rather than prior to the bloom, as predicted). Perhaps condition is more closely aligned with the peaks in availability of larger zooplankton prey species that would occur after the peak primary production bloom (Mackas et al. 2013), rather than the peak timing of the primary production. As zooplankton prey

density increased, so did age-0 herring condition to a point and then leveled off; it is unclear if this was due to the low number of samples at high zooplankton densities or if, at the highest zooplankton abundances, age-0 herring became prey-saturated and their condition was maximized, or some other factor began to limit age-0 herring condition. Examining zooplankton species composition might provide further insights into factors affecting age-0 herring condition in the SOG. Age-0 herring condition increased with temperatures warmer than 8.2°C, which was somewhat consistent with our hypothesis that SST is a proxy for prey availability during the first months of feeding.

Results provided no evidence of top-down control or negative effects on herring abundance by juvenile salmon predators or competitors. Counter to predictions, age-0 herring abundance increased as predator and competitor abundance increased; therefore, we conclude that when ocean conditions were favourable for age-0 herring abundance, they were also favourable for juvenile salmon abundance. This supports previous observations in 2007 of common patterns in juvenile herring and juvenile salmon production in the SOG (Beamish et al. 2012). Negative effects of predators were observed for age-0 herring condition, but not abundance. In the SOG, when predator abundances were high, age-0 herring may have spent time and energy reserves avoiding predators rather than feeding. Low growth and condition could have implications for age-0 herring survival because they must store enough energy reserves to survive their first winter, when food is scarce (Paul et al. 1998, Foy & Paul 1999). Other studies have shown that predator avoidance (including changes in spatial distribution) can negatively affect fish growth and condition (e.g. Casini et al. 2014). Changes in the spatial distribution of fish were not examined in this study and might offer further insights into the dynamics of herring in the SOG.

Sources of uncertainty in this study included the limited number of competitor and predator species examined. We utilized the relative abundance of juvenile salmon as an indicator of predator or competitor abundance. In the SOG, there are other predators, such as adult Chinook *O. tshawytscha* and coho salmon *O. kisutch*, Pacific hake *Merluccius productus*, Pacific spiny dogfish *Squalus suckleyi*, and potentially pinnipeds. There are time series of abundance for indicator salmon stocks (e.g. www.psc.org/publications/technical-reports/technical-committee-reports/chinook/, accessed 28 August 2017); however, they are not necessarily representative of all

stocks occupying the SOG between July and October or they are not available for several years (e.g. there are limited southern BC coho salmon abundance estimates for 1998 to 2003; see www.psc.org/publications/technical-reports/technical-committee-reports/coho/, accessed 28 August 2017). Similarly, there are no continuous time series of Pacific hake or Pacific spiny dogfish abundance in the SOG for the years we examined in this study. Also, the proportion of age-0 herring (as opposed to other age classes) in pinniped diets is not known. These issues can be resolved with modeled predator abundance estimates for years with missing data and with trophodynamic studies that examine both prey species and stage in predator diets. Finally, other factors, such as summer temperatures, summer zooplankton densities, zooplankton community composition and energy densities, and adult herring spawning duration, might improve the amount of deviance explained by the age-0 herring abundance GAM.

Unique to this study was the examination of both age-0 herring abundance and condition. As herring spawning biomass increased, age-0 herring abundance also increased but their condition decreased, indicating the potential for density-dependent growth. Density-dependent processes can affect fish abundance and condition; for example, Dingsør et al. (2007) found that compensatory density-dependent survival was an important process for a few fish species, including Norwegian spring spawning herring. In contrast, Casini et al. (2014) identified the inverse relationship between density and condition for Baltic Sea sprat as spurious, and instead related the reduction in fish condition to predation. Raid et al. (2010) noted that the increased recruitment of Gulf of Riga herring was driven by favourable temperatures that compensated for an observed decrease in herring condition. In the case of the SOG, more spawning adult herring produced more age-0 fish that may have competed for limited resources during their first months after yolk absorption. Thereby, density dependence may have resulted in reduced body condition during the age-0 phase due, in part, to intraspecific competition.

Two types of intraspecific competition include competitive (scramble) and interference (contest). We applied a test that was developed for distinguishing between these types of competition (as developed by Ferrer et al. 2006). A linear relationship between the mean and skewness of age-0 herring condition might be indicative of scramble competition because as density increases, individual animals in optimal habitats could maintain a good condition while individu-

als that are pushed to suboptimal habitats might have a reduced condition, creating an overall left-skewed distribution of condition (Ferrer et al. 2006, 2008). There was not a linear relationship between skewness and the mean age-0 herring condition (Fig. 9), indicating that interference competition may be an important process in the SOG. This is consistent with Reum et al.'s (2013) study of Pacific herring in Puget Sound, which found evidence for interference competition.

The predictive value of the SOG age-0 herring abundance time series has been demonstrated by Hay et al. (2003) and Schweigert et al. (2009), who showed that abundance was positively correlated with age-structured stock assessment model estimates of age-3 recruits (double log transformed and lagged by 3 yr to match the year class), at least through the 2004 year class. Since those 2 analyses, the time series of age-0 herring and age-3 recruits (DFO in press) have been extended (to 2014) and the correlation is significant ($R^2 = 0.80$, $p < 0.001$). However, 2 years with both low age-0 herring and low age-3 recruit abundances (e.g. 2005 and 2007; Fig. 10) are the primary drivers of this correlation. The age-0 herring survey may therefore provide a leading indicator of low recruitment years. The persistence of the relationship also highlights the importance of continuing this type of monitoring so that future changes in recruitment can be anticipated.

