Fine-scale spatiotemporal variation in juvenile Chinook Salmon distribution, diet and growth in an oceanographically heterogeneous region

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ABSTRACT

The existence of fine-scale structure in the abiotic and biotic characteristics of pelagic habitats is widely recognized, but the ecological significance of that structure is understudied. Logistical considerations have meant that research on the ecology of commercially and ecologically important marine species generally occurs at relatively coarse spatial and temporal scales. Many populations of Chinook Salmon (*Oncorhynchus tshawytscha*) in the Northeast Pacific are currently experiencing low productivity. The hypothesis that survival, and hence recruitment, of Chinook Salmon is related to growth early in marine residence has led to intensive research on the trophic ecology of this species during the first year at sea. We employed a small vessel-based methodology to simultaneously characterize fine-scale spatial and temporal variation in physical and biological oceanography, and juvenile Chinook Salmon distribution, size, diet, temperature exposure, and growth from July through October at five sites within the Southern Gulf Islands of the Salish Sea. Densities of zooplankton prey of Chinook Salmon declined to very low levels by the end of the study period. Juvenile Chinook Salmon stomach fullness and growth also declined by early fall while frequency of empty stomachs and importance of fish in diets increased. We found that both oceanographic conditions and trophic ecology of juvenile Chinook Salmon varied among sites only a few (2–23) kilometers apart. Juvenile Chinook Salmon were larger and faster growing at sites where fish (generally Pacific Herring *Clupea pallasii*) constituted a larger proportion of the diet. Overall, the most important prey of juvenile Chinook Salmon by mass proportion (25.6%) was Pacific Herring; however, only 8.4% of individuals contained *C. pallasii*. Analysis of co-occurrence of diet items suggested alternate foraging strategies, with some individuals specializing on Pacific Herring while others targeted a variety of small crustacean zooplankton. Juvenile Chinook Salmon which had consumed Pacific Herring had greater mean stomach fullness than those which had not. Predation on Pacific Herring was strongly related to juvenile salmon length, suggesting that age-0 Pacific Herring may have been too large to be consumed by smaller Chinook Salmon. Our results reinforce the importance of the transition to piscivory in the trophic ecology of juvenile Chinook Salmon. Further research is necessary to determine if fine-scale distribution of larger, piscivorous juvenile salmon is linked to the distribution of their forage fish prey and to understand the role of prey to predator size ratios in limiting the ability of juvenile salmon to transition to piscivory.

1. Introduction

Historical research efforts and conservation strategies for anadromous salmonids focused primarily on freshwater life history stages (Hayes and Kocik, 2014; Flitcroft et al., 2019), likely due to ease of observation and the existence of evident anthropogenic impacts on rivers and streams (e.g., Hartman et al., 1996; Williams et al., 2005). This focus has shifted as evidence grows that ocean conditions play a key role in controlling recruitment (Beamish and Bouillon, 1993; Welch et al., 2021) and as we learn more about the potential of anthropogenic climate change to alter the capacity of marine ecosystems to support salmonids (Abdul-Aziz et al., 2011). Recent research focused on the marine ecology of juvenile Pacific Salmon (genus *Oncorhynchus*) has been driven by a growing body of evidence that growth and size during the first summer after ocean entry may play a key role in regulating survival. Support for this hypothesis includes greater reconstructed first

ocean-summer sizes of adult survivors (based on scales and otoliths) compared to juveniles sampled in their first summer at sea (Moss et al., 2005; Zavolokin and Strezhneva, 2013; Howard et al., 2016; but see Beacham et al., 2018 for a critique of this approach); and evidence that cohorts which exhibit elevated early marine growth (or achieve greater size) experience relatively greater survival (Holtby et al., 1990; Tovey, 1999; Duffy and Beauchamp, 2011; Tomaro et al., 2012; Graham et al., 2019). Beamish and Mahnken (2001) proposed a framework within which size is positively related to survival at two critical periods during the first year at sea. The first period occurs soon after ocean entry, when rates of size selective predation are hypothesized to be high (Parker, 1971; Holtby et al., 1990). The second period occurs during the first marine winter, when fish which have not achieved adequate size (or in later formulations of the hypothesis, adequate lipid reserves, Beamish et al., 2008) experience mortality due to a nutrient deficit. This hypothesized link between growth and survival has led to a proliferation of

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studies focused on diet and growth during the first marine year (e.g. Duffy et al., 2010; Ferriss et al., 2014; Hertz et al., 2015; Journey et al., 2018; Chamberlin et al., 2017; Chittenden et al., 2017; Gamble et al., 2018; Davis et al., 2020).

Despite this focus on early marine growth, knowledge of the spatial and temporal scales at which juvenile salmon trophic ecology is structured in the ocean still lags that for freshwater, where studies of fine-scale processes have a long history (e.g. Lister and Genoe, 1970; Everest and Chapman, 1972; Sagar and Glova, 1988; Nislow et al., 1998; Metcalfe et al., 1997; Gries and Juanes, 1998). Recent work has demonstrated differences in diet and growth of juvenile salmon among estuarine, nearshore and offshore habitats (Duffy et al., 2010; Chittenden et al., 2017; Gamble et al., 2018; Davis et al., 2020). For estuarine and nearshore habitats, fine-scale studies have also attempted to link habitat structure, habitat use, and trophic ecology (e.g. Levy and Northcote, 1982; Munsch et al., 2016; Chalifour et al., 2019; Davis et al., 2019). Marine sampling programs for juvenile salmon which have dispersed from estuaries and littoral habitats generally employ large, expensive vessels capable of deploying seine or trawl nets. The cost and availability of such vessels typically limit investigations to seasonal snapshots, with spatial analyses limited to region, basin, or sub-basin comparisons (e.g. Beamish et al., 2000; Ferriss et al., 2014; Hertz et al., 2015; Journey et al., 2018, 2020). Trawl sampling integrates linear tracks generally measured in kilometers, limiting inference about fine-scale spatial processes (Peterson et al., 2010). While such studies have provided valuable insights, it is also important to understand finer scale processes in these epipelagic habitats.

Most pelagic marine organisms cannot survive on average prey densities and rely on aggregating mechanisms on various scales to generate foraging patches (Steele, 1980). Such patches may occur at convergent fronts, where water masses of different densities meet, concentrating buoyant particles or zooplankton which swim actively against downwelling currents (Wolanski and Hamner, 1988; Genin, 2004). Internal waves (gravity waves occurring at density interfaces within the ocean rather than at the surface) may also concentrate surface-oriented zooplankton by a similar mechanism (Jillett and Zeldis, 1985; Shanks and Wright, 1987). In a stable water column, zooplankton may concentrate at the depth corresponding to a chlorophyll maximum (Harris, 1988) potentially facilitating more efficient predation by planktivores. The interaction of ocean currents with topography may also generate localized foraging opportunities by concentrating and changing the vertical distribution of zooplankton prey and providing an increased flux of prey past waiting predators (Dower and Mackas, 1996; Zamon, 2002; Genin, 2004). Where physical mechanisms concentrate zooplankton prey, zooplanktivorous fish and their predators may also become aggregated, leading to trophic energy transfer becoming focused in space (Zamon, 2000, 2003; Genin, 2004).

While limited, previous attempts to link fine-scale oceanography to juvenile salmon trophic ecology have provided intriguing results. Sampling inside, outside and at the interface between river plumes and oceanic water has suggested that both prey and juvenile salmon densities may be elevated within or at the edge of plumes (St. John et al., 1992; de Robertis et al., 2005). However, the latter authors did not detect fuller stomachs or different prey in juvenile salmon sampled in frontal regions and suggested that the transient nature of plume fronts might prevent their exploitation by salmon. Off California, stomach fullness of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) was positively related both to recent upwelling and proximity to thermal fronts detected by remote sensing (Sabal et al., 2020). Moulton (1997) also encountered larger and more diverse catches of juvenile salmon within tidal rip lines in Cook Inlet, Alaska. More work is needed to elucidate linkages between fine-scale physical oceanography and juvenile salmon trophic ecology.

Chinook Salmon, a species of particularly high cultural, economic and ecological value, have exhibited declines in marine survival throughout their North American range (Welch et al., 2021). Juvenile Chinook Salmon may migrate to sea in the year that they emerge from the gravel (ocean-type) or spend one or more years rearing in freshwater (stream-type). They generally then spend 2–4 years in the ocean before returning to their river of origin to spawn (Quinn, 2018). Marine survival of Chinook Salmon is calculated by marking smolts with coded wire tags and measuring the subsequent catch and return to the river of surviving adults; the smolt to adult survival. Within the Salish Sea (Strait of Georgia, Strait of Juan de Fuca, and Puget Sound; Fig. 1), perception of synchronous declines in smolt to adult survival of Chinook Salmon (Riddell et al., 2009), along with those of Coho Salmon (*O. kisutch*, Beamish et al., 2010; Zimmerman et al., 2015) and Steelhead Trout (*O. mykiss*), led to the inception of the Salish Sea Marine Survival Project (SSMSP), a binational, five year initiative to understand factors influencing marine survival of these species. While detailed analysis of survival time series suggests that Chinook Salmon survival trends are quite variable within the Salish Sea (Ruff et al., 2017), low abundance of many stocks relative to historical levels led to unprecedented restrictions on Canadian recreational, commercial and First Nations fisheries beginning in 2019.

A considerable body of research has investigated factors influencing diet and growth of juvenile Chinook Salmon during their first summer in the Salish Sea. Much of this work has occurred in Puget Sound, where the average size achieved by July is positively related to survival to adulthood of Chinook Salmon cohorts (Duffy and Beauchamp, 2011). Individuals in offshore habitats (defined as generally greater than 30 m bottom depth) consume more decapod larvae and fish (Duffy et al., 2010) and grow more rapidly (Gamble et al., 2018) than those in estuarine or nearshore habitats. For fish in offshore habitats, diet and growth also vary by sub-basin, with greater growth associated with greater consumption of fish prey (Davis et al., 2020). Chamberlin et al. (2017) found that larger juvenile Chinook Salmon grew faster than smaller individuals in regions of Puget Sound where small Pacific Herring (*Clupea pallasii)* were abundant, suggesting that larger size may facilitate a transition to piscivory. To date, no research has investigated the potential role of fine-scale (kilometers to tens of kilometers) variation in physical and biological oceanography in structuring the diet, distribution and growth of juvenile Chinook Salmon during the first summer at sea.

