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Historical fluctuations and recent observations of Northern Anchovy *Engraulis mordax* in the Salish Sea

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ABSTRACT

Many small pelagic fish species exhibit dramatic fluctuations in abundance accompanied by range expansions during periods of favorable environmental conditions. The location and extent of suitable habitats also shift in response to both short term variability and long term trends in climate. Near the margins of a contemporary range, trends in abundance may reflect a continuation of historical variability but may also foreshadow future changes in distribution. The Salish Sea (all inland marine waters of Washington State and British Columbia; made up of the Strait of Georgia, Strait of Juan de Fuca, and Puget Sound) is a highly productive estuarine system at the northern end of the distribution of Northern Anchovy (*Engraulis mordax*). An apparent recent (2014–2016) increase in Northern Anchovy abundance has generated interest in the dynamics of this species in the Salish Sea. We compiled recent and historical data to understand spatiotemporal patterns of distribution and fluctuations in abundance over the last century. Spatially-consistent occurrence of eggs, larvae, and juveniles, and year-round presence of multiple age classes, confirm that successful spawning and recruitment of Northern Anchovy occurs within the Salish Sea. Most periods of elevated Northern Anchovy abundance in the last century have corresponded to, or lagged, periods of elevated ocean temperature. While a 2005 peak in abundance within the Salish Sea also corresponded to higher abundance of Northern Anchovy in adjacent regions of the coastal Pacific Ocean, it seems unlikely that Salish Sea abundance is controlled primarily by advection or migration from external populations. Persistence of elevated ocean temperatures like those observed from 2014 to 2016 could lead to consistently high abundance of Northern Anchovy within the Salish Sea, with implications for trophic relationships and ecosystem function.

Key Words: forage fish; temperature effects; fishery sciences, climate

1. Introduction

Small pelagic fish populations are often characterized by dramatic changes in abundance through time. At global and ocean basin scales, synchronous fluctuations of geographically distant populations may ultimately be linked to climatic regime shifts (Chavez et al., 2003; Tourre et al., 2007). Density dependence and interspecific competition may also interact with climate to drive changes in population productivity and size (Schwartzlose et al., 1999; Lindegren et al., 2013). Changes in abundance of small pelagic fish at the local scale may or may not be related to global scale causes depending on the regional intensity of resulting effects. When regional biotic and abiotic conditions are favorable, a stock may expand well beyond core production areas into habitat where it otherwise has been contemporarily absent (MacCall, 1990), resulting in patterns of appearance and disappearance that have little to do with local conditions. During periods of low abundance, remnant populations may contract into easily-observed nearshore habitats within their core range, giving a false impression of abundance to fishers and the public (MacCall et al., 2016; Davidson et al., 2017). Superimposed on such periodic fluctuations are long-term trends in climate that may be shifting the geographic limits of suitable ranges, allowing expansion into new habitats (Beare et al., 2004; Sabatés et al., 2006). These shifts in distribution may have major ecosystem-level consequences. Due to their abundance and trophic position, small pelagic fish play a critical role in the flow of energy from primary producers and primary consumers to higher trophic levels (Cury et al., 2000; Bakun, 2006). To understand marine ecosystems, it is therefore important to determine if changes in abundance of small pelagic fish reflect intrinsic variability in food web dynamics or foreshadow future ecosystem trajectories.

Northern Anchovy (*Engraulis mordax*; henceforward ‘anchovy’) occur off the West Coast of North America from Mexico to British Columbia. They support fisheries which can periodically be very valuable, and are an important prey species for marine birds and mammals (Velarde et al., 2015; McClatchie et al., 2016) and commercially important fish species (Brodeur et al., 2014; Dale et al., 2017). Three aggregations of anchovy abundance have been characterized on the Pacific Coast (McHugh, 1951). The northern-most of these is the northern subpopulation, which extends from northern California to central British Columbia. The Columbia River Plume was identified as the primary spawning site for this subpopulation by Richardson (1981); with peak spawning occurring in July. Other studies have recorded the presence of anchovy eggs as early as April (reviewed by Parnel et al., 2008), and during recent anomalous warm conditions (2015–16) larvae have been captured throughout the winter on the Newport hydrographic line off Oregon (Auth et al., in press). Previous stock assessments of the northern subpopulation of anchovy have been limited to the Columbia River plume region (Richardson, 1981; Emmett et al., 1997). Litz et al. (2008) reviewed available commercial catch and fishery-independent sample data for the northern subpopulation in the California Current. These authors suggested that strong variability in abundance was likely driven by bottom-up regulation of larval survival in the preceding year. Therriault et al. (2002) reviewed anchovy biology and fisheries in Canadian waters. This review described low and fluctuating abundance of anchovy in British Columbia and concluded that it was uncertain whether these stocks were resident or whether abundance was controlled by migration from more southerly components of the northern subpopulation. We are not aware of previous work that has specifically addressed that status or history of anchovy within the Salish Sea (SS), the combined inshore waterways and basins of southern British Columbia and Washington State.

Since 2014, evidence from multiple sources has suggested a widespread surge in abundance of anchovy within the SS. These observations were sufficiently unusual that they attracted the attention of the public and media.[1] Independent observations by resource users and fisheries research agencies prompted questions about the scale, cause(s), and ecological significance of the increase in abundance. Consequently, we reviewed available literature and assembled data to piece together the biology and recent dynamics of anchovy in the SS. We characterized spatiotemporal patterns of distribution and seasonal shifts in size and life-history stage. We attempted to define periods of high and low abundance from 1940 to the present by collating qualitative and quantitative fishery-dependent and -independent data. To assess the plausibility of alternative hypotheses underpinning population increases (spillover from adjacent population centers versus increased habitat suitability), we related periods of inferred high and low abundance to sea surface temperature (SST), salinity and dynamics of adjacent anchovy populations.

2. Materials and Methods

2.1. Study Area

The Salish Sea (SS) is a complex estuarine system on the north-west coast of North America with three dominant regions: Strait of Georgia (SoG), Strait of Juan de Fuca (SJF) and Puget Sound (PS; Figure 1). The Strait of Georgia (Figure 2) is the largest basin and is strongly influenced by large freshwater inflows from the Fraser River that promote stratification and high productivity and drive estuarine circulation (Thomson, 1981). The Strait of Juan de Fuca, which links the SS to the Pacific Ocean, is a tidally-mixed passage that remains comparatively cold throughout the year. To the south, Puget Sound (Figure 3) is a complex network of basins and fjords; the northern portion adjacent to the Strait of Juan de Fuca stays tidally-mixed and cool throughout the year while the more embayed regions can become thermally stratified and quite warm during the summer (Moore et al., 2008).

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[1] http://vancouversun.com/news/local-news/anchovy-schools-are-back-in-session-with-phenomenal-numbers-spawning-in-howe-sound; accessed 1 July 2017.

The SS is home to species of commercial, recreational, and cultural importance. It provides rearing habitat for Pacific salmon (*Oncorhynchus* spp.) from the Fraser River, Canada's most important salmon producing watershed, and many other rivers draining Washington State, mainland British Columbia, and Vancouver Island. Survival of juvenile Chinook (*O. tshawytscha*) and Coho (*O. kisutch*) Salmon entering the SS declined dramatically two decades ago and has not rebounded (Beamish et al., 2010; Zimmerman et al., 2015). This conspicuous change provided the impetus for a multiyear, binational science initiative (the Salish Sea Marine Survival Project-SSMSP-www.marinesurvivalproject.org) that seeks to identify and explain changes in ecosystem function. Several other marine species occurring in the SS have also experienced substantial population declines over the last several decades and are at risk of extirpation or extinction, resulting in listings under the U.S. Endangered Species Act (Yelloweye Rockfish *Sebastes ruberrimus*, Bocaccio *S. paucispinis*, Eulachon *Thaleichthys pacificus*, Bull Trout *Salvelinus confluentus*, Green Sturgeon *Acipenser medirostris*, Marbled Murrelet *Brachyramphus marmoratus;* see http://www.westcoast.fisheries.noaa.gov/about_us/ protected_resources_division.html) and the Canadian Species at Risk Act (SARA) (Marbled Murrelet, Southern Resident Killer Whales *Orcinus orca;* see https://www.registrelep-sararegistry.gc.ca).

The forage fish community of the SS is currently dominated by Pacific Herring (*Clupea pallasii*) and, to a lesser extent, Pacific Sand Lance (*Ammodytes personatus*) and various species of smelt (Osmeridae) (Therriault et al., 2009). While numerous sources have documented the presence of anchovy in the SS (e.g., Therriault et al., 2009; Beamish, 2014; Greene et al., 2015), they have not generally been considered to play an important role in the ecosystem. Recent anecdotal observations of large concentrations of anchovy in the SS, along with increased frequency of catches in fishery-independent surveys, suggest that this may no longer be the case. The present work seeks to clarify recent and historical dynamics of anchovy in the SS to inform ongoing efforts to understand the ecology of this valuable ecosystem.

2.2. Spatiotemporal Patterns in Distribution and Size Frequency

To characterize spatiotemporal patterns of distribution and seasonal shifts in anchovy size and life-history stage we assembled available fishery-independent survey data for the SS (Table 1). No surveys specifically target anchovy in the SS; however, anchovy are encountered as incidental catches in surveys for other species and as part of broad-based ecosystem surveys using non-selecting gear. We assembled results of six fishery-independent surveys that provided informative spatial and/or temporal coverage. These included ecosystem monitoring programs and targeted assessments of commercially important marine fish species.

Locations of gear deployments ('sets') and catches (either log(x+1) transformed catch per set or catch per hour) were mapped using the "PBSmapping" package (Schnute et al., 2008) in R (R Core Team 2016). Specific details for each dataset are provided in section 2.4 and Table 1.

Length data were available for anchovy captured in four of these datasets, facilitating inference of life-history stage-specific temporal patterns of distribution within the SS. Different surveys employed different types of length measurements (i.e., standard, total, and fork lengths). To allow comparisons among surveys, seasons, and years we converted all lengths to fork length (FL) using rearrangements of length-weight regression formulae of Gartz (2004), where *FL* = fork length, *TL* = total length, and *SL* = standard length.

$$FL = (TL^{3.1423}\,(0.5683))^{0.3242}$$

$$FL = (SL^{2.922}\,(2.7148))^{0.3242}$$

2.3. Trends in Abundance

We attempted to define periods of high and low abundance from 1940 to the present using a combination of quantitative and qualitative fishery-dependent and -independent data. For quantitative analysis, we assembled ten fishery-independent datasets (Table 1) that used different gear types and varied in the metrics used to record anchovy catch (counts, total weights, and/or individual measurements). Therefore, we limited our analysis of inter-annual variation to frequency of sets that captured anchovy (ie. % presence). These proportions were arcsine square root transformed to improve normality and converted to anomalies from the mean for each dataset. These anomalies were then averaged across datasets for each year to derive a quantitative index of anchovy abundance for all years in which there were data. To investigate temporal links between environmental variables and abundance we fit linear models ("lm" in the base stats package in "R"; R Core Team 2016) relating this quantitative abundance index to annual indices of Salish Sea SST, Coastal SST, and Salish Sea salinity (see section 2.4.13 for details). Models were fit to environmental indices averaged over the last 1 to 3 years and lagged by 0 to 3 years. Lags were chosen based on an assumption that most anchovy encountered in Salish Sea surveys would between age-0 and age-3 (Pike, 1951). Data were weighted by the number of data sources contributing to the anchovy abundance index for each year.

This quantitative approach could not be applied to all the datasets collated in the present study, including all data prior to the 1960s. We therefore employed a qualitative approach to combine all available data. Quantitative datasets described in the previous paragraph were converted to qualitative scores: for net gears (trawl, purse seine, and beach seine) we defined > 30 % presence as 'abundant' (score = 1), 5 % to 30 % as 'present' (score = 0.5), and < 5 % as 'scarce to absent' (score = 0); for zooplankton sampling gears we defined ≥ 5 % as 'abundant', < 5 % as 'present', and 0 % as 'scarce to absent'. We also assembled available anchovy fishery landing records for the SS and qualitative accounts of presence and abundance from management agency documents. For these datasets, we established criteria to assign qualitative scores (‘abundant’, ‘present’, or ‘scarce to absent’ on a case-by-case basis (described in section 2.4). Finally, we reviewed the literature for reports of surveys with spatial and temporal coverage that would have been expected to encounter anchovy if present; and scored these as ‘abundant’, ‘present’, or ‘scarce to absent’, as above. We assembled the results of all fishery-independent, fishery-dependent, and literature time series (n = 15), and calculated mean categorical scores for each year. Where two or more data sources were available for a given year, mean categorical abundance values of < 0.5 were considered to represent periods of likely scarcity and values of > 0.5 periods of likely abundance. To assess the plausibility of alternative mechanisms influencing anchovy dynamics in the SS, we graphically related periods of high and low abundance to environmental indices (previous paragraph and section 2.4.13) and indices of anchovy abundance in adjacent open coast regions (see section 2.4.12).