The correlation between age-0 herring condition and age-3 recruit abundance was insignificant, with a

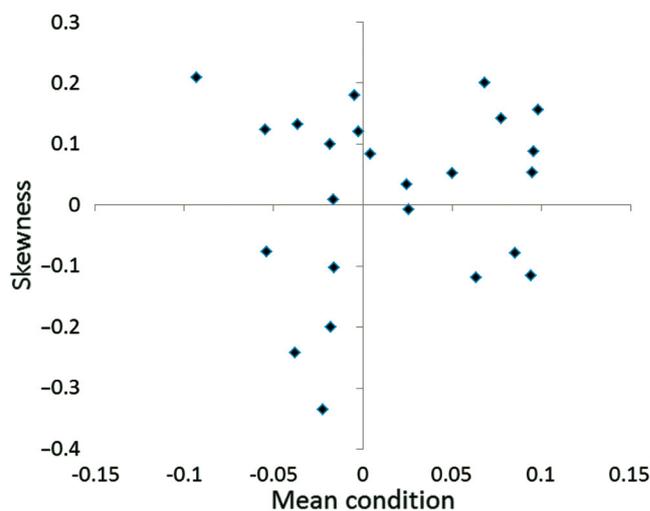


Fig. 9. Skewness as a function of mean condition (i.e. length-weight residuals from a double log-transformed length-weight relationship) of age-0 Pacific herring in the Strait of Georgia, September and October 1992 to 2016 (except 1995)

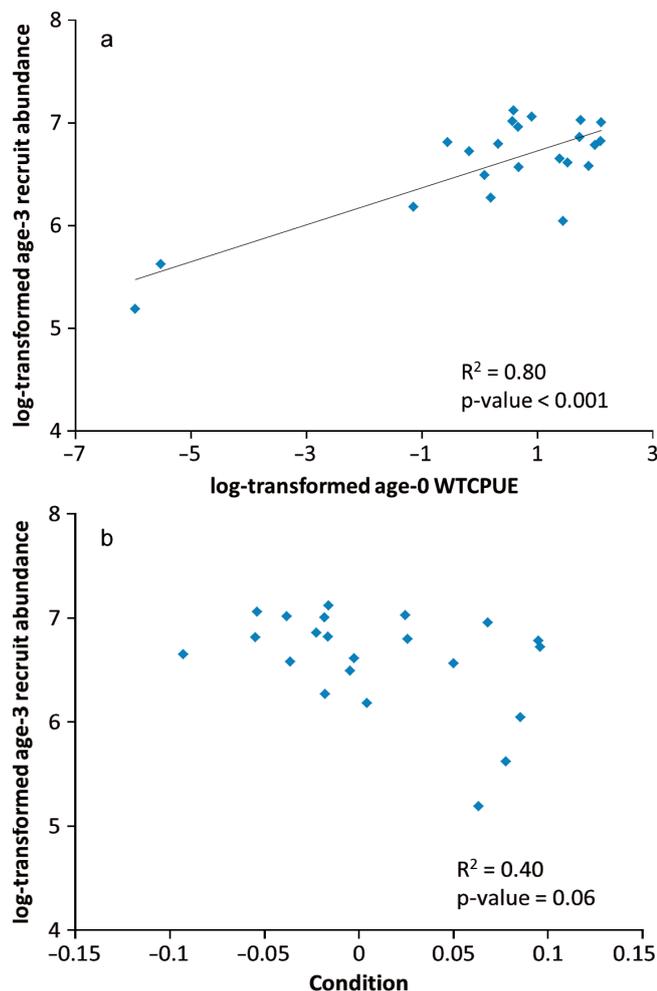


Fig. 10. Age-3 recruit abundance (millions, log transformed, lagged by 3 yr) from an age-structured stock assessment model (a) as a function the age-0 Pacific herring abundance index (log transformed; weight catch per unit effort [CPUE]; $g\ m^{-2}$) and (b) as a function of age-0 herring condition (length-weight residuals) in the Strait of Georgia from 1992 to 2016

tendency for lower age-3 recruit abundance to be associated with higher age-0 condition (lagged by 3 yr; $R^2 = 0.41$, $p = 0.06$; Fig. 10). Other studies have found that increased condition could have implications for fecundity and hence reproductive success and recruitment (Raid et al. 2010). Also, fish in good condition have improved survival during their first winter (Paul et al. 1998, Foy & Paul 1999, Frisk et al. 2015). Perhaps a measure of fish condition in late fall (e.g. November), rather than in September and October, would be more indicative of energy stores age-0 herring have acquired prior to their first winter and might have been more strongly correlated with age-3 recruit abundance. Other factors, such as overall abundance of age-0 herring, may be more important

in determining recruitment to the adult population, or factors such as predation may be important during the following 2 yr prior to recruitment to the adult population. Finally, the variance of SOG age-0 herring condition values decreased during the time series, indicating that perhaps more age-0 herring were experiencing favourable feeding conditions in recent years. Further study of the causes and effects of variability in age-0 herring condition are warranted.

In conclusion, this study illustrates that primarily bottom-up processes affect age-0 herring abundance and condition in the SOG, while top-down processes are limited to potential effects on age-0 herring condition. The temporal match between herring and their prey appears to be important, and density-dependent processes, such as interference competition, may affect age-0 herring abundance and condition. The factors affecting herring through their first months of life determine their ability to survive their first winter and eventually recruit to the adult population. Age-0 herring indices of abundance may provide a leading indicator of poor recruitment 2.5 yr in advance. Data from long-term monitoring programs will become increasingly important as climate change influences bottom-up processes that affect herring through spatial and temporal variability in prey and predators.

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