We employed hook and line sampling (microtrolling; Duguid and Juanes, 2017) to conduct a fine-scale investigation of size, diet, and growth of juvenile ocean-type Chinook Salmon through summer and early fall in an oceanographically heterogeneous region (the Southern Gulf Islands in the Strait of Georgia; Fig. 1). Concurrent with fish sampling we used small vessel-based oceanography to characterize spatio-temporal variation in physical (temperature) and biological (zooplankton composition and abundance) oceanography. Within a framework of three specific hypotheses, we sought to determine whether variability in Chinook Salmon diet and growth was present at finer spatial scales than typically considered in studies of juvenile salmon at sea. We hypothesized that locations with a more stratified water column would be selected by juvenile salmon and support faster growth due to generation of prey patches through mechanisms such as internal waves (Jillett and Zeldis, 1985; Shanks and Wright, 1987) and for the potential ability of salmon to select optimum temperatures for growth (Burke et al., 2013). Our study region in the Southern Gulf Islands included a narrows (Sansum Narrows; Fig. 1) and we hypothesized that the tidal jet generated at this location on the flood tide might also represent a 'hot spot' of juvenile abundance and growth if upwelling and/or flux of zooplankton concentrated forage fish (primarily Pacific Herring) and their predators (Dower and Mackas, 1996; Zamon, 2002; Genin, 2004). We also hypothesized that juvenile Chinook Salmon foraging could be influenced at fine temporal scales by tidal shifts in water column properties and zooplankton availability. Our results will facilitate an improved understanding of how juvenile Chinook Salmon use the topographically complex coastal waters during the latter part of their critical first summer at sea.
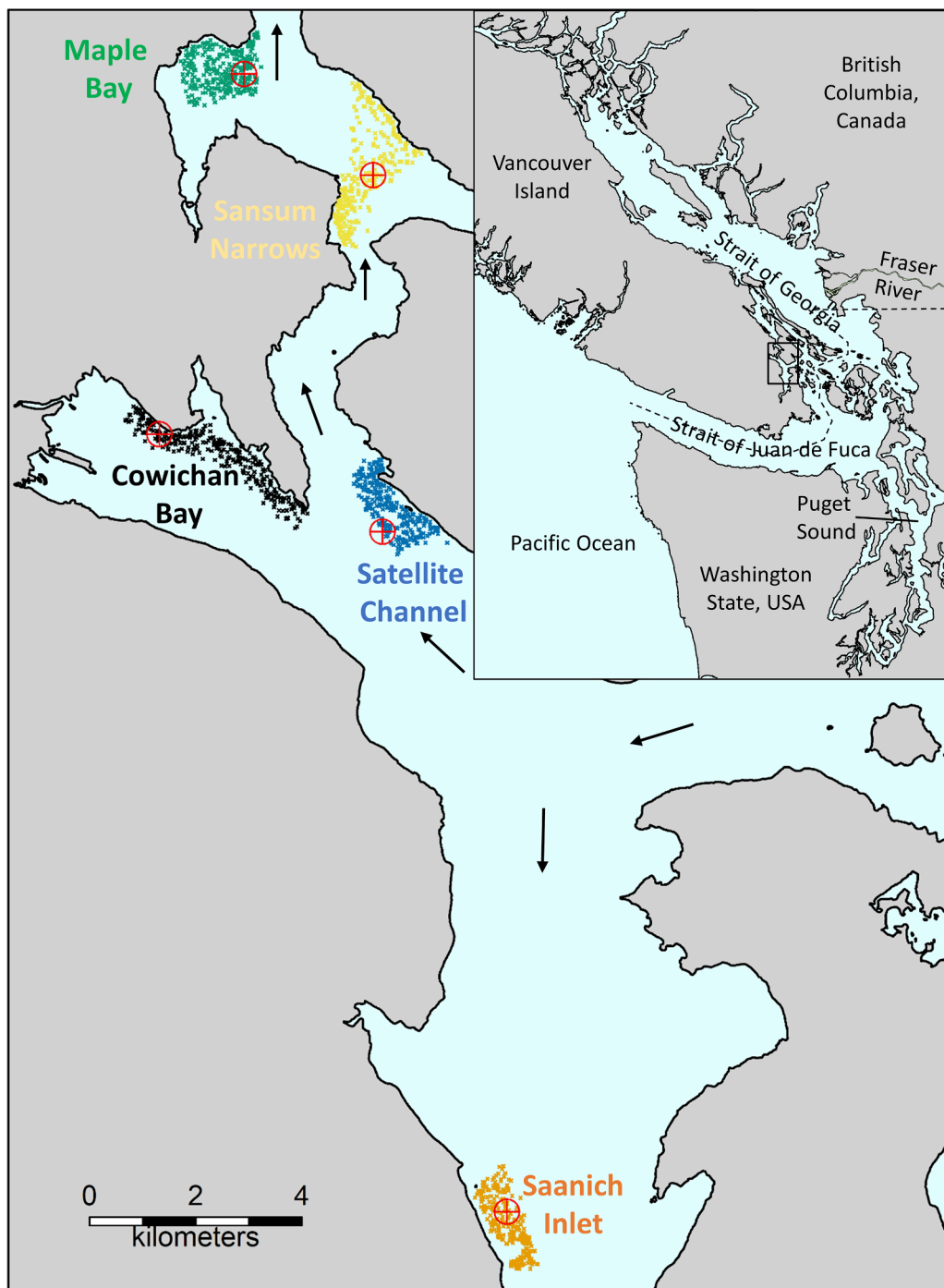
Fig. 1. Five sites in the Southern Gulf Islands of the Salish Sea (combined waters of the Strait of Georgia, Strait of Juan de Fuca, and Puget Sound) where oceanographic and fish sampling were conducted from 6 July to 23 October 2015; focal region is indicated by the rectangle in the larger scale inset. Coloured crosses indicate the locations of individual fishing events (colours used to represent sites are consistent with subsequent figures) while red quartered-circle symbols indicate the location of the oceanographic station at each site. Arrows indicate the approximate direction of the flood tide current with the ebb tide flowing in the opposite direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Study area

The Southern Gulf Islands region (Fig. 1) is oceanographically diverse. It adjoins the strongly tidally mixed waters of Haro Strait and the seasonally stratified waters of the Southern Strait of Georgia and Saanich Inlet (Harrison et al., 1983). This region contains Stuart Channel, a well stratified basin (Waldichuk et al., 1968), and a number of passages with strong tidal currents. Sansum Narrows, within our study area, is a narrow (500 m) passage with tidal currents reaching >4 knots. Interpretations of the quality of the Southern Gulf Islands as juvenile salmon habitat are inconsistent. Healey (1978), using seine surveys to

collect juvenile salmon throughout the Strait of Georgia, concluded that this region was an important nursery area. Journey et al. (2020) found poor recent growth (as indexed by low IGF-1 concentrations and negative residuals of an IGF-1 to fork length relationship) of Coho Salmon in the Southern Gulf Islands and suggested that this could be due to a lack of stratification resulting in low primary, and hence secondary, productivity. The Southern Gulf Islands has also been identified as a potential model system to study early marine survival of juvenile Chinook Salmon, as smolts from the Cowichan River, a Pacific Salmon Commission indicator stock, apparently rear almost exclusively in this region during their first summer at sea (Beamish et al., 2012).

Table 1

Oceanographic and fish sampling effort at five sites (Cow = Cowichan Bay, Map = Maple Bay, Saan = Saanich Inlet, Sans = Sansum Narrows, Sat = Satellite Channel) in the Southern Gulf Islands of the Salish Sea (see Fig. 1). Oceanographic sampling was conducted twice daily with CTD casts immediately before or after zooplankton tows.

Site	Sampling Days	First Day	Last Day	Fishing Events	Oceanographic Samples
Cow	12	2015–07-09	2015–10-23	306	24
Map	12	2015–07-17	2015–10-13	293	24
Saan	11	2015–07-22	2015–10-16	260	22
Sans	11	2015–07-12	2015–10-20	297	22
Sat	12	2015–07-11	2015–10-15	301	24
Total	58	2015–07-09	2015–10-23	1457	116

See Table S1 for details.

2.2. Oceanographic sampling

Each sampling day spanned two tidal phases at one of five sites in the Southern Gulf Islands of the Strait of Georgia (Fig. 1). Sampling occurred between 9 July and 23 October 2015 with 11 to 12 days at each site (Table 1). Where possible, successive days at the same site alternated between ebb to flood and flood to ebb transitions (Table S1). A single station within each site (Fig. 1) was occupied twice on each sampling day, once on the ebb and once on the flood. Oceanographic sampling generally occurred between the middle and the end of each tidal phase. A CastAway CTD was deployed from the surface to within 10 m of bottom (up to a maximum depth of 90 m) to record temperature and salinity. A 50 cm diameter, 2 m long, 350 μm mesh zooplankton net weighted with a 4.5 kg lead ball and equipped with a TSK flowmeter was towed vertically from 30 m to the surface using an Ace Brutus electric line hauler capable of retrieving at ~0.5 m/s. The weight was suspended from the tow line to prevent damage to the net and the cod end was clipped to the weight to ensure the net would sink vertically and not capture zooplankton on the downcast. While deploying and hauling the net, the vessel maneuvered to maintain as close to a vertical cable angle as possible. On the initial five sampling days (10 tows) the CastAway CTD was deployed below the weight (2.5 m below the net rim), to confirm that the target depth was reached. Zooplankton were washed down to the cod end of the net from the outside using pumped surface water and preserved in 10% formalin in seawater.

2.2.1. Zooplankton processing

In the laboratory, zooplankton retained on a 1 mm Nitex sieve were examined in a Bogorov Chamber using a stereomicroscope. Organisms were identified to taxonomic and life-stage groups (see Table 2) with taxonomic resolution varying by group based on a combination of ease of identification and frequency of occurrence. For example, hyperiid amphipods were identified to species, brachyuran megalopae were identified to family, and brachyuran zoeae were treated as a single group. Prey items were separated into groups, blotted on Kimwipes, and weighed to the nearest 0.00001 g. Where very high numbers of a given taxon were observed (11/116 samples) the sample was split using a Folsom plankton splitter and the total number and weight of that taxon in the sample was extrapolated from the subsample.

2.3. Fish sampling

2.3.1. Salmon capture

Fish sampling occurred over two tidal phases on all sampling days in the interval between occupation of oceanographic stations. Two Chinook Salmon captured on a reconnaissance day in Cowichan Bay on 6 July were also included in the analyses. Juvenile salmon were captured by 'microtrolling' (Duguid and Juanes, 2017) using a 6.7 m vessel and modified recreational fishing gear. Up to six lines per side (12 lines total) were deployed at 5 m intervals from 5 m to up to 30 m (depending on

water depth) using Scotty electric downriggers weighted with 6.8 kg lead balls. For the majority of sampling, terminal gear consisted of 2.5 cm "Trout Killer" Apex plastic lures (Hot Spot Fishing & Lures Ltd.) modified to accept small #12 barbed fly-tying hooks with a 5 mm point-shank gap. In general, a translucent pink Apex (finish #138: pink haze/UV) was fished on one side of the boat while an opaque white, black, white and silver (finish # 304: black n' white) Apex was fished on the other.

Fishing activity occurred haphazardly within predefined sites (Fig. 1). On each day, as much of the sampling site was covered as possible on both tidal phases. Microtrolling occurred in standardized gear deployments (Duguid and Juanes, 2017). Start time was logged at the beginning of each gear deployment. Once all lines were at the intended depth, a five-minute period was timed on a stopwatch. At the end of five minutes, gear was retrieved, and the end time was recorded when all lines were out of the water. To record actual speed through water a General Oceanics Flowmeter weighted with a 0.5 kg weight was suspended 1 m below the surface at the start and retrieved at the end of each fishing event. The vessel track during the fishing event was logged with GPS and the event location was assigned as the location at the mid-point between the start and end time. Hobo Tidbit thermistors were deployed at each depth on the clip connecting the leader to the down-rigger cable to provide *in situ* temperature data. As temperature was inversely related to depth over the study period, the minimum temperature recorded between the start and end time of the gear deployment was taken to be the temperature-at-depth. Data were manually screened to exclude the limited periods where air temperature was colder than water temperature at the end of the season. Salmon catch was logged at the level of the individual hook (Duguid and Juanes, 2017).