2.4. Data Sources

2.4.1. Strait of Georgia Zooplankton Database

The Institute of Ocean Sciences (DFO) in Sidney, British Columbia maintains a database of zooplankton samples collected during both annual monitoring programs and focused studies by researchers from DFO and other institutions. These sampling programs and the database are described in more detail by Mackas et al. (2013). We examined all records in this database for the SS beginning in the year 2000 (n = 1920). Samples prior to 2000 had been analyzed to varying levels of taxonomic resolution and anchovy presence could have been missed. Sample collection methods were diverse, ranging from ring nets and bongo nets to Tucker trawls and depth stratified multi-nets. Gears were also fished over different depth ranges.

We limited our analysis to annual percent presence of anchovy eggs, larvae, and juveniles, and only included gear deployments that sampled from a depth of at least 15 m and that included the surface. The zooplankton database characterizes fish under 10 mm as larvae and over 10 mm as juveniles. This likely misclassifies some larval anchovy, as transformation takes place between 35 and 40 mm (Watson and Sandknop, 1996). We grouped these size classes as larvae for analysis. As anchovy eggs and larvae were only encountered between March and September, only months within this range were considered for analysis of trends in abundance. A total of 1420 gear deployments between 2000 and 2016 met these criteria. Spatial coverage of zooplankton samples in the SoG has increased significantly since 2014 as part of the Salish Sea Marine Survival Project, and the majority of anchovy have been encountered in 2015 and 2016. We therefore limited our mapping of spatial and seasonal patterns of occurrence to the latter two years.

2.4.2. Strait of Georgia Age-0 Pacific Herring Purse Seine Surveys

Standardized night-time (6–7 hours beginning near dusk) surveys for age-0 Pacific Herring have been conducted by Fisheries and Oceans Canada (DFO) in the Strait of Georgia since 1992 (except 1995) as an index of future (age-3) recruitment to the population (Schweigert et al., 2009; Boldt et al., 2015; Thompson et al., 2016). A single purse seine set is conducted at each of up to 48 standard stations along 10 transects during September–October. Transect locations are spaced around the perimeter of the SoG (Figure 2). Stations along each transect extend from nearshore (approximately 15 m depth) out into open water at 1–2 km intervals, or from one side of a channel to the other. Station water depths range from 11 to 340 m with an average of 83 m. Significant numbers of anchovy were encountered in these surveys for the first time in 2005; since then, a sample of the catch has been measured for standard length. For the present study, we evaluated presence or absence of anchovy at the set level for all years (mean annual sets = 44, range = 24–48, total = 1056).

The standardized nature of these age-0 Pacific Herring surveys also provided an opportunity to evaluate the effect of water depth on the fine scale distribution of anchovy. To test the hypothesis that anchovy were more likely to be present in shallow water, we fit a mixed effects binomial glmm (logit link) relating the presence (1) or absence (0) of anchovy in each set to the random categorical variables ‘Year’ and ‘Transect’ and the continuous variable ‘Depth (m)’ using the “glmer” function in the package “lme4” (Bates et al., 2015) in R (R Core Team 2016).

2.4.3. Strait of Georgia Juvenile Salmon Trawl Surveys

Surveys to capture juvenile salmon have been conducted by DFO every summer (June/July) and fall (September/October) since 1998 in the Strait of Georgia and associated waters, primarily aboard the CCGS R/V W.E. Ricker. Surveys employ a modified mid-water trawl (approximately 14 m high by 30 m wide; mesh tapering to a 1 cm liner in the cod end) fished at 8–9 km/h and at variable depths (Beamish et al., 2000). A standard track line is sampled during each survey (~80–100 sets); other regions were fished as time permits including mainland inlets, the Southern Gulf Islands, PS, and SJF. For the present study, we reviewed a total of 458 sets from surveys conducted in 2015 (24 June–9 July and 16 September–6 October) and 2016 (5–14 July and 17–26 October). In both years standard track lines were surveyed in addition to PS and the vicinity of Cowichan Bay in the Southern Gulf Islands. Surveys in 2015 were somewhat more extensive and included Desolation Sound, Whidbey Basin and South PS. Approximately 1/2 of tows were conducted with the headrope at the surface, 1/3 at 15 m, 1/6 at 30 m, and the balance at 30 to 80 m. Fork lengths were measured on board for a subset of anchovy captured in summer and fall surveys in both 2015 and 2016.

2.4.4. Fraser River Plume Study (Tow Net)

Two-vessel surface trawls (henceforward this sampling method is referred to as a “tow net”) were conducted by the Fisheries Research Board of Canada as part of a study of the Fraser River plume from 1966 to 1969 and again in 1973. The trawl net was approximately 6 m by 3 m and included a 350 µm mesh plankton net integrated into the cod end to catch zooplankton and larval fish. The net was deployed for standardized 10-minute tows. A full description of gear and methods is provided in Barraclough (1967). While some of these data were published in the Fisheries Research Board manuscript report series shortly after they were collected, the Fraser River plume data from 1968, 1969, and 1973 were not. They were recovered recently during a data archaeology project (McKinnell and Perry, 2016). Surveys occurred in the southern Strait of Georgia between April and July but anchovy occurred only in the months of June and July. We therefore considered only tows during these months (n = 196) for catch maps and abundance analyses.

2.4.5. Strait of Georgia R/V Neocaligus Trawl

From 2014 to 2016, DFO conducted experimental trawl surveys in the southern Strait of Georgia using the CCGS R/V Neocaligus. These surveys employed a 4 m by 4 m trawl in 2014 and 2015 and a 15–20 m by 5–6 m trawl in 2016. Coverage in these surveys varied by year, with 2014 and 2015 focusing on the edge of Robert’s Bank at the Mouth of the Fraser River and 2016 focusing on Howe Sound. Additional sets were also conducted in Cowichan Bay. Due to the very different spatial coverage of these surveys among years we did not include them in the analysis of trends in abundance; however, we did compare the size distribution of anchovy captured from 2014–16 to those captured in other survey programs.

2.4.6. Puget Sound Mid-Water Trawl Survey

The Washington Department of Fish and Wildlife (WDFW) conducted bimonthly mid-water trawl surveys from February 2016 to February 2017 to investigate seasonal and spatial changes in the distribution of the mid-water fish community of PS (we report only survey results from February 2016 to December 2016). The F/V Chasina, a 17.7 m commercial fishing vessel, performed the surveys using a mid-water Polish rope trawl with a maximum 7.3 m by 7.3 m opening and a 1 cm mesh liner in the cod end. The trawl was deployed in standardized 15-minute deployments to depths identified by a lead acoustics vessel as having the highest concentration of fish targets. Tow depths ranged from 15 to 141 m (mean = 54 m). Bimonthly surveys consisted of between 16 and 38 sets (184 total) and covered all major basins of PS, also extending into the southern SoG and SJF.

2.4.7. Skagit Bay Surface Trawl Survey

Two-vessel surface tow net surveys have been conducted in Skagit Bay, PS by the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center (NWFSC) since

2001. A Kodiak trawl (3.1 m deep by 6.1 m wide; mesh tapering from 76 mm in forward sections to 6 mm in the cod end) was fished at 4–5.5 km/h for 10 minute sets at a series of standard stations (see Rice et al., 2011 for details). Some sampling has occurred between February and November, but the number of sets and seasonal coverage has varied by year. The months with the most consistent coverage were July (all but 2016), August (all years), and September (all but 2004). To assess trends in abundance we limited analysis to percent presence in tows conducted in the latter two months. The number of tows conducted in this period ranged from 16 in 2012 to 90 in 2002 (total = 871; mean = 54).

2.4.8. Historical Tow Net Surveys

Greene et al. (2015) synthesized results of historical two vessel surface 'tow net' surveys conducted in the southern SoG (referred to as 'Rosario Basin'), Whidbey Basin, Central PS, and Southern PS from 1972 to 1985, and again in 2003 and 2011. Methods for this work were similar to those for Skagit Bay tow net surveys (section 2.4.7) and are described in detail in Rice et al. (2011) and Greene et al. (2015). The number of tows for each region and year varied from 4 to 158 (mean = 41), with all tows included in the analysis occurring from June to September (n = 1380). Sampling was conducted primarily at night from 1973–85 and during the day in 1972, 2003, and 2011.

2.4.9. Elwha and Snohomish Beach Seines

From 2001 to 2010 the NWFSC and Tulalip Tribes conducted a beach seine program to monitor juvenile salmon utilization of the Snohomish River Estuary. A similar program has been conducted by the NWFSC at the Elwha River estuary since 2005. These programs employed a 37 m by 3.1 m beach seine with a 3.2 mm mesh bag following methods outlined by Miller et al. (1990). Some seine sites at these locations were primarily freshwater habitats, so to assess annual variation in percent presence we utilized data only for sites where anchovy were encountered at least once. Similarly, we only included sets in months where anchovy were encountered; April to September for the Elwha estuary (total sets = 1031; range = 5–161; annual mean = 86) and August and September for the Snohomish estuary (total sets = 139; range = 5–23; annual mean = 14).

2.4.10. Catch Data

Commercial catch data for anchovy in PS were provided by the WDFW. Catches have been sporadic and we were unable to account for changes in fishing effort and closures of the fishery. We therefore could not use these data to infer periods of scarcity. We defined landings of greater than 10,000 kg as reflecting abundance (score = 1), while any landings less than 10,000 kg reflected presence (score = 0.5). British Columbia commercial catch data were compiled from Canadian fisheries statistics by Warren Wulff (DFO) for a 2002 stock status review (Therriault et al., 2002). Landings prior to 1947 were identified by region, while those from 1947 to 1951 were not. All catch data after 1951 were from outside of the SS. Again, we were unable to use these data to infer absence of anchovy, but we considered years with a documented SoG catch of greater than 10,000 kg to constitute abundance (score = 1).

2.4.11. Literature Sources

Annual reports (1925–1980) of work conducted by the Pacific Biological Station, DFO Pacific Stock Assessment Review Committee Annual Reports from 1987 to 1997, and sources cited within these documents were examined for references to anchovy (all reports reviewed but not cited in the text are listed in the supplementary material). Where abundance or scarcity within the SoG was mentioned, we assigned a score of 1 or 0, respectively. Beamish et al. (1976) reported results of 50 purse seine sets in the southern SoG in July and August of 1974. DFO conducted 400 thirty-minute sets with a 4 m by 4 m surface trawl in the Fraser River plume in early summer from 1989–1994. The methodology of these surveys is reported in Beamish and Neville (1995) with total catches and number of sets reported in Beamish (2014). These surveys were scored for abundance/scarcity based on the same criteria described for other net-based gears in section 2.3.

2.4.12. Anchovy Abundance Beyond the Salish Sea

The abundance of the northern subpopulation of anchovy is not assessed routinely; however, they are caught in surface trawl surveys (targeting juvenile salmon) conducted annually in the Columbia River plume in June by the NWFSC (see Brodeur et al., 2005 for methods). Annual anomalies (deviations from log of mean catch per km) from 1998 to 2016 were provided by Cheryl Morgan (Oregon State University). The number of tows per year ranged from 27–59 (mean = 46). Sampling methodology and sampling area has been standardized throughout the study, although a marine mammal excluder device was installed beginning in 2014 (37 of 47 hauls). This device was installed in the net with the opening facing upward in 2014 and with the opening facing downward for all hauls in 2015 and 2016.

Coastal (non-Puget Sound) Washington and Oregon landing data (weight) for anchovy were obtained from WDFW harvest records. Fisheries for anchovy in Washington and Oregon have used purse seines and lampara nets to provide live bait primarily for recreational and commercial fishers (Litz et al., 2008). Catch data from 1970–2016 were obtained from the Washington fish ticket database, while data from 1929 to 1969 were obtained from a WDFW database containing data derived from annual Washington State Department of Fisheries Statistical Reports. Data for 1969 were not divided by region and may also include PS catch. Data are reported as anomalies from the mean.

2.4.13. Environmental Data

Daily SST and salinity has been measured using consistent methodology at a number of lighthouses on the British Columbia Coast and at the Pacific Biological Station in Departure Bay over various time periods beginning in 1914 and continuing up to the present. Data for Departure Bay (1914–2016), Active Pass (1967–2012), Cape Mudge (1936–1985), Chrome Island (1961–2016), Entrance

Island (1936–2016), and Race Rocks (1921–2016) were retrieved from http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html. Sea surface temperatures (1992 to 2016) from weather buoys maintained by Environment Canada at Sentry Shoal and Halibut Bank in the SoG were obtained from the Marine Environmental Data Section of DFO. For each time series, daily SST and salinity data were converted to monthly anomalies from the monthly mean for all years between 1935 and 2016. Months with less than 15 days of data were excluded. Annual temperature and salinity indices were then derived by averaging monthly anomalies for all years with at least 11 months of data. To avoid splitting the coldest or warmest part seasons, years were centered on 1 October (ie. 2016 would include 1 October 2015 to 31 September 2016). For the purpose of modeling the relationships with SS anchovy abundance these SoG SST and salinity indices were used as a proxies for the entire SS. An index of SST for the coastal Northeast Pacific as a whole was derived from NOAA Extended Reconstructed SST data (monthly data; 1854 – present; 2° lat/long grid) - Version 4 (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v4.html). Grid points directly adjacent to the coast between 40° N and 60° N were selected for analysis (one grid point for every 2° of latitude). Monthly SST anomalies from long-term monthly mean were calculated for each grid point. Where a datum was missing the mean of the preceding and following month were used when available, or else the anomaly was set to zero. A principal component analysis was applied to monthly anomalies. The first principal component explained 93% of covariance in the data. Monthly scores for this principal component were averaged for each year (centered on 1 October as above) to derive an annual coastal SST index.

3. Results

3.1. Spatiotemporal Distribution and Body Size

3.1.1. Regional Patterns in Distribution

Anchovy were captured throughout the SS in a variety of surveys, but some spatial patterns were evident. Within the SoG, Malaspina Strait was an area of consistent occurrence in zooplankton tows (Figure 4). At one station in Malaspina Strait (see arrow in Figure 4a) eggs or larvae were encountered in 7 of 9 surveys conducted between 11 May and 14 August 2015. Eggs and larvae were also caught at many stations in and around Baynes Sound. The only records of anchovy in the zooplankton data in SJF and Haro Strait were larvae/juveniles captured in March and April 2015, prior to the main occurrence of eggs or larvae within the SoG (with the exception of a single sample in the Fraser River plume; Figure 4).

Anchovy were encountered in age-0 Pacific Herring surveys on all transects (Figure 5). The highest frequency of occurrence was on transects 9 – 11 along the northeast shore of the SoG (including Malaspina Strait) and on transect 2 in the Gulf Islands. Most anchovy catches in juvenile salmon trawl surveys also occurred along the northeastern shore of the SoG or in the Fraser River plume (Figure 6). All large catches in these salmon trawl surveys occurred in the Fraser River plume or mainland inlets (Howe Sound and Desolation Sound). Of juvenile salmon trawl sets conducted by DFO in Puget Sound, anchovy were encountered only in South Puget Sound in the fall of 2015 (Figure 6). Surveys in summer 2015 and in 2016 did not extend into the South Puget Sound due to limited ship time. Historical (1967–69) tow net surveys provide more information on distribution near the Fraser River plume. In 1967 and 1968 anchovy catches were concentrated to the north of the mouth of the Fraser River, while in 1969 catches were dispersed throughout all sampled areas of the central SoG (Figure 7).

The 2016 WDFW mid-water trawl survey provided a relatively complete spatial and temporal snapshot of anchovy distribution in PS in a year of apparent high abundance. Anchovy were encountered in all the main basins of the Sound. In general, catches were greater within embayments further from the entrance to the Sound (Figure 8). The largest and most consistent catches occurred in South PS. Almost no anchovy were caught in either the June or August mid-water trawls surveys in PS, with the only significant catch occurring in the South Sound in August. The largest catches occurred in October and December (Figure 8). In 2015 and 2016, larval and post-larval anchovy were caught in the Skagit Bay tow net survey, primarily in retention areas such as embayments where they were caught in large numbers (data not shown).

3.1.2. Fine Scale Distribution

Qualitative assessment of within-transect catch distribution from the SoG age-0 Pacific Herring surveys suggested that anchovy were more likely to be captured closer to shore (and therefore in shallower water). For example, for transect 11 near Pender Harbour (highest anchovy occurrence for any transect in the survey: 26%, SE = 4%), frequency of occurrence was very high for the station closest to shore (63%, SE = 10%), while anchovy have never been captured at the most offshore station across 18 years of sampling (Figure 5 inset). A mixed effects logistic regression model confirmed that the log-odds of encountering anchovy in purse seine sets declined with water depth (intercept = -1.78, slope = -0.006, standard error of slope = 0.002, $P < 0.001$).

3.1.3. Life History Stage Timing and Length Frequency Distributions

Anchovy eggs and larvae were present in the SoG from March to August of 2015 and 2016, with a peak in June (Figures 4 and 9). Many of the anchovy encountered in the late summer and fall surveys described in the present study were small, post-larval young of the year. Of 2245 fish measured from surface trawl catches in the Southern SoG in June and July of 1967–69 only 11 individuals were greater than 100 mm FL. The other 2234 ranged from 7 to 92 mm FL (mean = 26.7 mm). Of 626 fish measured in fall SoG age-0 Pacific Herring surveys since 2005, 548 (88%) were less than 100 mm FL. A mode of fish (≤ 75 mm FL) first appeared in July in the R/V Neocaligus surveys in 2015, but were not caught in July in either 2014 or 2016 (Figure 10). In 2016, a mode of fish ≤ 75 mm FL was evident in the R/V

Neocaligus trawl surveys in Howe Sound in August and in age-0 Pacific Herring surveys in September (Figure 11). The same mode was apparently present in juvenile salmon trawls in October and PS mid-water trawls in October and December, but had increased to between 75 and 100 mm FL. The length of age 1+ anchovy caught in February in PS mid-water trawls was primarily between 75 and 100 mm, whereas the length of those caught in April was bimodal with modes at 105 and 145 mm. The length of anchovy caught in Howe Sound in May by the R/V Neocaligus corresponded to this larger mode. Anchovy caught in July in the juvenile salmon trawl surveys in the SoG had a length distribution that overlapped with the samples from the R/V Neocaligus in Howe Sound but also included larger fish (145–160 mm). In August 2016, most fish in the PS survey were > 125 mm. A mode between 125 and 150 mm was present in all surveys from September to December (albeit almost non-existent in PS in December).

3.2. Fluctuations in Abundance

3.2.1. Abundance Time Series

A number of sources indicated a period of anchovy abundance in the SS in the 1940s. Commercial landings occurred annually in the SoG between 1940 and 1946, ranging from 47,000 kg to just over 1 million kg. Commercial catches of 17,000 and 21,000 kg were recorded in PS in 1946 and 1947 respectively (Figure 12). The annual reports of the Pacific Biological Station make specific reference to anchovy abundance within the SoG in 1940, 1941 and 1947. From the late 1940s to the 1950s information is sparse. Commercial catches for BC were reported in 1947, 1948 and 1950, but these were not broken down by region so it is not possible to tell if part of the catch was made in the SoG. The annual report of the Pacific Biological Station for 1948 indicated that anchovy were scarce in that year (Foerster, 1948). The report for 1951 (Hart, 1951) indicated that large schools of age-1 anchovy appeared in the SoG in that year, but there is no evidence that these fish persisted. The report of 1969 (Radway, 1969) indicated that anchovy had not been abundant in the SoG since 1951, but this is the only reference to this two-decade period.

A peak in abundance at the end of the 1960s was evident in results of the Fraser River plume study (Figures 7 and 13). Small commercial catches were also reported for PS in 1969–1971 (Figure 12). No anchovy were encountered in Fraser River plume study in 1966 or 1973. A purse seine survey in the SoG in 1974 (Beamish, 1976) encountered no anchovy despite suitable gear and considerable effort (50 sets). From the early 1970s to the early 1990s information regarding anchovy abundance comes primarily from tow net surveys conducted in the southern SoG and PS. A small number of tows conducted in the southern SoG and Central PS (18 total) suggested a possible year of higher abundance in 1976, and tows in Whidbey Basin suggested elevated abundance from 1983–85 (Figure 13). Surface trawl surveys in the Fraser River Plume from 1989 to 1993 (Beamish, 2014) encountered no anchovy in 400 sets.Beginning with age-0 Pacific Herring surveys in the early 1990s, various fishery-independent data sets provide a fairly coherent picture of trends in abundance up to the present (Figures 13 and 14). Elevated frequency of occurrence was observed in age-0 Pacific Herring surveys, Skagit Bay tow net surveys, and Snohomish River estuary beach seines in 2005. No anchovy were encountered in zooplankton tows at stations in the SoG in 2005; however, eggs and larvae were encountered in 2006. This result contrasted with other survey programs, which did not detect abundance in 2006 (Figure 13). A noteworthy increase in abundance was detected in 2015 and 2016. Only Elwha beach seine data were inconsistent with this trend.

3.2.2. Relationship with Environmental Variables and Northern Subpopulation Abundance

Some, but not all, periods of qualitatively inferred SS anchovy abundance corresponded to, or closely lagged, periods of elevated SST in the Salish Sea and along the Pacific Coast (Figure 14). However, no evidence of anchovy abundance was detected during other warm periods (eg. late 1990s). Some periods of abundance also corresponded to or lagged periods of lower salinity, but this pattern was weak. Catch per unit effort in Columbia Plume trawl surveys was relatively constant, with one strong peak in 2004 and 2005 which corresponded to inferred abundance of anchovy in the SS in 2005. Coastal Washington and Oregon commercial anchovy catch was also relatively constant with a small peak in 2009 and a very dramatic increase in 2016.

A quantitative anchovy abundance index was significantly related to an index of Salish Sea SST only when SST was unlagged and averaged over two years (slope = 0.46, $P = 0.04$; Figure 15). At a lag of 3 years, the relationship between the 2- and 3-year averaged SST index and anchovy abundance became significantly negative. The unlagged index of coastal SST was positively and significantly related to anchovy abundance whether averaged over 1, 2 or 3 years; at a 1-year lag only SST for a single year was significantly related to abundance. Three year-averaged coastal SST lagged by 3 years was significantly negatively related to anchovy abundance. The relationship between coastal SST and abundance was most significant for the unlagged index averaged over 2 years (slope = 0.57, $P < 0.01$). A possible negative relationship between the unlagged SS salinity index and anchovy abundance was marginally nonsignificant.

4. Discussion

4.1. Life-History Distribution Within the Salish Sea

Our results suggest that when anchovy are abundant in the SS they consistently utilize certain regions including the Fraser River plume, mainland shore of the SoG, and South Puget Sound. This is generally consistent with historical accounts and recent anecdotal observations of anchovy in the SS. Hart (1934) cited results of a survey of fishers indicating that within the SoG, locations noted for anchovy abundance were the coastal area between Victoria and Ladysmith on the southeast side of Vancouver Island and the eastern shores between Boundary Bay and Pender Harbour. Canadian fisheries statistics for catches between 1940 and 1946 indicated that fishing occurred in the vicinity of the Fraser River, Howe

Sound, and along the mainland shore of the SoG. Only in 1946 were small catches recorded from the western SoG (near Nanaimo). The 1942 report of the Pacific Biological Station (Foerster, 1942) reported that anchovy were important in diets of Chinook Salmon from the east coast of the SoG but not elsewhere, and the 1947 report (Foerster, 1947) indicated that anchovy occurred regularly on the lower east coast of the SoG but were rare elsewhere. In 2016, recreational fishers observed anchovy schools around the entrance to Howe Sound from spring through late fall. Schools were often on the surface and very close to shore, and were being fed on by seabirds, harbor seals (*Phoca vitulina richardii*), and humpback whales (*Megaptera novaeangliae*) (Jason Assonitis, pers. com.). This historical and observed distribution of Northern Anchovy in the SoG is consistent with an association with lower salinity water. Engraulids are frequently associated with the influence of rivers (Checkley et al., 2017). Richardson (1981) suggested that the Fraser River Plume could provide suitable conditions (stable and productive) for anchovy spawning and might represent a secondary spawning center for the northern subpopulation. The plume of the Fraser River turns north once it enters the SoG (Thomson, 1981), and the waters of the mainland shore are lower in salinity than the northwestern shore (Tully and Dodimead, 1956). The salinity of Howe Sound and the other major inlets is also affected by inflows from large mainland rivers.