2.3.2. Catch processing

All salmon were landed directly into a 150 L insulated live well partially filled with seawater aerated and maintained at ≤17 °C using ice blocks. Fish were individually transferred into an anaesthetic bath (5 L of 80 mg/L Tricaine methanesulfonate) for sampling. All salmon were assessed for an adipose fin clip and checked for coded wire tag and passive integrated transponder (PIT) tag presence. Nose to fork length was measured to the nearest millimeter. Scale sampling (for genetic stock ID and growth analysis) and PIT tagging (Chinook Salmon which did not exhibit obvious hooking damage) followed Duguid et al. (2018). Chinook Salmon stomach contents were sampled non-lethally by gastric lavage (Duguid and Juanes, 2017) and then preserved in ≥5% formalin in 50 mL tubes for quantitative laboratory analysis (see below). Total time under anesthesia was approximately 3 min. Fish were returned to the live well and allowed to regain equilibrium before being released near the site of capture.

2.3.3. Chinook Salmon genetic stock identification

As we PIT tagged all uninjured Chinook Salmon as part of a separate study of Cowichan River Chinook Salmon survival (Pacific Salmon Foundation, 2017), genetic stock identification was required to determine which fish originated from the Cowichan River. After pressing (see Section 2.3.5), scale books were transferred to the Molecular Genetics Laboratory at the DFO (Fisheries and Oceans Canada) Pacific Biological Station where DNA was extracted using Qiagen DNeasy kits. Fish were assigned probabilities of belonging to each of 296 stocks of North American Chinook Salmon following methods similar to those of Beacham et al. (2012). All Chinook Salmon samples were analyzed as a single mixture using the program cBayes (Neaves et al., 2005), which estimates the stock composition following Pella and Masuda (2001). Highest probability stock assignments for each fish were grouped by region and primary life history type (supporting Table S2). To avoid confounding effects of life history type and the tendency of larger fish within a stock to disperse more quickly from natal areas (Freshwater et al., 2016), analyses of size, diet, growth, and patterns of catch per unit

Table 2

Overall absolute and proportional mass, counts, and frequency of occurrence of zooplankton groupings identified in 116 vertical 30 m zooplankton tows with a 0.5 m diameter 350 µm ring net over 58 sampling day between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea. Zooplankton groups were aggregated into analysis categories for spatiotemporal patterns in composition and biomass of important juvenile Chinook Salmon prey.

Zooplankton Group	Analysis Category	Composition Analysis	Prey Biomass Analysis	Total Mass (g)	Mass Proportion	Total Count	Frequency of Occurrence
Brachyuran Zoea	Decapod Zoea	Yes	Yes	4.1360	29.48%	7743	97.41%
Calanoid Copepod	Copepod	Yes	No	2.8177	20.08%	8597	97.41%
Caridean Zoea	Decapod Zoea	Yes	Yes	2.7208	19.39%	6710	96.55%
Cyphocaris challengeri	Gammarid	Yes	No	1.0573	7.54%	358	36.21%
Lophopanopeus bellus Megalopa	Decapod Megalopa	Yes	Yes	0.6120	4.36%	479	75.00%
Hyperoche sp.	*Hyperoche* sp.	Yes	Yes	0.6053	4.31%	804	93.10%
Porcellanid Zoea	Decapod Zoea	Yes	Yes	0.5309	3.78%	313	51.72%
Cancrid Megalopa	Decapod Megalopa	Yes	Yes	0.4484	3.20%	121	50.00%
Themisto pacifica	*Themisto* sp.	Yes	No	0.2821	2.01%	555	90.52%
Grapsid Megalopa	Decapod Megalopa	Yes	Yes	0.1510	1.08%	115	35.34%
Polychaete	Polychaete	Yes	No	0.1408	1.00%	438	63.79%
Unidentified Anomuran Zoea	Decapod Zoea	Yes	Yes	0.1072	0.76%	127	44.83%
Euphausiid Larva	Euphausiid	Yes	Yes	0.0865	0.62%	329	64.66%
Unidentified Decapod Zoea	Decapod Zoea	Yes	Yes	0.0852	0.61%	227	3.45%
Pteropod	Pteropod	No	No	0.0697	0.50%	1	0.86%
Insect	Insect	No	No	0.0567	0.40%	38	8.62%
Larval Fish	Larval Fish	Yes	Yes	0.0282	0.20%	45	25.86%
Pagurid Megalopa	Decapod Megalopa	Yes	Yes	0.0211	0.15%	17	11.21%
Majid Megalopa	Decapod Megalopa	Yes	Yes	0.0163	0.12%	17	13.79%
Other	Other	No	No	0.0154	0.11%	9	5.17%
Unidentified Gammarid	Gammarid	No	No	0.0121	0.09%	1	0.86%
Caridean Post Larva	Decapod Post Larvae	No	No	0.0120	0.09%	8	5.17%
Pinnotherid Megalopa	Decapod Megalopa	Yes	Yes	0.0116	0.08%	13	8.62%
Mysid	Other	No	No	0.0014	0.01%	6	4.31%
Hyperia medusarum	*Hyperia medusarum*	No	Yes	0.0013	0.01%	2	1.72%
Caligid Copepod	Copepod	Yes	No	0.0010	0.01%	1	0.86%
Pinnotherid Post Larva	Decapod Post Larvae	No	No	0.0008	0.01%	1	0.86%
Unidentified Amphipod	Unid. or Other Amphipod	No	No	0.0006	0.00%	1	0.86%
Primno sp.	Unid. or Other Amphipod	No	No	0.0004	0.00%	1	0.86%
Gelatinous Zooplankton	Gelatinous Zooplankton	No	No	0.0000	0.00%	39,507	100.00%

effort were limited to ocean-type stocks from river systems draining into the Strait of Georgia. Ocean-type Chinook Salmon from the South Thompson stock aggregate were also excluded as these fish have an unusual late ocean entry timing (Beamish et al., 2010).

2.3.4. Chinook Salmon diet

Laboratory analysis of samples followed methods described for Zooplankton under Section 2.2.1. For samples with very numerous, small prey (8/325 samples), only a subsample was examined. The remainder of these samples was blotted and weighed in bulk, and weight proportions and counts were assigned in proportion to results for the subsample. Given the importance of cancrid megalopae in Chinook Salmon diets that became evident over the course of processing samples, up to 10 cancrid megalopae per stomach were re-examined from a subsample of stomachs (N = 44) *post hoc* to determine species composition (312 individual megalopae). Where possible, heavily digested fish were identified on the basis of bone morphology using index collections maintained in the Anthropology Bone Lab at the University of Victoria.

2.3.5. Chinook Salmon growth indices

Determination of Chinook Salmon circulus spacing followed Duguid et al. (2018). Impressions were produced at the DFO Pacific Biological Station by pressing scale cards onto acetate sheets using a heat-transfer press following Hudson and Crosby (2010). Acetate impressions of up to three scales per fish were photographed under brightfield illumination with a stereomicroscope-mounted camera. Only scales with a clearly defined origin (non-regenerated) were photographed. The anterior scale radius and width of all circuli along the long axis of the scale were measured using a combination of CellSens software and custom code in the R language. Where the independently measured scale radius differed by more than 1% from the sum of the radius of the origin and all circuli, the scale was remeasured. Where residuals from linear regressions of scale diameter on fork length and circulus count exceeded 200 μm, scales were excluded from analysis. Scales with a measured radius of the origin of <40 μm or >110 μm were also excluded. As it was not always possible to tell if the outermost measured circulus was partially or completely formed, the average of the second and third to last circuli were used as an index of growth rate over the preceding 12–27 days (assuming outermost circuli ranging from negligible to fully formed and a circulus formation duration of 6–9 days as discussed in Duguid et al., 2018). Where more than one good scale was measured for the same fish this circulus spacing based growth index (henceforward "circulus spacing") was averaged across scales.

2.4. Data visualization and statistical analyses

2.4.1. Oceanographic sampling

2.4.1.1. Physical. Temperature, salinity, and density data for both the downcast and upcast of the CTD were integrated using CastAway software. For plotting and analysis, data were averaged for each meter of depth (1 m therefore represents the average of data from 0 to 1 m). To visualize spatiotemporal variation in thermal stratification we averaged temperature profiles across the two daily tows and employed linear interpolation of temperature across dates using the 'interp' function in the package 'akima' in R. We plotted heatmaps of temperature by depth and date for all five sites. To visualize flood vs. ebb shifts in water column properties at each site we calculated the within-day difference of flood tide vs. ebb tide values of temperature, salinity, and density within each meter of depth and plotted the mean and standard deviation of these values over the study period for each site. We also employed generalized additive modelling (GAM) to examine the relationships between stratification and date, site, and tidal phase. The response variable for this analysis was an index of stratification calculated as the density difference between the second and fiftieth meter of the water column. Models were fit in the package 'mgcv' in R with the identity link and using maximum likelihood (ML) to estimate smoothing parameters (Wood, 2011). We specified our model based on the *a priori* hypotheses that stratification would differ among sites, would change non-linearly through time, would change differently among sites, and would exhibit site-specific differences between tidal phases (ebb vs. flood). Our model therefore included a global smooth term for day of the year (DOY), separate smooth terms for DOY by site, and parametric terms for site, phase of the tide (flood vs. ebb), and the interaction of site and phase of the tide. To allow non-linear, site-specific changes in stratification with date to be compared to global changes in stratification with date, we applied a first derivative penalty to the site-specific smoothers rather than the default second derivative penalty (coded as m = 1 in the 'gam' function in the package 'mgcv'). Rather than penalizing the degree of curvature of the smoother, this approach penalizes deviance from a flat function. In the presence of a global smoother for the same variable, this is effectively penalizing deviance from this global smoother (Pedersen et al., 2019). Deviation coding of the categorical variable 'site' facilitated comparison of stratification at each site to the average across sites. Model fit was validated using function 'gam.check' which indicated that the model was under-smoothed using the default (10) maximum degrees of freedom (k) in 'mgcv'. We therefore increased the maximum degrees of freedom until the p-values of the k-index of all smoothers (an indication of patterns in the residuals of that smoother) was > 0.05. The final maximum degrees of freedom selected by this process for smooth functions of day of the year was 13. To visualize the fit of our model we used the function 'gam.predict' to generate predicted stratification indices and associated standard errors at the five sites over the study period and plotted these predictions together with observed values. Residual diagnostics for all gams implemented in this study employed a residual simulation approach using the 'DHARMa' package (Hartig, 2020).