While the trawl data that we report indicated the presence of anchovy throughout PS, the most consistent occurrence was in South Sound. Observations by South Puget Sound residents that various size classes of anchovies are present year-round (Duane Fagergren, pers. com.) corroborate this result. Catches in WDFW trawls were consistently low in the SJF and opening of PS. This region is subject to strong tidal mixing (Moore et al., 2008) and may represent an area of depressed primary productivity and poor foraging for planktivorous fish, as was found at the northern exit from the SoG (McKinnell et al., 2014). Interestingly, our results contrast with the scat-based harbor seal diet analysis of Lance and Jefferies (2009) which suggested that anchovy were relatively important in seal diets in Hood Canal and the San Juan Islands but not South PS. This difference could reflect a shift in anchovy distribution since the period of these scat studies (1995–1997). Alternatively, it could be partially due to different temporal coverage among regions, with only Hood Canal and the San Juan Islands sampled in 2005, a year of high anchovy abundance based on results of the present study. One interesting result of 2016 WDFW PS mid-water trawls was that catches were very infrequent in summer (June and August). Catches were also almost absent when Canadian juvenile salmon surveys extended into PS in June/July and September/October. It is unclear if this pattern is a consequence of movement of anchovy out of PS, redistribution to areas less vulnerable to mid-water trawl gear, or a shift to a patchier distribution during the summer months.

The egg and larval timing and size frequency shifts documented in the present study are consistent with year-round residence, spawning, and successful recruitment of anchovy within the SS.

Early fishery scientists in British Columbia believed that spawning occurred within the SoG (Foerster, 1941) and Pike (1951) inferred that spawning occurred in Southern BC due to the presence of ripe females in mid- to late- summer. Richardson (1981) suggested the Fraser River plume as a possible spawning location for anchovy. However, because eggs had not been observed in the SoG at the time, Therriault et al. (2002) remained uncertain whether anchovy reproduced in British Columbia waters. Our results suggest that spawning can occur in the SoG as early as March, peaks in June, and continues to at least September. Small, age-0 fish appear in net-based surveys in July or August and remain present through fall and winter, with a size mode between 75 and 100 mm by late fall and close to 100 mm by the following spring. This is consistent with the results of Pike (1951) who found that average lengths of age-1 anchovy in BC were 107 mm for females and 105 mm for males. While winter data in the present study are limited to PS trawl surveys, other threads of evidence confirm that age 1+ anchovy are present in the SS throughout the year. Schools of anchovy were observed being pushed into shallow water by harbor seals (*Phoca vitulina*), sea lions (*Zalophus californianus* or *Eumetopias jubatus*), river otters (*Lontra canadensis*), and birds in January of 2016 near the entrance to Howe Sound, with scales and mortalities washing up on shore (Dianne Sanford, pers. comm.). Anchovy were also present in 11 of 27 Chinook Salmon stomachs caught by recreational anglers in Howe Sound and near Vancouver from December 2016 to March 2017, standard lengths of these fish ranged from 123 to 168 mm (J. Qualley, unpublished data).

Timing and distribution of anchovy catches reported in the present study should be considered in any future effort to assess abundance in the SS. Mid-water trawl surveys in open water may be a poor method to assess anchovy abundance. While multiple lines of evidence suggest that anchovy were abundant in 2016, SoG juvenile salmon trawl surveys only caught anchovy in 10 of 93 tows in July and 3 of 84 tows in October (albeit 4 of these catches were very large). This contrasts with anchovy encountered in 17 of 48 age-0 Pacific Herring survey purse seine sets conducted in September, despite purse seine sets sampling a volume of water at least three orders of magnitude smaller than the trawl sets. The significant negative effect of bottom depth on likelihood of encountering anchovy in the age-0 Pacific Herring surveys suggests the possibility of a very nearshore distribution in the SS by late summer and fall. This nearshore distribution is also consistent with observations by fishers and members of the public. Spawning biomass assessments of anchovy in the California Current have relied on egg and larval density-based methods (Richardson, 1981; Emmett et al., 1997; MacCall et al., 2016). Given evidence of patchy and nearshore distribution of adult and sub-adult anchovy in the SS, it is likely that any future attempts at formal stock assessment should also focus on early life-history stages in mid-summer.

4.2. Fluctuations in Abundance

Anchovy have been intermittently abundant in the SS throughout the period of historical and paleo-archaeological record. In Burrard Inlet (Vancouver, BC) anchovy were the third most abundant fish in First Nations archaeological sites up to 3000 years old (Pierson, 2011), and McKenchie and Moss (2016) report that anchovy remains were present at 37% of 94 First Nations archaeological sites within the SS. Anchovy scales were present in the majority of laminated strata dated to the period from 1861 to 1900 in the anoxic basin of Saanich Inlet, but were scarce in the 20th century (O'Connell, 1998). Nineteenth century accounts of fishery resources describe anchovy as abundant or formerly abundant (Suckley, 1860). In British Columbia, anchovy were described by Langevin (1873) as being "taken with great ease in any quantity," although it is not clear if this refers to waters within the SS. Swan (1894) characterized anchovy as so abundant in PS as to be harvested by bucket. Unfortunately, accounts prior to the 1940s are not detailed enough to define periods of abundance and scarcity, although it is clear that both occurred. Hart (1934) makes reference to a questionnaire on fish distributions and abundance that was distributed to fishers throughout BC. Three respondents to this questionnaire indicated that anchovy became abundant in 1928 after an absence of approximately 15 years. The Pacific Biological Station report for 1935 (Hart, 1935) includes the statement: "…all enquiries elicit the information that in southern British Columbia this species is much less common than it was two or three years ago. This apparent decline in abundance has occurred in spite of the fact that the species has been practically free from exploitation." These statements are consistent with a period of abundance between 1928 and the early 1930s; however, given a lack of specific reference to abundance in the SoG we did not include this in our reconstructed time series.

The data sources assembled for the present study suggest several periods of anchovy abundance in the SS since the 1940s, separated by periods of scarcity. While data were inadequate to characterize abundance through large sections of the time series, it would be surprising if sustained high abundance of anchovy would have gone un-documented in the scientific literature or management agency records. Since 2000, multiple data sources provide a generally consistent picture. One inconsistency among data series was the absence of anchovy in 2005 zooplankton samples and their presence in 2006. Sampling gear and effort for surveys reported in the zooplankton database varied considerably from year to year, and 2005 was the year with the second lowest number of sets included in the analysis (23 as compared to a mean of 83). All samples with anchovy in 2006 were obtained using a Tucker trawl. This gear type samples a larger volume of water than most other gear types reported in the zooplankton database and was only utilized in 2000, 2006, and 2007. Another inconsistency in the data was the Elwha beach seine program, which did not detect a period of abundance in 2015–16. The Coastal Watershed Institute has also been conducting beach seine surveys in the Elwha estuary since 2007, and while anchovy were caught in several sets in 2007 and a single set in 2010, no anchovy were caught in other years including 2015 or 2016 (Anne Shaffer, pers. comm.). It seems possible that the strongly tidally mixed JDF does not exhibit the same trends in anchovy abundance as PS and the SoG.

We detected a more significant positive relationship between coastal SST and anchovy abundance than between SST within the SS and anchovy abundance. This could suggest that SS abundance is controlled by reproduction and recruitment on the outer coast, or that our reconstructed SST index did a poor job of reflecting the environmental conditions influencing reproduction and recruitment success within the SS. Nevertheless, both our quantitative and qualitative results suggest that periods of SS anchovy abundance have tended to correspond to, or closely lag, periods of elevated ocean temperature. As the SS is close to the northern edge of the distribution of anchovy it seems likely that periods of warmer ocean temperature could result in higher productivity. The northern population of anchovy generally spawn later than the central subpopulation, which spawns throughout the winter (Richardson, 1981; Emmett et al., 1997; the present study, see Auth et al., 2018). Therefore, in the SS, warm water temperatures may be necessary to facilitate rapid growth by larvae and juveniles to achieve an adequate size to survive the winter. Winter temperatures in the SS could also present problems for anchovy in cold years; mean minimum January SST in the southern SoG is between 6 and 7 °C (based on Departure Bay SST), close to the critical lower temperature (6.5 °C) demonstrated by Brewer (1976) for anchovy. Observations of anchovy schooling in very shallow water, and mortalities on the beach near Howe Sound in January of 2017 (Dianne Sanford pers. comm.) were consistent with the possibility of low temperature thermal stress. However, deep waters of the SS do not get as cold in the winter (Thomson, 1981; Chandler et al., 2016), and could provide a thermal refuge if utilized.

Due to the lack of a continuous time series of stock size for the northern subpopulation of anchovy outside the Salish Sea, we were unable to directly test the hypothesis that this population expands into the Salish Sea during periods of high abundance. Anchovy catch in Columbia River plume surveys has remained relatively low and consistent from 1998 to 2016, with the exception of a marked increase in 2004 and 2005, which did correspond to an increase in SS anchovy (Figure 14). The status of anchovy in the Columbia River plume region in 2015 and 2016 is very uncertain, low CPUE in the Columbia River plume surveys could indicate low abundance, or could be a consequence of some combination of the introduction of a marine mammal excluder device reducing catches and the highly unusual oceanic conditions of the warm water “blob” changing anchovy distributions (Cheryl Morgan, pers. comm.). A very unusual event also occurred in the northern subpopulation commercial fishery in 2016, with by far the largest landings on record (Figure 14). The significance of this event is uncertain. The fishery concentrated on anchovy primarily within the Columbia Estuary. Increased effort may also have been driven by a shift from marketing anchovy exclusively for bait to marketing it for human consumption, and by reduced purse seine fishing opportunities (Cyreis Schmitt, Oregon Department of Fish and Wildlife, pers. com.). Whether this high catch reflects a real increase in the northern subpopulation, a contraction into nearshore habitat during low population abundance (MacCall et al., 2016; Davidson et al., 2017), or a response to unusual oceanographic conditions remains uncertain.

If fluctuations in SS anchovy abundance were driven by fluctuations of adjacent coastal populations, it follows that fish would need to move into the SS at some point during their life history. The SJF, the main connection between the inner SS and adjacent shelf habitat, is characterized by net outward estuarine surface flows during summer (Thomson, 1981). It seems unlikely that the very small age-0 anchovy (< 50 mm FL) that are encountered in the SoG in mid-summer could have migrated from the outer coast against this prevailing flow. However, when infrequent, low-pressure systems result in a switch to poleward winds during summer, estuarine circulation can break down, and low salinity surface water from the northern Washington shelf can be transported far into the SJF at relatively high velocity (Thomson et al., 2007). Interestingly, 2005, a year where coastal anchovy abundance corresponded to SS anchovy abundance, was characterized by a very late spring transition (switch to northerly winds) with strong southerly wind stress events occurring into late May (Kosro et al., 2006). Transient summer inflows of coastal surface waters provide a plausible mechanism for anchovy recruitment to the SS in some years.

Laroche and Richardson (1981) inferred from catch patterns that mature anchovy in the northern subpopulation moved offshore to spawn in mid-summer, with only immature individuals remaining nearshore in bays and estuaries, and that all life history stages overwintered together nearshore. Pike (1951) found that most age-2 anchovy females were mature, at a mean SL of 128 mm. The results of the present study suggest that fish of this size are present in the SS in June and July, and have not all migrated offshore to spawn. However, low encounter frequency of anchovy in summer mid-water trawl surveys in Puget Sound could be consistent with part of the mature population migrating offshore. While it remains possible that adult anchovy in the SS are exclusively the product of spawning outside of the SS, it seems unlikely that this is the case, at least for the recent (2015–2016) increase in abundance for which size frequency and distribution data are available. If fluctuations in abundance are driven primarily by conditions within the SS, some remnant population must remain even during poor conditions. The fact that at least some anchovy have been caught in all 24 years of the SoG age-0 Pacific Herring surveys suggests that this is plausible. Early accounts (Swan, 1894) describe anchovy as arriving in SS waters from elsewhere as a distinct run, being present from May to November. It is possible that historical abundance was driven by migration of fish from outside the SS (possibly during a period of very large coastal populations), while contemporary dynamics are driven by recruitment within the SS. If the frequency and duration of warm periods increases, anchovy may become a more persistent and important component of the SS ecosystem.

4.3. Ecosystem Implications

The Salish Sea is an ecosystem in a state of flux, and when abundant, anchovy may play pivotal roles as competitors, prey, or predation buffers. The changing quality of the SS as a nursery for culturally, economically and ecologically valuable Pacific salmon stocks has received considerable recent attention (e.g., Beamish et al., 2000; Beamish et al., 2010; Beamish et al., 2012; Zimmerman et al., 2015). Some species and stocks of Pacific salmon exhibited drastic declines in early marine survival in the 1970–80s and have not yet recovered. It is currently unclear how abundant anchovy could influence survival of juvenile Pacific salmon in the SS. Chamberlin et al. (2017) suggested that while abundant Pacific Herring (the dominant forage fish in the Salish Sea) may inhibit juvenile Chinook Salmon growth through competition, larger juvenile Chinook Salmon may experience enhanced growth when Pacific Herring small enough to utilize as prey are abundant. Anchovy are planktivorous, and potentially could also act as competitors to juvenile salmon. As anchovy spawn throughout the summer in the SS, larvae and small juveniles may be more accessible to piscivorous juvenile salmon than larger age-0 Pacific Herring produced by late winter spawning. Indeed, in 2016 larval and post-larval anchovy were observed in the stomach contents of juvenile Chinook Salmon captured in summer juvenile salmon trawl surveys in the SoG (C. Neville, unpublished data) and in hook and line sampling in the Southern Gulf Islands (W. Duguid, unpublished data). Recent work in the California Current has suggested that age-0 anchovy abundance may be a key regulator of juvenile Chinook Salmon growth during the transition to piscivory (Litz et al., 2016). If anchovy become consistently abundant in the SS it will be important to consider their role in the trophic ecology of juvenile Pacific salmon.

In addition to acting as competitors or prey, abundant anchovy could potentially reduce predation pressure on juvenile salmon and other species in the SS. The presence of one highly abundant prey species has the potential to buffer predation mortality and increase survival of other prey species in an ecosystem (eg. Willette et al., 1999; Weitkamp et al., 2011; Wells et al., 2017). Harbour seal abundance has increased dramatically in the SS in recent decades, and there is mounting evidence that seal predation is impacting juvenile salmon survival (Berejikian et al., 2016; Thomas et al., 2016; Chasco et al., 2017). Harbor seals in the Salish Sea do eat anchovy, particularly in winter and spring (Lance and Jefferies, 2009; Lance et al., 2012), and could be expected to target them when abundant. Concurrent with increased abundance of anchovy, acoustic tag-based survival estimates for Nisqualley River juvenile Steelhead (*Oncorhynchus mykiss*) migrating out of PS increased from 6% to 38% between 2014 and 2016 (Megan Moore, NOAA, pers. com.). Predation buffering by abundant anchovy is one hypothesis to explain this change. Interactions among predators and multiple prey species may also exhibit more complex dynamics. For example, off California predation pressure on juvenile Chinook Salmon by common murres (*Uria aalge*) is low when juvenile rockfish (*Sebastes spp.*) are abundant offshore, but increases when murres switch to feeding on anchovy which overlap spatially with the juvenile salmon closer to the coast (Wells et al., 2017).

Given that anchovy have been scarce during the bulk of the period of intensive fisheries research in the SS, hypotheses about their role in the ecosystem remain very speculative. Nevertheless, British Columbia coastal waters are warming (Chandler et al., 2016), and results of the present study suggest that this warming may lead to more consistent abundance of anchovy in the SS. It has been suggested that warming of the SS may be directly and/or indirectly related to declines in survival of juvenile Pacific Salmon, particularly Coho Salmon (Beamish et al., 2010) and Chinook Salmon (Beamish et al., 2012). If anchovy become more abundant they could exacerbate the negative effects of warming as competitors and/or mitigate warming effects as prey and/or buffers against predation. Conversely it is also conceivable that changes in the SS due to warming, including reduced predation by juvenile salmon, could play a causal role in increased anchovy abundance through higher juvenile anchovy survival. Regardless of the polarity of causal relationships, our results suggest that anchovy should be taken account in attempts to model the response of the SS ecosystem to a changing climate.

4.4. Conclusions

Anchovy have not been considered an important species in the Salish Sea ecosystem during the period of modern fisheries research. However, this species was at least periodically abundant in the SS prior to the 20^{th} century, and has experienced periodic spikes in abundance over the past century. Probably the most pronounced of these periods since the 1940s began in 2014 or 2015 and has extended at least into the spring of 2017. Historical and contemporary data indicate that anchovy exhibit consistent patterns of distribution in the SS. The Fraser River plume and mainland shore of the SoG and South PS appear to be regions of consistent occurrence. Spawning, possibly concentrated in the Fraser River Plume, peaks in mid-summer. Age-0 anchovy may be concentrated in nearshore habitats by fall and adults are present in the SS year-round. Abundance of anchovy in the SS appears to correspond to, or lag, periods of elevated ocean temperature, and is positively correlated with two year-averaged indices of Salish Sea and coastal SST. While plausible mechanisms exist by which abundance of anchovy in coastal regions could influence abundance within the Salish Sea, this does not seem to be a necessary cause for fluctuations in abundance. Continued warming of the Salish Sea may lead to greater abundance and persistence of anchovy, with potentially important consequences for the ecosystem as a whole. Population genetic research is warranted to test the hypothesis that anchovy within the SS are largely reproductively isolated from the rest of the northern subpopulation. Development of a systematic survey to assess spawning stock biomass in the SS may also be warranted. Studies investigating the current and future trajectories of the

SS ecosystem should consider possible interactions between temperature, anchovy abundance, and other species in the ecosystem.

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7. Tables

Table 1. Data sets utilized to investigate spatiotemporal distribution and trends in abundance of Northern Anchovy in the Salish Sea. 'Spatial Sets' indicates the number of gear deployments used in maps of spatiotemporal distribution. 'Time Series Sets', indicates the number of gear deployments used in developing a quantitative index of anchovy abundance. 'Qualitative Time Series' indicates whether or not a given data set was included in a qualitative index of anchovy abundance.

	Gear/Deployment Time	Figures	Depth Range (m)	Years Used	Months Used	Spatial Sets (N)	Time Series Sets (N)	Qualitative Time Series	Methods Reference	Comments
SoG Zooplankton Database	Various, analysis limited to sets fished from at least 15 m to the surface	4, 9, 13	0-420	2000-16	Mar-Sept	435	1420	Yes	Mackas et al. 2013	
SoG Age-0 Herring Surveys	183 by 27 m purse seine (9.5 mm mesh bunt)	5, 11, 13	0	1992-94, 1996-2016	Sept-Oct	1056	1056	Yes	Schweigert et al. 2009, Boldt et al. 2015, Thompson et al. 2016	Night time sets at standard stations
SoG Juvenile Salmon Trawl Surveys	~14 by 30 m rope trawl with 1 cm cod end liner, 30 minute tows	6, 11	0-80	2015-16	June-July, Sept-Oct	458	NA	No	Beamish et al. 2000	Most sets on standard (1998 to present) track lines.
Fraser River Plume Study (tow net)	3 by 6 m surface trawl; 1.3 cm cod end; integrated 350 μm plankton net,10 minute tows	7, 13	0	1966-69, 1973	June-July	196	196	Yes	Barraclough 1967, McKinnell and Perry 2016	Effort varied between years, trawl fished between two vessels
SoG R/V Neocaligus Trawl	4 by 4 m (2014-15) and 5-6 by 15-20 m (2016) trawls with ~1.3 cm cod end, 15 minute tows	10, 11	0-30	2014-16	May-Sept	NA	NA	No		Focused on edge of Robert's Bank in 2014-2015 and Howe Sound in 2016
Puget Sound Midwater Trawl	7.3 by 7.3 m trawl with 1 cm liner in cod end, 15 minute tows	8, 11	15-141	2016	Feb-Dec	184	NA	No		Sets at depth of acoustic targets identified by lead vessel
Skagit Bay Townet Surveys	3.1 by 6.1 m trawl, 6 mm cod end, 10 min tow	13	0	2001-16	Aug-Sept	NA	871	Yes	Rice et al. 2011	Two vessel trawl
Southern SoG Townet	3.1 by 6.1 m trawl, 6 mm cod end, 10 min tow	13	0	1974-77, 2003, 2011	June-Sept	NA	226	Yes	Greene et al. 2015	Two vessel trawl; primarily nighttime in 73-85 daytime in 1972, 2003, and 2011
Whidbey Basin Townet	3.1 by 6.1 m trawl, 6 mm cod end, 10 min tow	13	0	1972, 1983-85, 2003, 2011	June-Sept	NA	444	Yes	Greene et al. 2015	Two vessel trawl; primarily nighttime in 73-85 daytime in 1972, 2003, and 2011
Central Puget Sound Townet	3.1 by 6.1 m trawl, 6 mm cod end, 10 min tow	13	0	1976-85, 2002-03, 2011	June-Sept	NA	513	Yes	Greene et al. 2015	Two vessel trawl; primarily nighttime in 73-85 daytime in 1972, 2003, and 2011
South Puget Sound Townet	3.1 by 6.1 m trawl, 6 mm cod end, 10 min tow	13	0	1976-82, 2003, 2011	June-Sept	NA	197	Yes	Greene et al. 2015	Two vessel trawl; primarily nighttime in 73-85 daytime in 1972, 2003, and 2011
Snohomish Beach Seine	37 by 3.1 m (bag) beach seine, 3.2 mm mesh in bag, ideal swept area = 1200 m^2	13	0	2001-09	Aug-Sept	NA	139	Yes	Miller et al. 1990	Only included sets at sites where anchovy encountered at least once
Elwha Beach Seine	37 by 3.1 m (bag) beach seine, 3.2 mm mesh in bag, ideal swept area = 1200 m^2	13	0	2005-16	Apr-Sept	NA	1031	Yes	Miller et al. 1990	Only included sets at sites where anchovy encountered at least once
BC Commercial Catch Records	NA	12	NA	1940-2016		NA	NA	Yes		Commercial catch data specific to the SoG only reported for 1940-46
Puget Sound Commercial Catch Records	NA	12	NA	1940-2016		NA	NA	Yes		Provided by WDFW
Annual Reports of Pacific Biological Station and related documents	NA	NA	NA	See Suppl. Material		NA	NA	Yes	See Suppl. Material	
Beamish and Neville Plume Surveys	4 by 4 m trawl, 5 mm mesh cod end	NA	0	1989-93	June-July	NA	400	Yes	Beamish and Neville 1995	
Beamish Strait of Georgia Purse Seine	402 by 33 m purse seine, 6 mm bunt	NA	0	1974	July-Aug	NA	50	Yes	Beamish 1976	

8. Figures Captions

Figure 1. The Salish Sea consists of the Strait of Georgia (SoG), Strait of Juan de Fuca (SJF) and Puget Sound (PS). Inset box (a) corresponds to Figure 2 and maps of SoG zooplankton sample data (Figure 4) and age–0 Pacific Herring surveys (Figure 5); box (b) corresponds to Figure 3 and maps of PS mid–water trawl surveys (Figure 7). Bathymetry data are the GEBCO_2014 Grid, version 20150318, http://www.gebco.net.

Figure 2. The Strait of Georgia and northern Strait of Juan de Fuca. Sites referenced in the present study include (*SST and salinity data sites indicated in italics*): (JI) Jervis Inlet, (DS) Desolation Sound, *(CM) Cape Mudge, (SS) Sentry Shoal*, (TI) Texada Island, (PH) Pender Harbour, (HS) Howe Sound, (BS) Baynes Sound, (MS) Malaspina Strait, *(CI) Chrome Island, (HB) Halibut Bank*, (BI) Burrard Inlet, *(EI) Entrance Island, (DB) Departure Bay*, (RB) Roberts Bank, (BB) Boundary Bay, (L) Ladysmith, (SGI) Southern Gulf Islands, *(AP) Active Pass*, (SSI) Saltspring Island, (CB) Cowichan Bay, (SI) Saanich Inlet, (SJI) San Juan Islands, (HSt) Haro Strait, (V) Victoria, *(RR) Race Rocks*. Bathymetry data are the GEBCO_2014 Grid, version 20150318, http://www.gebco.net. Note: The deepest part of Jervis Inlet is depicted here as 500 m deep but in fact reaches depths of up to 670 m.

Figure 3. Puget Sound and the eastern part of the Strait of Juan de Fuca (SJF). Sites referenced in the present study include: (SSG) Southern Strait of Georgia, (SJI) San Juan Islands, (SB) Skagit Bay, (WB) Whidbey Basin, (EE) Elwha River Estuary, (SE) Snohomish River Estuary, (CPS) Central Puget Sound, (TN) Tacoma Narrows, (NE) Nisqually River Estuary, (SPS) South Puget Sound. Bathymetry data are the GEBCO_2014 Grid, version 20150318, http://www.gebco.net.

Figure 4. Locations (red filled points) of anchovy eggs (a–c) and larvae/juveniles (d–f) encountered in 435 zooplankton samples (x indicate tows with no catch of anchovy eggs, larvae, or juveniles) covering at least the top 15 m of the water column and collected between March and August of 2015 and 2016. Arrow in (a) indicates the location of a station in Malaspina Strait where eggs or larvae were encountered in 7 of 9 tows conducted between 11 May and 14 August 2015.

Figure 5. Proportion of sets encountering anchovy in fall (September or October) night time age–0 Pacific Herring surveys conducted by DFO between 1992 and 2016 in the SoG. One set was conducted annually (except 1995) at each of 3 to 5 stations on each numbered transect. Inset shows % presence at each station on transects 10 and 11 (Malaspina Strait); x indicates stations with no catches.