2.4.1.2. Biological. Prior to analysis of spatiotemporal variation in composition, zooplankton groups were aggregated into categories (Table 2). To reduce the influence of rarely encountered taxa, zooplankton categories were only included in analyses of spatiotemporal patterns in community composition if they occurred in more than 10% of tows. All analyses used an index of biomass density calculated as the mass of each category in each tow divided by the average volume sampled per tow, yielding an approximate biomass/m^3 (but see Section 3.1.2 for issues with quantitative zooplankton sampling). To investigate how zooplankton composition varied by site, date and water column stratification we employed canonical correspondence analysis (CCA; Ter Braak, 1986) of daily averaged of biomass indices. An initial full model was fit with day of the year and stratification (see Section 2.4.1.1) as continuous constraints and site as a categorical constraint. Significant constraints were selected using the 'ordistep' function in the package 'vegan' (Oksanen et al., 2019) with terms alternately added to and dropped from the model and significance determined using permutation (significance levels for adding and dropping terms were defined as 0.05 and 0.10 respectively). Significance levels of the final model and retained constraints were assessed using the 'anova.cca' function in vegan with 999 permutations. Constraints were assessed for multicollinearity using the function 'vif.cca.'

To examine the relationships between date, site, and tidal phase and the aggregate biomass concentration of important zooplankton prey of juvenile Chinook Salmon we employed a generalized additive modeling approach corresponding to that used for stratification (Section 2.4.1.1). The response variable for this analysis was an overall index of zooplankton biomass concentration derived by summing the category-specific indices in each tow (see previous paragraph). Prey categories included in this analysis were those which represented >2% of Chinook Salmon diets by weight (see prey biomass analysis column in Table 2). To account for the positively skewed nature of the response, the GAM

Table 3

Overall absolute and proportional mass, counts, and frequency of occurrence of prey groups in juvenile Strait of Georgia ocean-type Chinook Salmon with non-empty stomachs (N = 262) between 6 July 2015 and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea. Prey groups were aggregated into analysis categories to investigate spatiotemporal patterns in diet.

Prey Group	Analysis Category	Composition Analysis	Total Mass (g)	Mass Proportion	Total Count	Frequency of Occurrence
Clupea pallasi	Herring	Yes	25.7828	25.60%	25	8.40%
Cancridae - Megalopa	Decapod Megalopa	Yes	15.3313	15.22%	5005	69.47%
Teuthida	Cephalopod	Yes	7.1111	7.06%	12	3.82%
Hyperoche medusarum	*Hyperoche* sp.	Yes	6.5841	6.54%	6602	71.76%
Lophopanopeus bellus - Megalopa	Decapod Megalopa	Yes	5.2519	5.21%	5116	52.29%
Brachyura - Zoea	Decapod Zoea	Yes	3.8527	3.82%	2788	55.34%
Embiotocidae	Fish	Yes	3.8287	3.80%	2	0.38%
Osteichthyes - Post Larval	Fish	Yes	3.3198	3.30%	4	1.53%
Octopoda	Cephalopod	Yes	3.2242	3.20%	35	5.73%
Hyperia medusarum	*Hyperia medusarum*	Yes	2.9831	2.96%	294	42.75%
Osteichthyes - Fragments	Fish	Yes	2.6751	2.66%	41	14.50%
Osteichthyes - Larval	Fish	Yes	2.5693	2.55%	94	18.70%
Euphausiidae - Post Larval	Euphausiid	Yes	2.4734	2.46%	114	13.36%
Porcellanidae - Zoea	Decapod Zoea	Yes	1.9897	1.98%	1043	28.24%
Brachyura - Megalopa	Decapod Megalopa	Yes	1.7901	1.78%	2388	48.47%
Engaulis mordax	Fish	Yes	1.2567	1.25%	5	1.15%
Themisto pacifica	Themisto pacifica	Yes	1.2565	1.25%	711	25.57%
Amphipoda	*Unidentified or Other Amphipod*	Yes	1.1205	1.11%	97	27.10%
Myctophidae	Fish	Yes	1.1017	1.09%	1	0.38%
Cephalopoda	Cephalopod	Yes	1.0590	1.05%	5	1.91%
Gammaridae	Gammarid	Yes	0.9125	0.91%	73	13.36%
Syngnathus leptorhynchus	Fish	Yes	0.7952	0.79%	114	7.63%
Insecta	Insect	No	0.6962	0.69%	203	4.96%
Porcellanidae - Megalopa	Decapod Megalopa	Yes	0.6895	0.68%	411	27.86%
Other	Other	No	0.4847	0.48%	53	18.70%
Grapsidae - Megalopa	Decapod Megalopa	Yes	0.3231	0.32%	298	31.30%
Pinnotheridae - Megalopa	Decapod Megalopa	Yes	0.2723	0.27%	260	32.06%
Pinnotheridae - Post Larval	Decapod Post Larvae	No	0.2452	0.24%	14	3.82%
Pleuronectidae - Larval	Fish	Yes	0.2422	0.24%	8	3.05%
Hymenoptera	Insect	No	0.2068	0.21%	22	1.53%
Copepoda	Copepod	Yes	0.2010	0.20%	377	11.45%
Polychaeta	Polychaete	No	0.1520	0.15%	27	6.87%
Calanoidea	Copepod	Yes	0.1373	0.14%	388	20.61%
Cirripedia - Adult Exuviae	Other	No	0.1325	0.13%	102	5.73%
Mysidae	Other	No	0.1105	0.11%	7	1.15%
Cyphocaris challengeri	Gammarid	Yes	0.1052	0.10%	8	0.76%
Majidae - Megalopa	Decapod Megalopa	Yes	0.1012	0.10%	95	16.79%
Digested Material	Other	No	0.0743	0.07%	8	3.05%
Caridea - Post Larval	Decapod Post Larvae	No	0.0673	0.07%	14	4.58%
Decapoda - Megalopa	Decapod Megalopa	Yes	0.0601	0.06%	34	4.20%
Pteropoda	Pteropod	No	0.0414	0.04%	18	4.20%
Decapoda	Other	No	0.0405	0.04%	2	0.76%
Caridea - Zoea	Decapod Zoea	Yes	0.0170	0.02%	19	4.96%
Sebastes sp.	Fish	Yes	0.0148	0.01%	1	0.38%
Paguridae - Megalopa	Decapod Megalopa	Yes	0.0132	0.01%	13	4.20%
Brachyura - Post Larval	Decapod Post Larvae	No	0.0098	0.01%	1	0.38%
Arachnida	Other	No	0.0051	0.01%	1	0.38%
Gastropoda - Larval	Other	No	0.0042	0.00%	4	1.53%
Diptera	Insect	No	0.0029	0.00%	1	0.38%
Caprellidae	Unidentified or Other Amphipod	Yes	0.0023	0.00%	1	0.38%
Caligidae	Copepod	Yes	0.0014	0.00%	1	0.38%
Isopoda	Other	No	0.0010	0.00%	1	0.38%
Monstrilloidea	Copepod	Yes	0.0009	0.00%	2	0.76%
Pycnogonidae	Other	No	0.0008	0.00%	1	0.38%
Euphausiidae - Zoeae	Euphausiid	Yes	0.0004	0.00%	1	0.38%
Cumacea	Other	No	0.0003	0.00%	1	0.38%
Paguridae - Zoea	Decapod Zoea	Yes	0.0002	0.00%	1	0.38%
Euphausiidae - Furcilia	Euphausiid	Yes	0.0002	0.00%	1	0.38%
Cnidaria - Medusae	Gelatinous Zooplankton	No	NA	NA	2	0.38%
Pleurobrachia	Gelatinous Zooplankton	No	NA	NA	1	0.38%
Siphonophora	Gelatinous Zooplankton	No	NA	NA	3	1.15%

was fit with a gamma distribution and log link. As k-index p-values did not suggest undersmoothing, default (k = 10) maximum degrees of freedom were used.

2.4.2. Chinook Salmon diet, size and growth

Analysis of spatial and temporal variation in Chinook Salmon diet followed the same framework as described for zooplankton composition. Aggregation of prey groups into categories for analysis is outlined in Table 3. Only prey groups which occurred in at least 10% of non-empty stomachs were included in analyses of diet composition. As we did not weigh live fish we were not able to convert the weight of diet components into fullness values (i.e. prey weight/predator weight). In order to prevent stomach contents of large fish disproportionately influencing analyses we converted the mass of each diet category in each fish into an index of partial stomach fullness (PF) following Magnussen (2011). The PF index for a given prey category in an individual juvenile Chinook Salmon was calculated as $PF = 1000(w)/L^3$ where w is the weight of that prey category in grams and L is the length of the juvenile Chinook Salmon in centimeters. Canonical correspondence analysis was conducted on individual diets as outlined for zooplankton composition in Section 2.4.1.2 with the addition that fork length was included in the full model as a potential constraint (in addition to day of year, site, and density stratification).

To visualize volumetric contribution of different prey groups we also aggregated prey into coarse categories (herring, other fish, decapod larvae, other crustacean zooplankton, euphausiid, cephalopod and other) and plotted the means of aggregate partial fullness scores for these categories across months and sites. To investigate foraging selectivity of individual fish we employed a distribution-free, probabilistic model that compared the incidence of pairwise co-occurrence of prey categories within individual stomachs to the expected incidence of co-occurrence given that prey categories occurred randomly and independently from each other (Veech, 2013). This analysis was implemented using the package 'cooccur' in R (Griffith et al., 2016). As our goal was to observe patterns of co-occurrence among prey categories, we did not apply a correction for multiple comparisons to the significance level of the co-occurrence analysis (α = 0.05).

To test how juvenile Chinook Salmon length, stomach fullness, occurrence of empty stomachs, capture temperature, and growth varied by site and through the season we employed a GAM approach similar to that applied to stratification and zooplankton biomass. In each case the response variable - nose to fork length in mm, total stomach fullness index (the sum of PF scores for each prey type in each fish), binomial occurrence of empty stomachs, temperature at capture depth in °C, and mean spacing of second and third outermost circuli - was related to a parametric term for site and both global and site-specific smooth terms for day of the year. To test for an effect of stratification, a smooth term for the density stratification between 2 and 50 m was included in each model based on the average of density stratification values derived for the flood and ebb on each sampling day (see Section 2.4.1.1). As stratification data were not available for all sampling days, this term was dropped from the model when non-significant (P > 0.05). To prevent over-fitting where simple non-linear relationships were anticipated, smooth terms were constrained to a maximum of three knots. Where all site-specific smoothers for day of the year were non-significant (P > 0.05), site-specific smoothers were dropped from the model. Given the importance of Pacific Herring in diets which became evident in the course of this work (see results) we also included diet groupings as a parametric term in each model (except the empty stomach model). We grouped juvenile Chinook Salmon as having empty stomachs, having preyed on Pacific Herring, or not having preyed on Pacific Herring. As juvenile Chinook Salmon scale circulus spacing has been demonstrated to be related to fork length independently of growth rate (Duguid et al., 2018), we included a smooth term for fork length as a covariate in the scale circulus spacing (growth rate) model. To accommodate positively skewed distributions, fork length, stomach fullness, and capture

temperature were modelled using the gamma distribution with a log link. Occurrence of empty stomachs was modelled as a binomial response (empty = 1, non-empty = 0) with a logit link and circulus spacing was modelled with a normal distribution and identity link.