Figure 6. Tow locations and log + 1 transformed anchovy catch per hour in DFO juvenile salmon trawl surveys in 2015 (a. 24 June to July 9 and b. 16 September to 6 October) and 2016 (c. 5 July to 14 July and d. 17 to 26 October); x indicates tows with 0 catch.

Figure 7. Tow locations and log + 1 transformed anchovy catch per tow (a–e) in June and July surface two–vessel trawl surveys in 1966–69 (a–d) and 1973 (e); x indicates tows with 0 catch.

Figure 8. Tow locations and log + 1 transformed anchovy catch (numbers) per tow in February (a), April (b), June (c), August (d), October (e), and December (f) for mid–water trawl surveys conducted by WDFW in 2016; x indicates tows with 0 catch.

Figure 9. Monthly % presence of anchovy eggs and larvae/juveniles in zooplankton samples from the Strait of Georgia and Strait of Juan de Fuca covering at least the top 15 m of the water column between February and October of 2015 and 2016. Error bars are standard error of proportions.

Figure 10. Monthly size frequency distribution (fork length in mm) of anchovy caught in DFO surveys by the R/V CCGS Neocaligus in 2014, 2015 and 2016. Fishing locations were the edge of Robert's Bank in 2014 and 2015 and Howe Sound in 2016.

Figure 11. Monthly size (fork length in mm) frequency distribution of anchovy caught in four survey programs between February and December 2016, sample sizes for each survey in each month are indicated on the panels.

Figure 12. Reported commercial catches of anchovy (kg) from 1940 to 2016 in a. Puget Sound and b. the Strait of Georgia (see section 2.4.10 and Table 1 for details). The dashed horizontal line indicates the threshold (10,000 kg) between catches considered to indicate 'abundance' (score = 1) vs those considered to indicate only 'presence' (score = 0.5) in generating a qualitative index of abundance. Note that vertical axis range differs between the two panels.

Figure 13. Proportion of sets capturing anchovy in a variety of fishery–independent surveys from 1966 to 2016 (see section 2.4 and Table 1 for details): a. SoG Zooplankton Database, b. SoG Age–0 Pacific Herring Surveys, c. Fraser River Plume Study (tow net), d. Southern Strait of Georgia tow net, e. Skagit

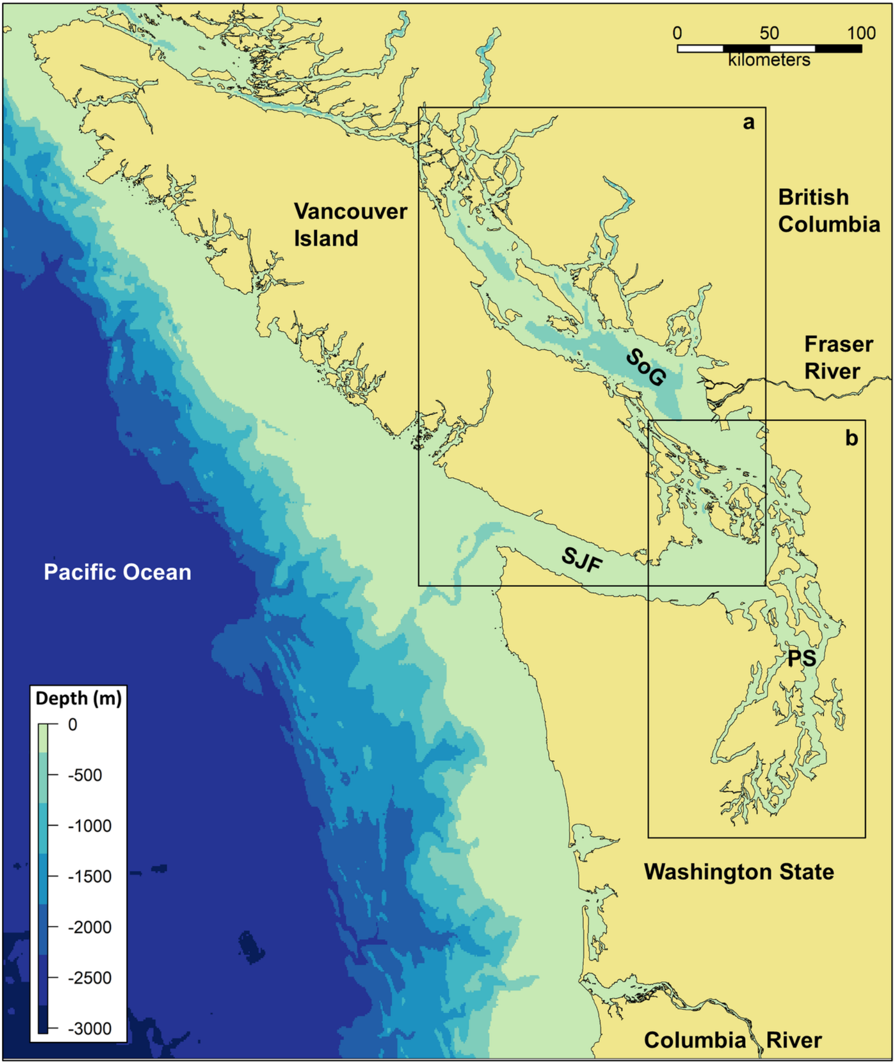
Bay tow net, f. Whidbey Basin tow net, g. Central Puget Sound tow net, h. South Puget Sound tow net, i. Snohomish Beach Seine, j. Elwha Beach Seine. The dashed horizontal lines indicate thresholds between catches considered to indicate ‘abundance’ (score = 1), ‘presence’ (score = 0.5), or ‘scarcity/absence’ (score = 0) in generating a qualitative index of abundance. Note that vertical axis range and threshold levels differ between (a) and (b–j). Error bars indicate standard error of proportion.

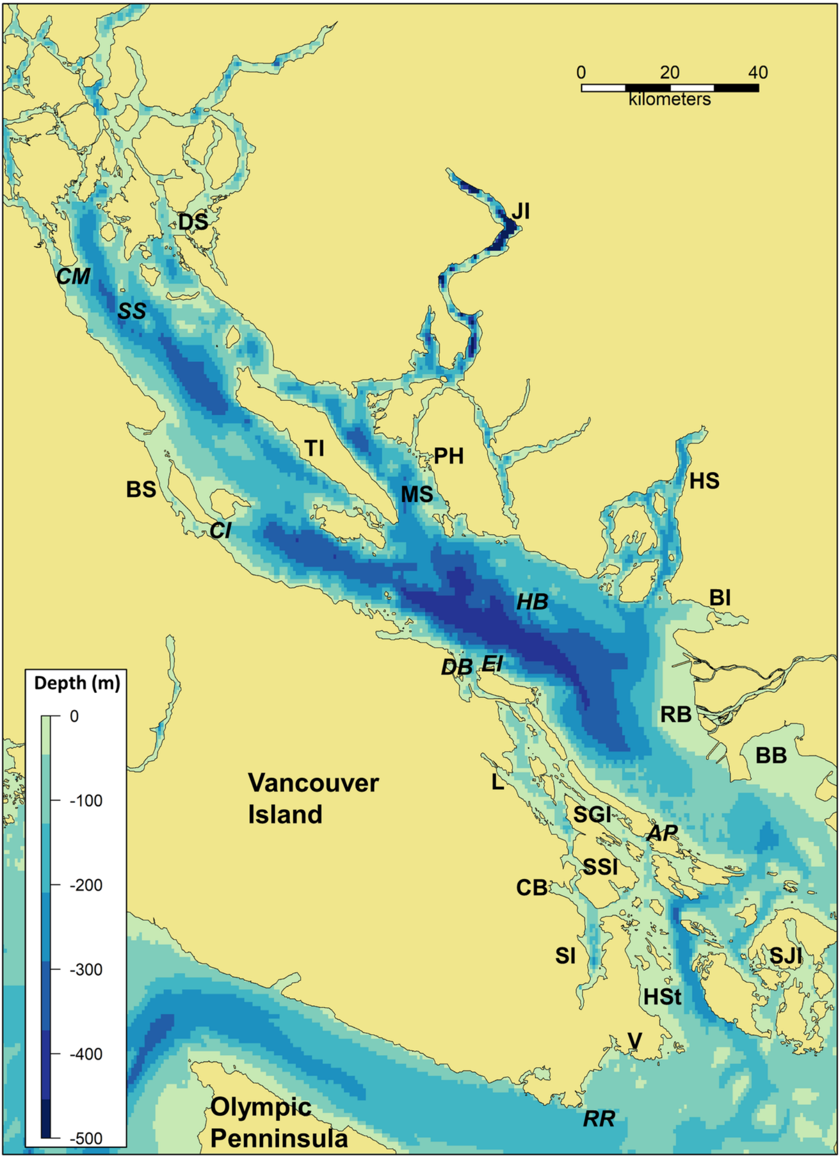
Figure 14. Indices of a. SST (Salish Sea and Coastal), b. Salish Sea Salinity, and c. abundance (densities in Columbia River plume surveys and outer coast commercial catch) of the northern subpopulation of Northern Anchovy off Washington and Oregon from 1936 to 2016. Details of how these indices were derived are provided in the text. Note that the 2016 value for commercial anchovy catch is off the scale of the y–axis (9.1). The grid along the bottom of the figure summarizes a qualitative index of anchovy abundance in the Salish Sea. Numbers in each grid cell indicate the number of contributing data sets for each year. Cells are shaded where at least two datasets contribute to the abundance index for that year. The top row (green) indicates years with and index > 0.5, the middle row (yellow) and index of 0.5, and the bottom row (red) and index of < 0.5. Periods of inferred abundance (index > 0.5, at least 2 contributing datasets) are highlighted in green across all index time series. More details of index derivation are provided in the text.

Figure 15. Coefficient estimates and 95% confidence intervals for linear regressions relating a Salish Sea Northern Anchovy abundance index derived from frequency of anchovy catches in fishery–independent surveys to a. a composite index of Strait of Georgia SST anomalies (1935 to 2016), b. first principal component scores of NOAA reconstructed monthly SST adjacent to the coast between 40° N and 60° N, c. a composite index of Strait of Georgia salinity anomalies (1935 to 2016). Predictor variables were averaged over 1 to 3 years and lagged over 0 to 3 years. Data points were weighted by the total number of data sets contributing to the quantitative anchovy abundance index for that year. All significant (alpha = 0.05) estimates are indicated with black circles. For additional details on how indices of anchovy abundance, temperature and salinity were derived refer to the text.

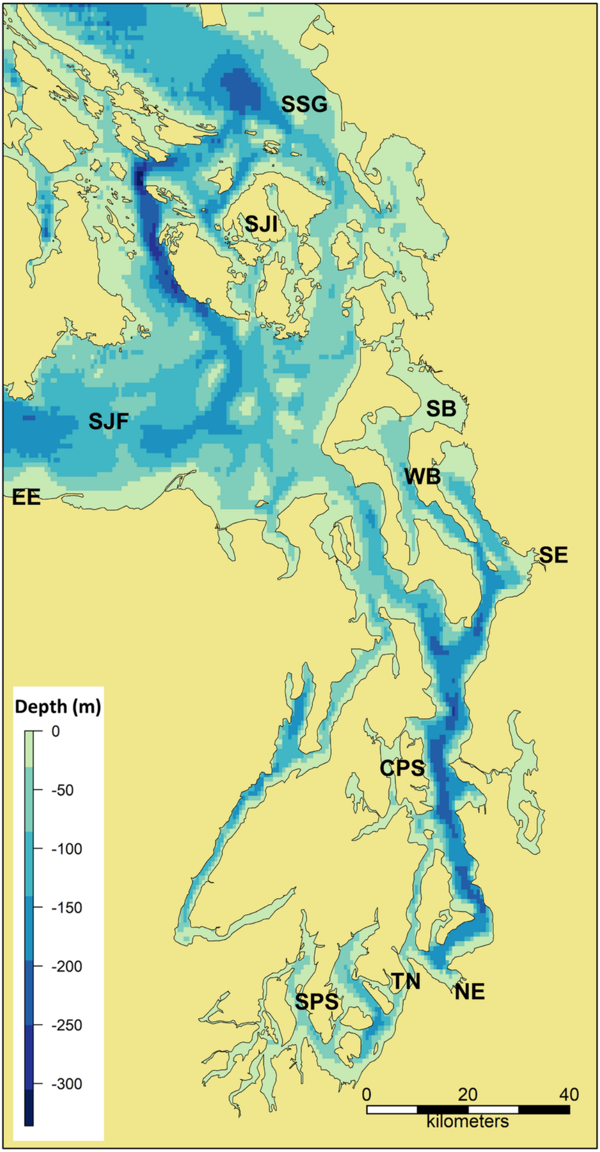
9. Supplementary Material

Literature sources reviewed for references to Northern Anchovy in the Salish Sea but not directly cited in the present study.

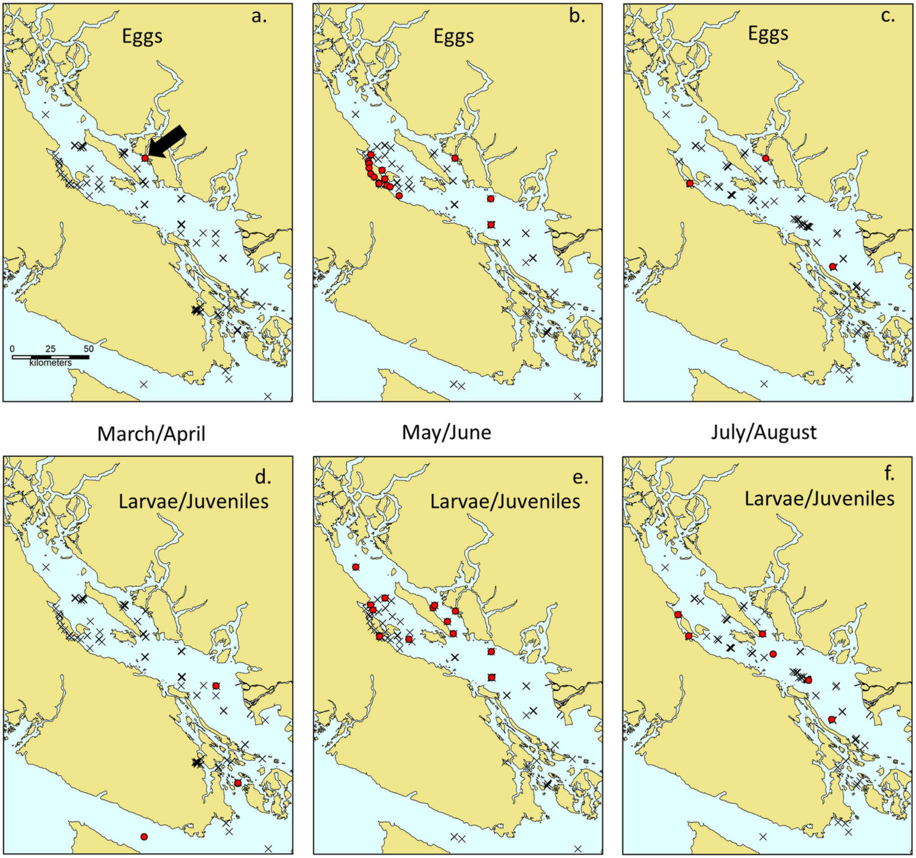

0
50
100
kilometers
a
b
Vancouver Island
British Columbia
Fraser River
SoG
SJF
PS
Pacific Ocean
Washington State
Columbia River
Depth (m)
0
-500
-1000
-1500
-2000
-2500
-3000

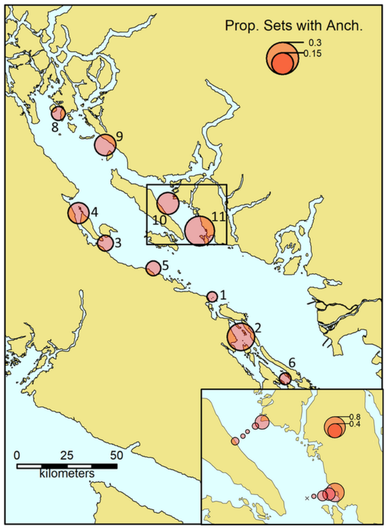


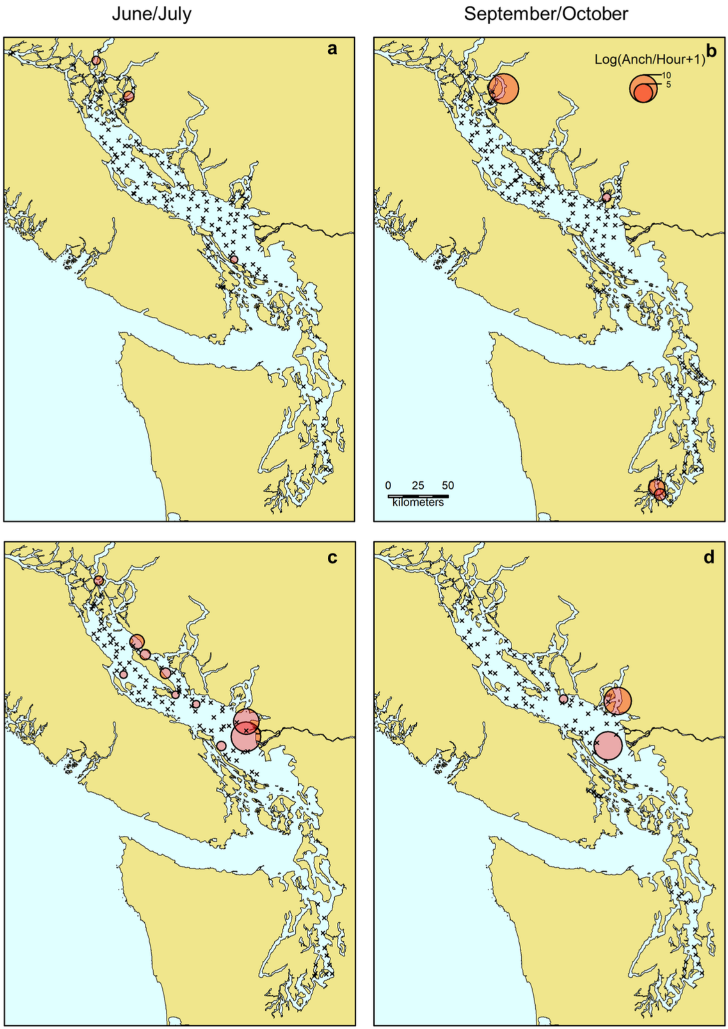
0
20
40
kilometers
JI
DS
CM
SS
TI
PH
HS
BS
MS
CI
BI
HB
DB
EI
Depth (m)
0
-100
-200
-300
-400
-500
RB
BB
Vancouver Island
L
SGI
AP
SSI
CB
SI
SJI
HSt
V
Olympic Penninsula
RR

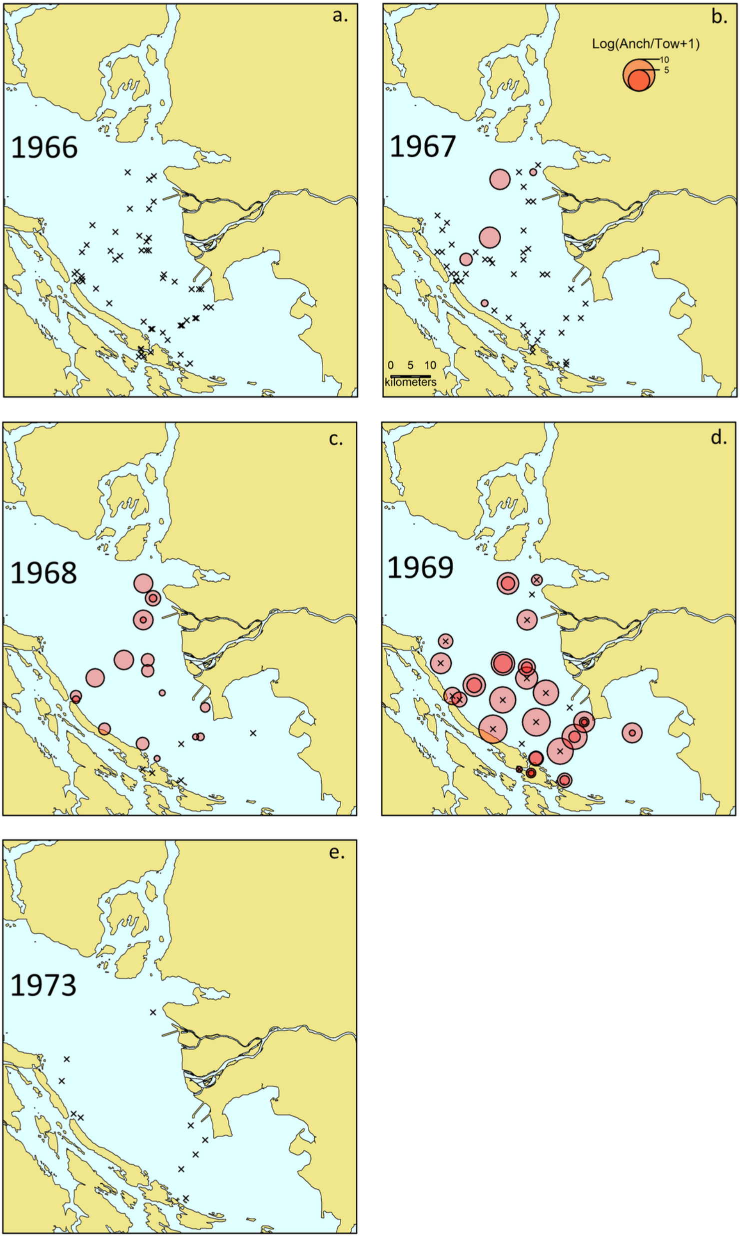


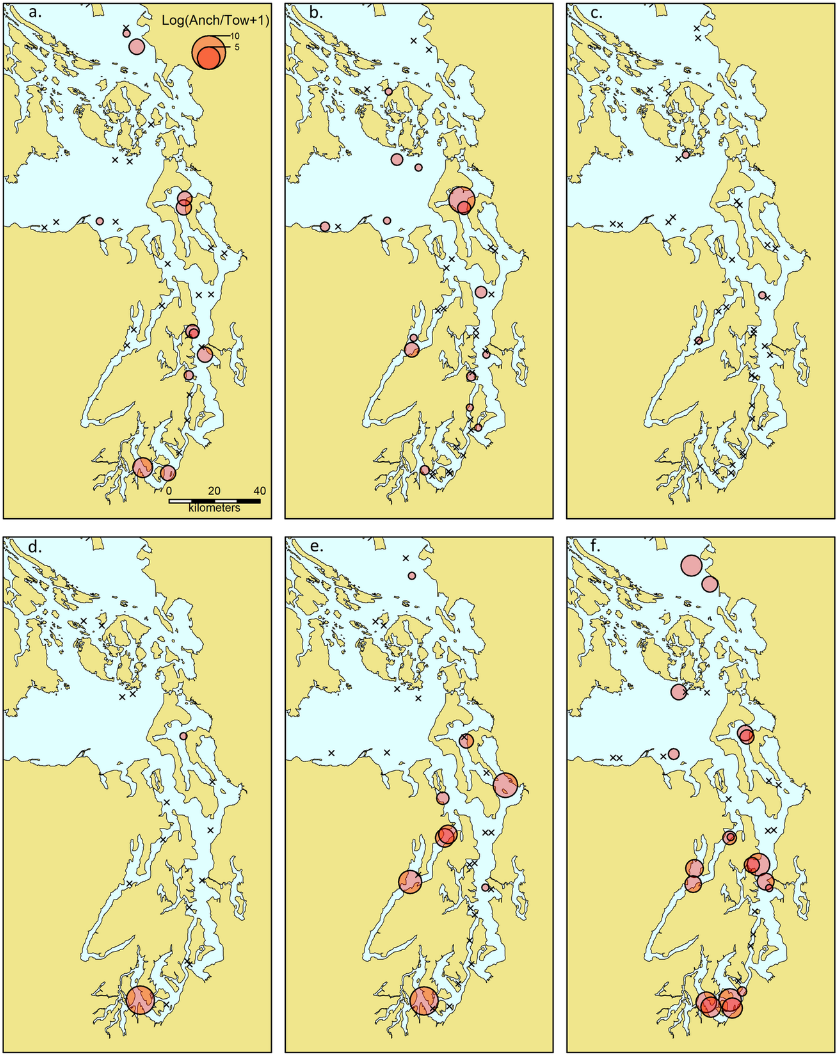
SSG
SJI
SB
SJF
WB
EE
SE
CPS
TN
NE
SPS
Depth (m)
0
-50
-100
-150
-200
-250
-300
0
20
40
kilometers

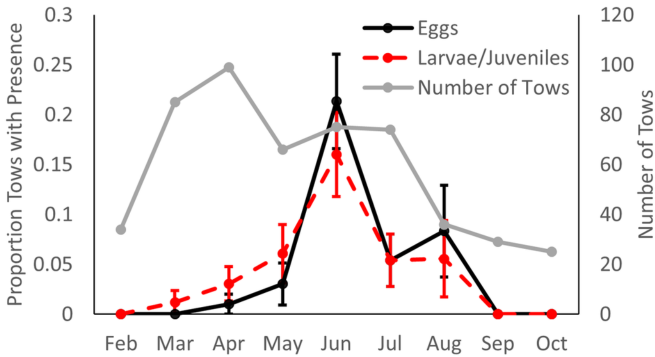

a.
Eggs
0
25
50
kilometers
b.
Eggs
c.
Eggs
March/April
May/June
July/August
d.
Larvae/Juveniles
e.
Larvae/Juveniles
f.
Larvae/Juveniles