2.4.3. Analysis of catch per unit effort

Catch per unit effort (CPUE) of first ocean year Chinook Salmon was analyzed at the level of the individual hook deployment based on a modification of the method of Duguid and Juanes (2017). Each hook where a Chinook Salmon was captured was scored as a 1 while all other hooks were scored as 0 s. To investigate how CPUE varied across sites, depths, time of day, DOY, and stage of the tide we specified a binomial GAM on the basis of *a priori* hypotheses. Specifically, we hypothesized that Chinook Salmon CPUE would differ among sites, and would vary globally and non-linearly by depth, DOY, density stratification, vessel speed through water, and hour of the day. We also hypothesized that site-specific non-linear relationships might exist between CPUE and depth, DOY, and stage of the tide. Our binomial GAM included a parametric term for site; global smooth terms for hour of the day, depth, and DOY; and site-specific smooth terms for DOY, depth, and tide. Speed through water and stratification data were available only for subsets of fishing events. To determine if these variables influenced Chinook Salmon CPUE, we fit separate models including the aforementioned variables and smooth terms for either speed or stratification to the subset of fishing events that included these variables. We calculated a continuous variable for stage of the tide (tide) based on hour relative to predicted low slack at Active Pass, the nearest tidal prediction site of the Canadian Hydrographic Service. This variable was negative during the ebb tide and positive during the flood tide. As minimum values of the variable 'tide' approximated high slack, and were therefore theoretically continuous with maximum values, we modelled the site-specific relationship between CPUE and tide using cyclic cubic splines (bs = "cc" in gam model formula) which have matching end points. Other smoothers employed default thin plate splines. Models were fit using maximum likelihood (ML). As discussed in Section 2.4.1, where both a global smoother and site-specific smoother were included in the model (DOY and depth), a first derivative penalty was applied to the site-specific smoothers. We limited the maximum degrees of freedom (knots) to 5 for smoothers of DOY, tide, and hour of the day, and 3 for depth. The clustering of hooks within an individual gear deployment represented a potential violation of the assumption of independence in our modelling approach. The GAM function in 'mgcv' allows the inclusion of random effects modelled similarly to smoothers as penalized regression terms (bs = "re" in 'gam' model formula; Wood, 2008). We used this approach to include fishing event as a random effect in our model, thereby generating a generalized additive mixed model (GAMM). Due to the relatively large size of the dataset (15,905 individual hooks deployed) this GAMM was fit using the function 'bam' rather than the function 'gam' in the package 'mgcv' in R. The function 'bam' is optimized for more computationally efficient fitting of generalized additive models to large datasets (Wood et al., 2015).

3. Results

3.1. Oceanographic sampling

3.1.1. Physical

Cast depths with the CTD varied by site due to differing bottom depth at the oceanographic sampling station. Plotting and analyses included only data down to the shallowest maximum depth reached by any cast at each site. These depths were Cowichan Bay: 50 m; Maple Bay: 84 m; Saanich Inlet: 89 m; Sansum Narrows: 82 m; and Satellite Channel: 68 m. The conductivity sensor on the CTD failed on a single cast on the flood tide at Satellite Channel on 11 July; this cast was excluded from analyses. A cast in Cowichan Bay on 7 October encountered a shallow (<3 m) layer of low salinity water, likely a consequence of localized input
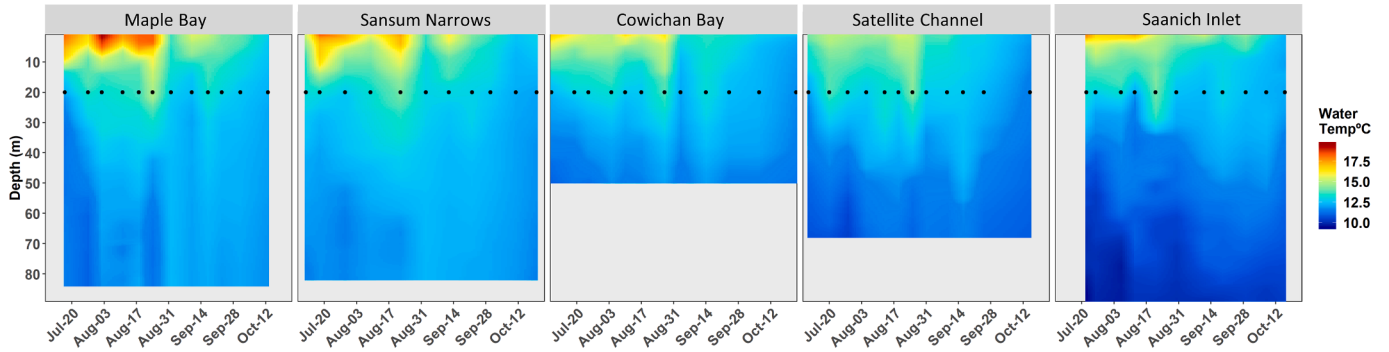
Fig. 2. Vertical and longitudinal interpolation of water temperature profiles averaged from twice daily (ebb and flood) CTD casts between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands (ordered from North to South; see Fig. 1 for site locations) of the Salish Sea. Black points indicate sampling dates, only one site was sampled on each date.
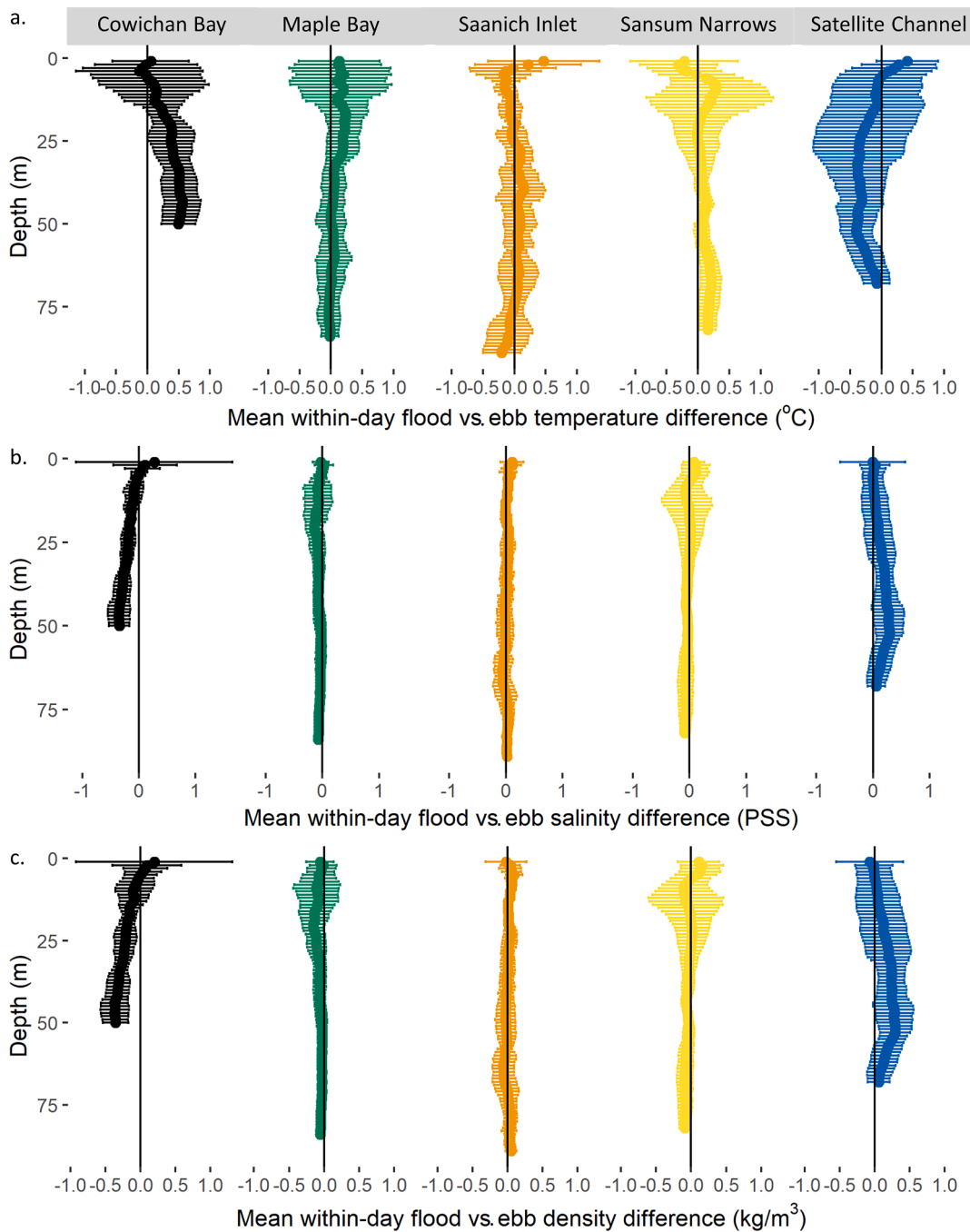

Fig. 3. Mean within-day difference between flood tide and ebb tide temperature (a), salinity (b), and density (c) for each 1 m of depth between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea (see Table S1, Fig. 1 for details). Horizontal error bars indicate standard deviation of the mean.

from the Cowichan River, this date was also excluded from generalized additive modeling of stratification.

The warmest water temperatures were observed in Maple Bay and Sansum Narrows, with maximum temperature in the top 1 m reaching 20.3 °C and 18.9 °C, respectively. Temperatures in the top 1 m also reached 18.6 °C in Saanich Inlet, but the layer of warm water was shallower than at the former two sites and the deep water was cooler (Fig. 2). Maximum temperatures in the top 1 m were lowest at Cowichan Bay (16.9 °C) and Satellite Channel (15.5 °C). Across sites, temperature in the top 1 m declined from 16.3 °C in July (SD = 1.4 °C) to 12.8 °C in October (SD = 0.60 °C). A decrease in surface water temperature and thermal stratification was evident at all sites at the end of August. The most pronounced within-day differences between flood tide and ebb tide water column properties occurred at Cowichan Bay and Satellite Channel. At Cowichan Bay the flood tide was associated with warmer, lower salinity and lower density water below about 5 m, while at Satellite Channel the opposite pattern was observed (Fig. 3). At Maple Bay there was a slight shift towards warmer, lower salinity, lower density water on the flood tide, particularly in the top third of sampled depths.

Sansum Narrows showed a similar pattern, but in the bottom third of sampled depths, and exhibited high variability in flood to ebb differences in water column properties in the top third of sampled depths. Water column properties varied little between flood and ebb in Saanich Inlet (Fig. 3).