Prop. Sets with Anch.
0.3
0.15
8
9
4
10
11
3
5
1
2
6
0
25
50
kilometers
0.8
0.4

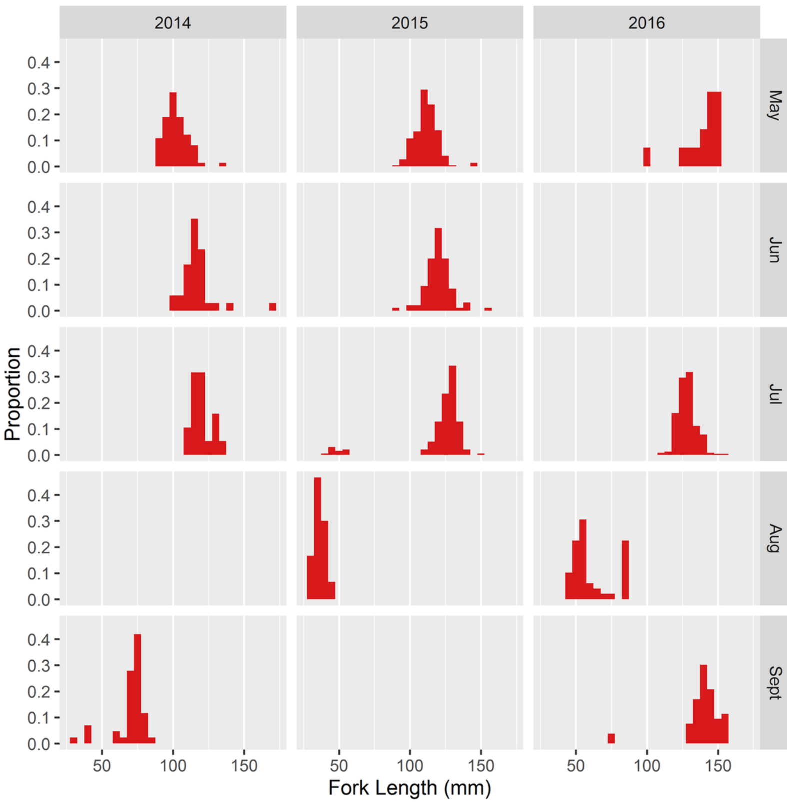

June/July
September/October
a
b
Log(Anch/Hour+1)
10
5
0 25 50
kilometers
c
d


a.
1966
b.
1967
Log(Anch/Tow+1)
10
5
0 5 10
kilometers
c.
1968
d.
1969
e.
1973

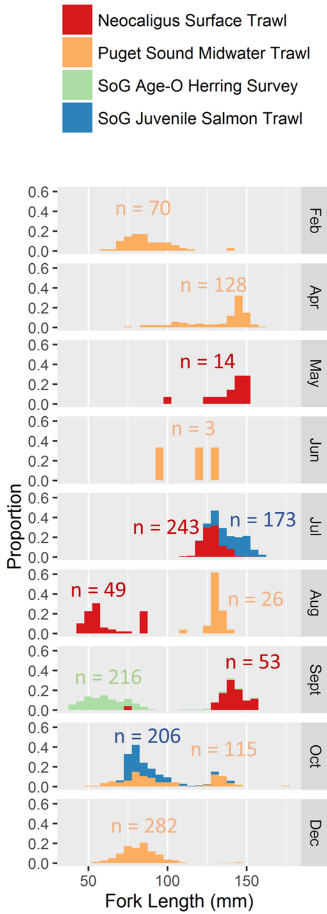

a.
Log(Anch/Tow+1)
10
5
0
20
40
kilometers
b.
c.
d.
e.
f.



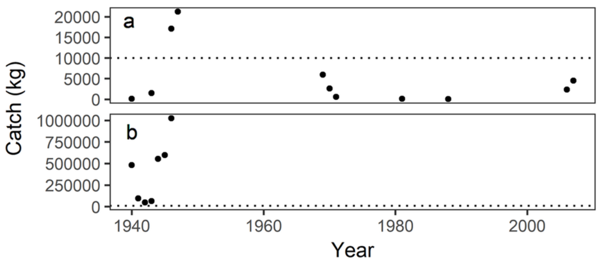
Proportion Tows with Presence
Number of Tows
Eggs
Larvae/Juveniles
Number of Tows
0.3
0.25
0.2
0.15
0.1
0.05
0
120
100
80
60
40
20
0
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct



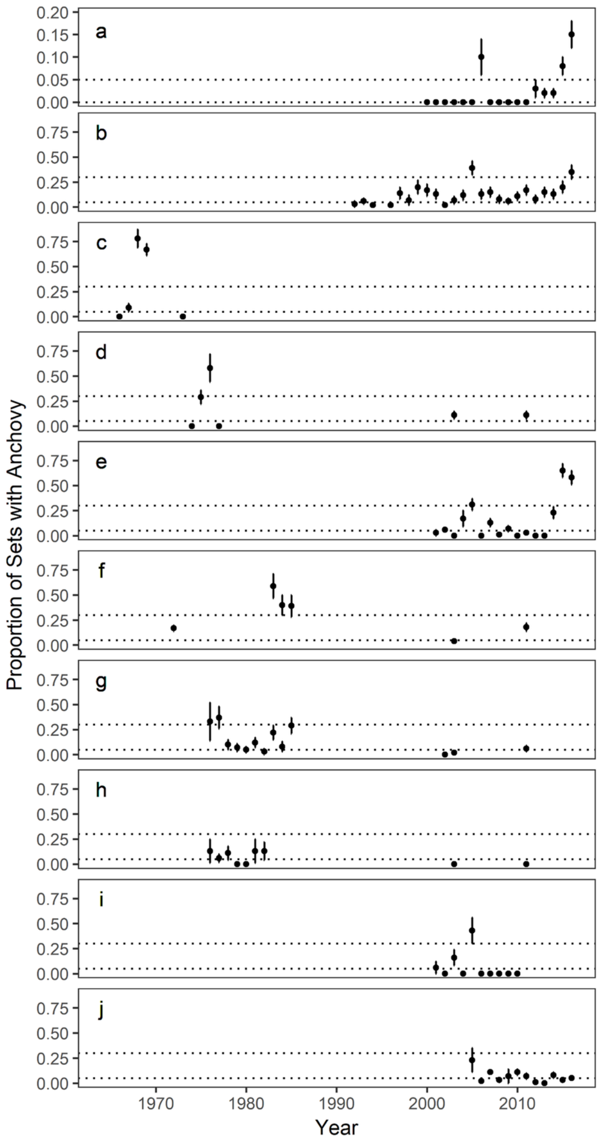
2014
2015
2016
May
Jun
Jul
Aug
Sept
Proportion
0.0
0.1
0.2
0.3
0.4
50
100
150
Fork Length (mm)

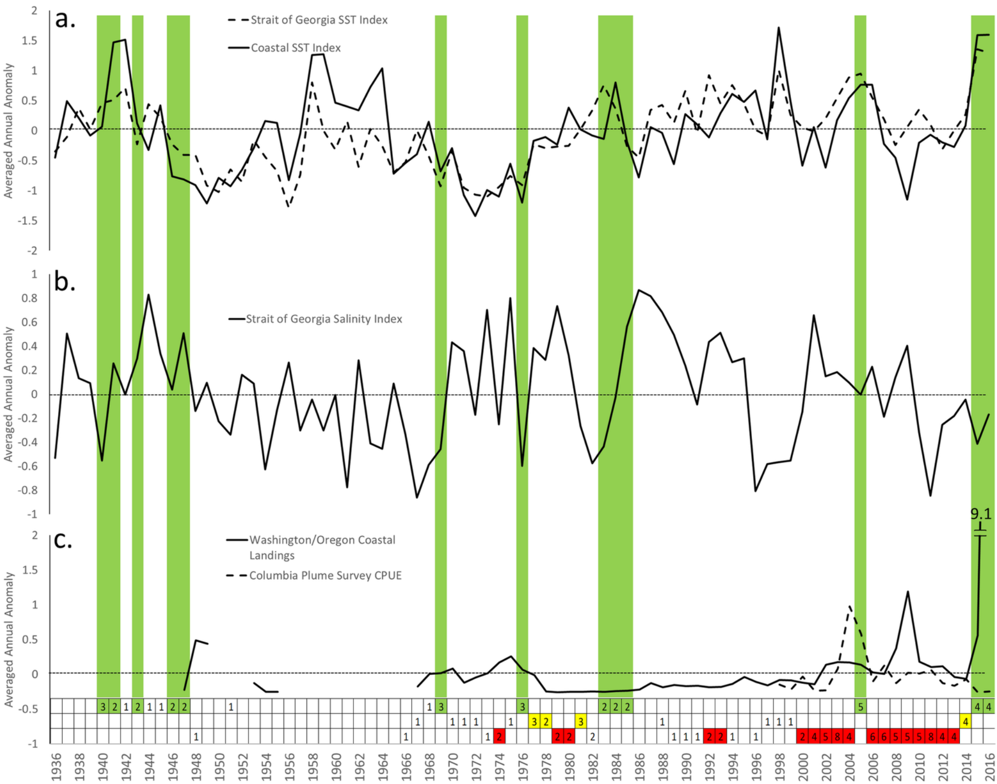


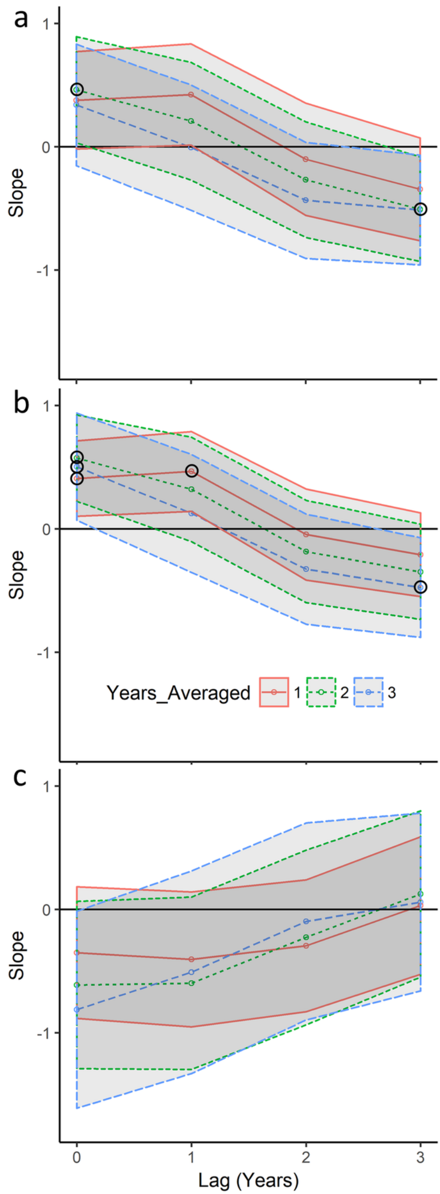
Neocaligus Surface Trawl
Puget Sound Midwater Trawl
SoG Age-O Herring Survey
SoG Juvenile Salmon Trawl
Proportion
0.6
0.4
0.2
0.0
n = 70
Feb
n = 128
Apr
n = 14
May
n = 3
Jun
n = 243
n = 173
Jul
n = 49
n = 26
Aug
n = 216
n = 53
Sept
n = 206
n = 115
Oct
n = 282
Dec
50
100
150
Fork Length (mm)



a
b
20000
15000
10000
5000
0
1000000
750000
500000
250000
0
Catch (kg)
1940
1960
1980
2000
Year


Proportion of Sets with Anchovy
Year
a
b
c
d
e
f
g
h
i
j
0.00
0.05
0.10
0.15
0.20
0.25
0.50
0.75
1970
1980
1990
2000
2010


a.
Strait of Georgia SST Index
Coastal SST Index
Averaged Annual Anomaly
b.
Strait of Georgia Salinity Index
Averaged Annual Anomaly
c.
Washington/Oregon Coastal Landings
Columbia Plume Survey CPUE
Averaged Annual Anomaly
9.1
1936
1938
1940
1942
1944
1946
1948
1950
1952
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016


a
b
c
1
0
-1
Slope
Years_Averaged
1
2
3
0
1
2
3
Lag (Years)