A GAM including parametric terms for site, phase of the tide, and their interaction, and global and site-specific smooth terms for day of the year, explained 93.5% of the deviance in density stratification between 2 m and 50 m. Relative to the global mean, density stratification was significantly higher at Maple Bay and Sansum Narrows and significantly lower in Satellite Channel (regression statistics provided in Fig. 4). The global smooth term for day of the year was significant (p = 0.010) but was penalized to a straight line with a negative slope (edf = 1). Site-specific smoothers differed significantly from this global trend for all sites and density stratification exhibited strong cyclic periodicity at all sites except Saanich Inlet. We detected no global effect of phase of the tide, and the interaction of site and phase of the tide was significant only for Cowichan Bay and Satellite Channel, with Satellite Channel more stratified on the flood and Cowichan Bay more stratified on the ebb
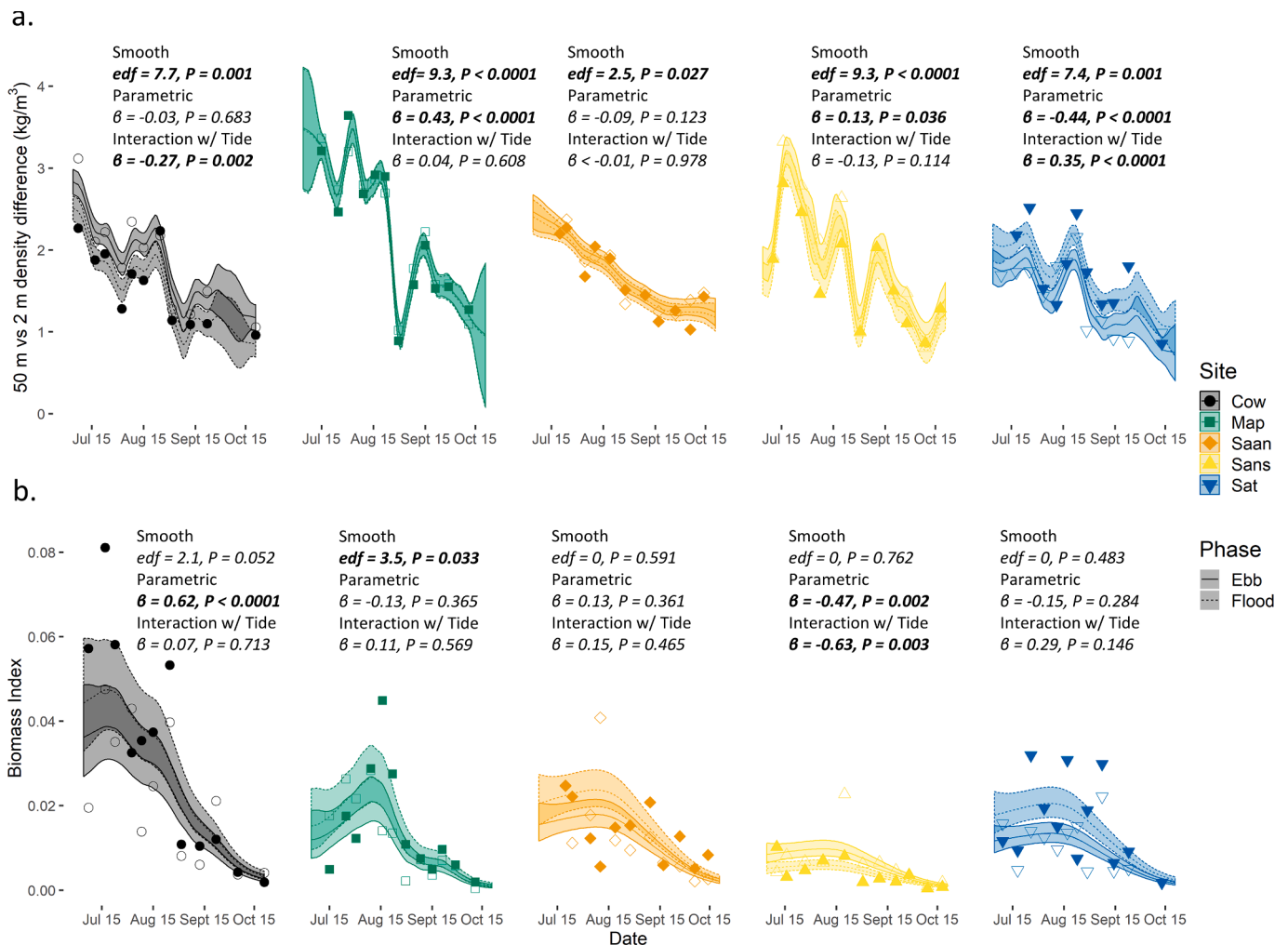

Fig. 4. Observed values (points) and generalized additive model (GAM) fits for a. an index of stratification (density difference between the 50th and 2nd meter of the water column), and b. an index of aggregate biomass concentration (g/m³) for important Chinook Salmon prey groups (contributing to > 2% of total diet by mass) sampled with vertical 30 m tows with a 0.5 m diameter 350 μm ring net between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea. Filled symbols indicate flood tide samples and open symbols indicate ebb tide samples. Lines indicate fitted values from GAMs relating smoothed terms for day of year and day of year by site and parametric terms for site and phase of the tide (and their interaction) to the density stratification (a) and biomass index (b); shaded ribbons indicate standard error of these predictions. For each site regression statistics are the estimated degrees of freedom (edf) of the smooth term and corresponding approximate P-value, the estimated coefficient (β) for the parametric term for site and corresponding P-value, and the coefficient (β) for the interaction of site and tidal phase and corresponding P-value. A significant global effect of tide was not detected in either GAM. Site names are defined in Table 1 and mapped in Fig. 1.
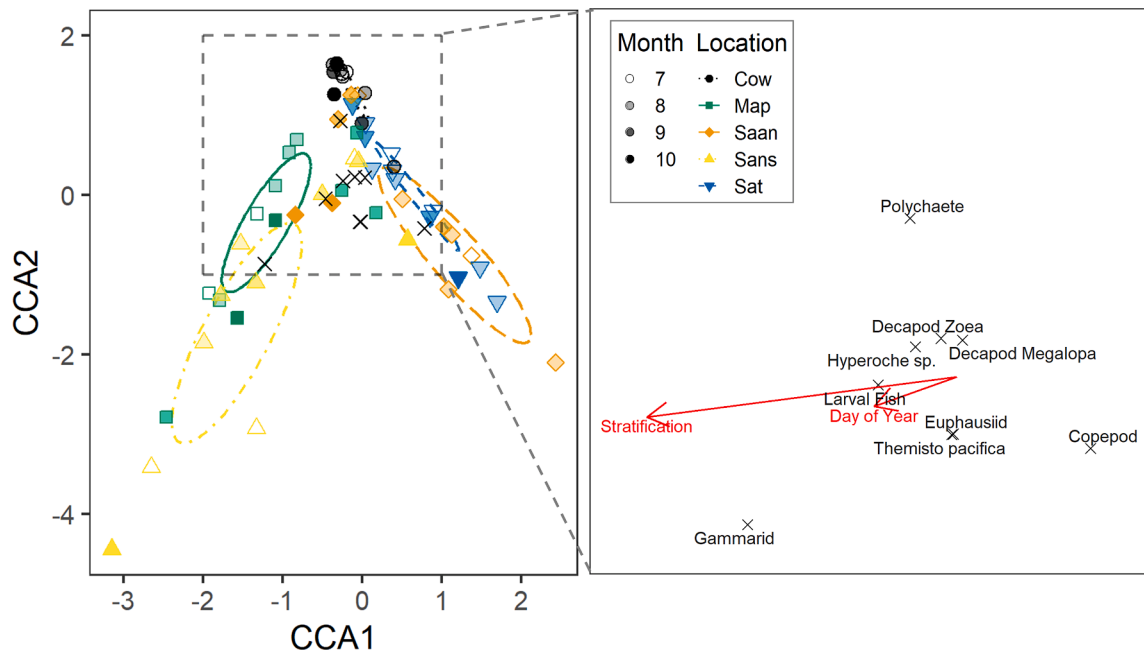
Fig. 5. Canonical correspondence analysis biplot of indices of biomass concentration (g/m^3) for potential zooplankton prey of juvenile Chinook Salmon sampled with vertical 30 m tows with a 0.5 m diameter 350 μm ring net (see methods for details) at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015. Points in the left-hand panel indicate daily averaged samples with ellipses indicating the 95% confidence intervals of site (location) centroids and x indicating zooplankton taxa locations. The right-hand panel is an inset (corresponding to region within the dashed lines) that provides the zooplankton taxa name for each point and arrows indicating direction of continuous constraints (density stratification and day of the year). Site names are defined in Table 1 and mapped in Fig. 1.

(Fig. 4).

3.1.2. Biological

Zooplankton tows were successful in sampling the intended depth (30 m) with trial CTD deployments (N = 10) 2.5 m below the net mouth ranging from 32.1 m to 33.3 m (mean = 32.7 m). Line hauling speed averaged 0.55 m/s (SD = 0.05 m/s; based on 106 timed 30 m tows). The retrieval speed through water was close to the threshold required to initiate recording by the TSK flowmeter, and in 34/116 tows the flow-meter either did not begin to spin or recorded implausibly low values (<50% of the mean value). Due to the very full and tide-dependent daily program of oceanographic sampling and fish capture it was not practical to repeat tows with problematic flowmeter readings. Zooplankton biomass values must therefore be considered relative indices rather than absolute estimates. Where flowmeter readings were plausible (N = 82 tows) the volume sampled averaged 5.6 m^3 (SD = 0.7; range = 3.4 to 10.0 m^3; net mouth area = 0.2 m^2; flowmeter calibrated at 6.57 revolutions/m).

Decapod zoeae, calanoid copepods, decapod megalopae, and gammarid amphipods collectively made up more than 90% by weight of the potential juvenile Chinook Salmon food sampled in our tows (Table 3). Of the decapod megalopae, almost half were of a single species, *Lophopanopeus bellus*, while almost all gammarid amphipods examined were *Cyphocaris challengeri*. Zooplankton categories encountered in a very low number of tows and therefore not included in analyses of species composition included decapod post-larvae (7 tows), *Hyperia medusarum* (2 tows), insects (10 tows), pteropods (1 tow), and unidentified amphipods (2 tows). The category with the minimum numbers of tows that was included in the analysis was larval fish which occurred in 30 tows.

Cumulative densities of zooplankton prey important to juvenile Chinook Salmon declined dramatically over the course of the study period, reaching very low levels in October (Fig. 4). A GAM model containing both global and site-specific smooth terms for day of year and parametric terms for site, phase of the tide, and the interaction of phase of the tide and site explained 77.1% of the variance in zooplankton

density. Relative to the overall average, zooplankton densities were significantly lower at Sansum Narrows, and significantly higher in Cowichan Bay. We did not detect a global effect of phase of the tide on zooplankton density; however, at Sansum Narrows densities were significantly lower on the flood tide (P = 0.003).

All constraints (day of the year, P = 0.001; density stratification, P = 0.010; and site P = 0.001) were significant and retained in a final CCA (P = 0.001) of zooplankton biomass indices averaged across the two daily tows at each site (Fig. 5). Variance inflation factors for these
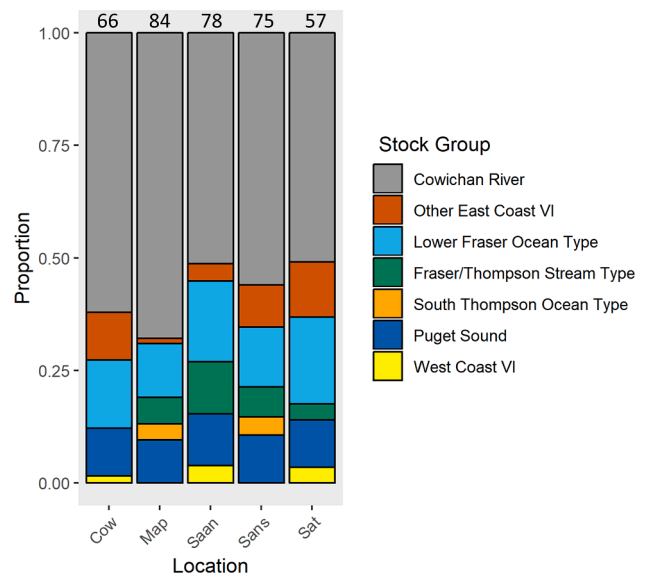

Fig. 6. Stock group proportions for first ocean year (<300 mm FL) Chinook Salmon captured between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea. Sample size is indicated by the numbers above each bar; for individual stocks making up each group see Table S2. VI = Vancouver Island. Site names are defined in Table 1 and mapped in Fig. 1.

variables were all low (<3). Collectively these constraints explained 56% of the inertia in zooplankton composition with the first two canonical axes accounting for 55% and 31% of explained inertia. Maple Bay and Sansum Narrows were negatively associated and Satellite Channel and Saanich Inlet positively associated with the first CCA axis. This likely reflected a greater biomass of gammarids at the former two sites and copepods at the latter two sites (Fig. 5, Supplementary Table S3). Confidence ellipses of site centroids overlapped for these two pairs of sites. Interestingly both day of the year and density stratification were negatively associated with the first CCA axis despite stratification declining with day of the year (Fig. 4). This may have been due to a global decline in decapod larval forms with day of the year and consistently low densities of decapods at Sansum Narrows (a significantly more stratified site; Fig. 4) throughout the study period (Supplementary Table S3). Cowichan Bay was positively associated with the second CCA axis, likely due to a consistently higher biomass density of polychaetes than at all other sites (Fig. 5; Supplementary Table S3).

3.2. Fish sampling

We conducted a total of 1457 fishing events totaling 15,905 hook deployments over 58 sampling days. The number of fishing events per day ranged from 15 to 33 (Table S1). Fishing event duration averaged 8.0 min (SD = 0.7 min), mean speed through water as logged by the

flowmeter averaged 0.55 m/s (SD = 0.02 m/s). In the field we identified our catch as 382 Chinook Salmon, 92 Coho Salmon, 1 Chum Salmon, 3 Copper Rockfish (*Sebastes caurinus*), 5 Spiny Dogfish (*Squalus acanthias*), and 1 Pacific Sandfish (*Trichodon trichodon*).

3.2.1. Chinook Salmon stock, origin, and size

In the course of genetic stock identification (GSI), one fish originally identified as a Chinook Salmon was revealed to be a Coho Salmon and 12 fish identified as Chinook Salmon were revealed to be Chinook Salmon-Coho Salmon hybrids. A manuscript investigating the phenomenon of Chinook-Coho Salmon hybridization in this region and including data for these fish is in preparation (Araujo et al., in prep). Of the 369 confirmed Chinook Salmon, 362 were < 300 mm FL and assumed to be in their first ocean year, and 7 were likely second ocean year fish ranging from 320 to 381 mm FL. Genetic stock identification (GSI) indicated that 58% of first ocean year Chinook Salmon were of Cowichan River origin (See Table S1 for detailed GSI results); the proportion of Cowichan River origin fish ranged from 51% to 68% among sites (Fig. 6). The remainder were primarily from East Coast Vancouver Island, Puget Sound, and the lower Fraser River. Small proportions of the catch were West Coast Vancouver Island ocean-type (2%) and middle and upper Fraser River ocean-type (2%) and stream-type (6%) stocks. All subsequently reported results and analyses refer to the 289 first year ocean-type juveniles originating from Strait of Georgia systems including the Cowichan River
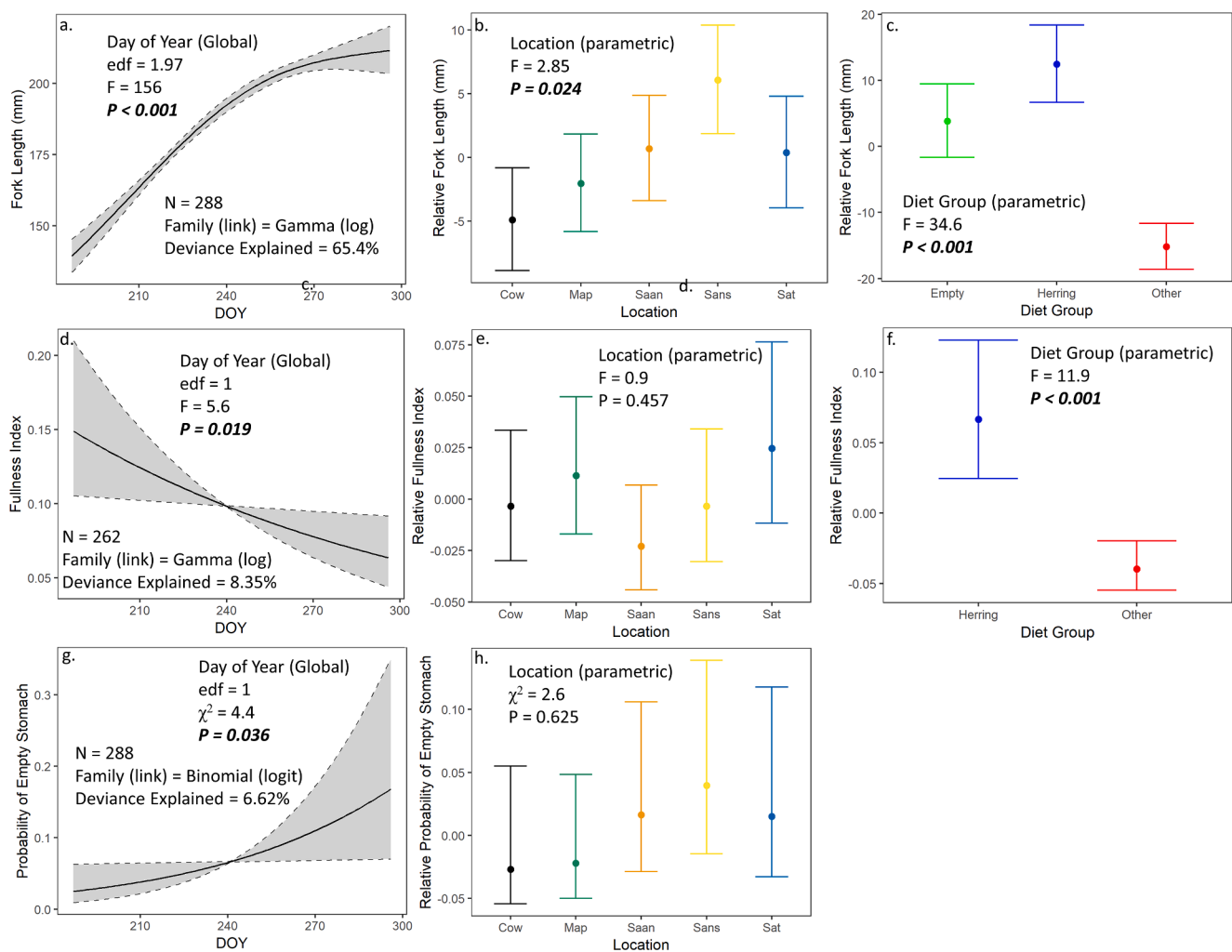

Fig. 7. Effects plots for generalized additive models relating day of the year (DOY), sampling location, and diet grouping to juvenile Chinook Salmon fork length (a-c), stomach fullness index (d-f), and occurrence of empty stomachs (g-h). Regression statistics and the error distribution and link function for each model are reported in the panels; significant terms (P < 0.05) are indicated in bold italics. Where effective degrees of freedom (edf) = 1 the relationship between the predictor and response is effectively linear. Site names are defined in Table 1 and mapped in Fig. 1.

(N = 209), Lower Fraser River (N = 55), and other East Coast Vancouver Island rivers (N = 25).

Hatchery origin was confirmed for 101/289 fish (36.7%) based on adipose clip, coded wire tag, or both; total hatchery proportion could not be determined as marking of Chinook Salmon is not universally employed at Canadian hatcheries. For Cowichan River-origin Chinook Salmon, where universal marking of hatchery fish did occur in 2015

(Kevin Pellett, DFO, pers. comm.) the overall hatchery marked proportion was 44% and remained relatively constant through the season (supporting Figure S1).

Mean fork length was 176 mm (SD = 27 mm), increasing from 145 mm (SD = 19 mm) in July to 202 mm (SD = 23 mm) in October. A GAM detected a non-linear apparent rate of increase in fork length which levelled off after mid-September (Fig. 7a). Fork length differed
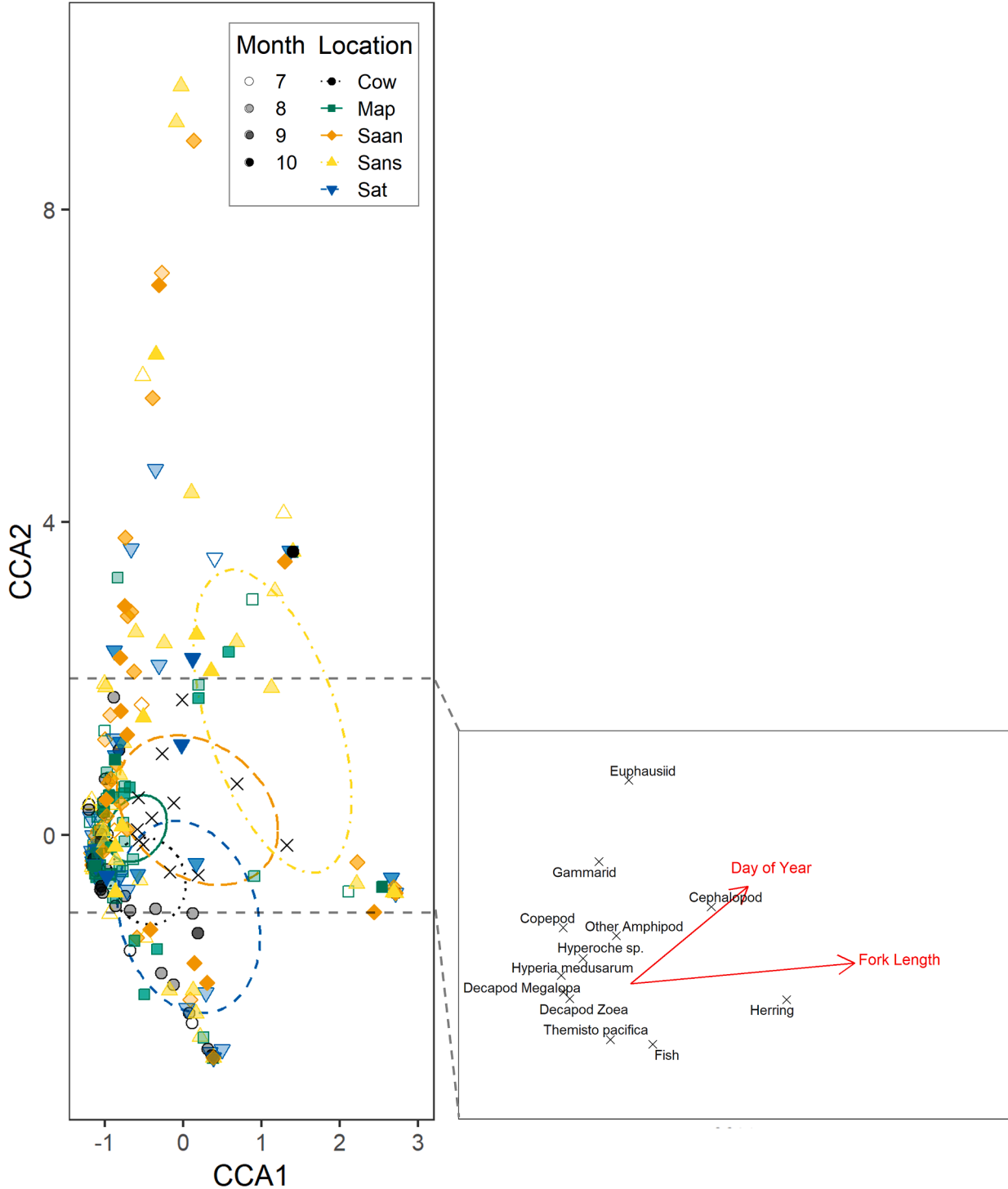
Fig. 8. Canonical correspondence analysis biplot of partial fullness values (see methods for details) for different prey categories of juvenile ocean-type Chinook Salmon sampled at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015. Points in the left-hand panel indicate diets of individual fish with ellipses indicating the 95% confidence intervals of site (location) centroids and × indicating prey taxa locations. The right-hand panel is an inset (corresponding to region between the horizontal dashed lines) that provides the prey taxa name for each point and arrows indicating direction of continuous constraints (fork length and day of the year). . Site names are defined in Table 1 and mapped in Fig. 1.
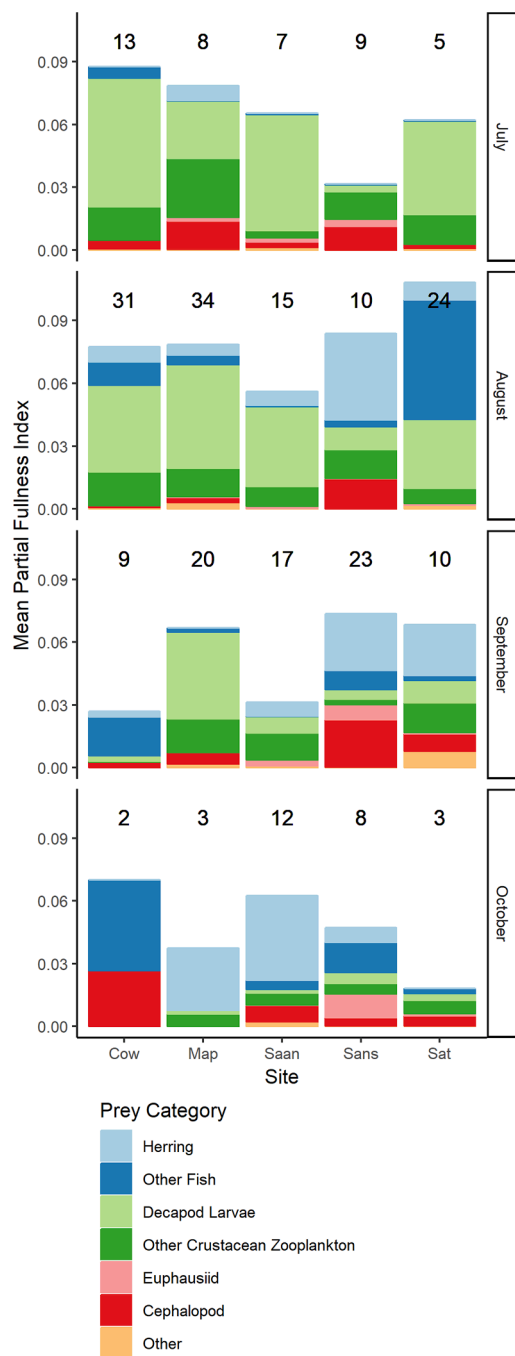
Fig. 9. Monthly mean partial fullness indices (see text for full definition) for broad taxonomic groupings of the prey of juvenile Chinook Salmon with non-empty stomachs sampled at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015. Sample sizes are indicated above each bar. The high partial fullness index for "Other Fish" at Satellite Channel in August was driven by an outlier, a 168 mm Chinook Salmon which contained two Shiner Surfperch (*Cymatogaster aggregata*) giving a partial fullness index of 0.80. Site names are defined in Table 1 and mapped in Fig. 1.

significantly among sites with the largest fish at Sansum Narrows and the smallest fish in Cowichan Bay (P = 0.024; Fig. 7b). Both fish with empty stomachs and those which had consumed Pacific Herring were significantly larger than fish which had consumed other diet items (P < 0.001; Fig. 7c). A smooth term for stratification and site-specific smooth terms for day of the year were all non-significant and were not included

in the final model.

3.2.2. Diet

Quantitative diet data were obtained for 262 of 265 juvenile Strait of Georgia-origin ocean-type Chinook Salmon with non-empty stomachs; 23 individuals had empty stomachs and 1 individual was not lavaged. Juvenile Chinook Salmon consumed a diverse assemblage of prey, with the most important prey categories by weight being Pacific Herring (25.6%; 62% of all fish prey) and cancrid megalopae (15.2%; Table 3). This diet proportion for Pacific Herring was a minimum estimate as unidentified post larval fish and fish fragments constituted an additional 6% of diets by mass. When diets were aggregated for all juvenile Chinook Salmon, including stock groups not included in analyses (N = 322), Pacific Herring represented 38.5% of diets by mass and 73.4% of fish prey (Table S4). Despite having the greatest importance by weight, Pacific Herring occurred in only 8.4% of non-empty stomachs, while cancrid megalopae occurred in 69.5%. For a subset of cancrid megalopae identified to species (N = 312), the majority (88.8%) were *Cancer productus,* with the balance being *Cancer oregonensis* (10.6%) and *Cancer gracilis* (0.6%). Of the zooplankton categories dominating our zooplankton tows (Table 2), calanoid copepods, decapod zoeae, and gammarid amphipods were relatively far less important in juvenile Chinook Salmon diets (Table 3). Quantitative stomach data were also collected from an additional 60 juvenile Chinook Salmon from non-focal stocks. A taxonomically nested, hierarchical summary (Buckland et al., 2017) of gravimetric composition and frequency of occurrence of prey identified in all 322 diets is provided in supplementary Table S5.

Site, day of the year, and individual fork length were all retained in a final CCA (P = 0.001) of taxon partial fullness scores in individual Chinook Salmon diets (P = 0.001 for all constraints). Density stratification was not significantly related to diet and was dropped from the CCA during stepwise selection. Variance inflation factors for all constraints were below 3. These constraints explained 19% of the total inertia in diets with the first and second canonical axes respectively accounting for 55% and 20% of explained inertia. Confidence intervals of site centroids overlapped considerably, but Sansum Narrows showed the least overlap with other sites, being associated positively with both primary CCA axes and shifted towards Pacific Herring, cephalopods and euphausiids (Fig. 5). Day of the year showed the same positive association with both CCA axes as Sansum Narrows, and fork length was strongly associated with the first CCA axis. Overall diets later in the season, and those of larger fish, shifted away from crustacean larvae and other small crustacean zooplankton (copepods and hyperiid amphipods) and towards Pacific Herring, euphausiids and cephalopods (Fig. 8). The importance of crustacean zooplankton prey (with the exception of euphausiids) declined dramatically from July to October, while fish (primarily Pacific Herring) became more important after July (Fig. 9). Crustacean zooplankton dominated diets at Maple Bay and Saanich Inlet into September while fish became the most important prey at Sansum Narrows and Satellite Channel in August and September. Sample sizes in October were very low (≤3) at all sites except Saanich Inlet and Sansum Narrows where fish dominated diets (along with euphausiids at Sansum Narrows; Fig. 9, Supplementary Table S4).

Several categories of small zooplankton prey including copepods, decapod larvae, and hyperiid amphipods all occurred together in diets more often than would be expected by chance. Only cephalopods and Pacific Herring occurred with any other prey categories significantly less often than expected by chance (2 and 7 of 15 potential pairings respectively; Fig. 10).

Overall stomach fullness declined significantly over the study period (P = 0.019) while the occurrence of empty stomachs increased (P = 0.036) (Fig. 7d, g). Neither overall fullness nor occurrence of empty stomachs differed significantly between sites (Fig. 7e, h). Juvenile Chinook Salmon which had consumed Pacific Herring had significantly fuller stomachs than fish with non-empty stomachs which did not contain Pacific Herring (P < 0.001; Fig. 7f). Smooth terms for
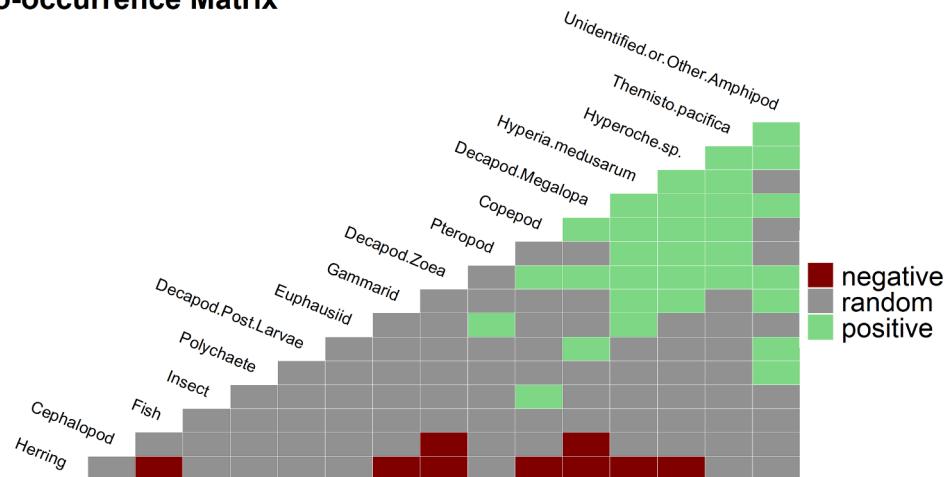
Fig. 10. Probabilistic analysis of whether pairs of juvenile Chinook Salmon prey categories occurred together in the same fish significantly more (green/lightest) or less (red/darkest) often than expected if prey occurred in Chinook Salmon diets randomly and independently of each other ($\alpha = 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stratification and site-specific smooth terms for day of the year were non-significant in models explaining both stomach fullness and occurrence of empty stomachs and were not included in final models.

3.2.3. Capture temperature

Temperature at the depth and time of capture was successfully measured for 267 of 289 juvenile ocean-type, Strait of Georgia-origin Chinook Salmon of which 264 were captured on days for which stratification data were available. The mean *in situ* capture temperature was highest in August at 14.0 °C (N = 111; SD = 1.0 °C) and declined to 12.3 °C (N = 29; SD = 0.3 °C) by October (Fig. 11). Capture temperature was also positively related density stratification. The relationship between capture temperature and date differed significantly from the global linear decline at Maple Bay (P = 0.004; Fig. 11e) and Sansum Narrows (P = 0.001; Fig. 11f); both of which exhibited more stable capture temperatures through the first part of the sampling period followed by a steeper decline than other sites. Capture temperatures did not differ significantly by site or diet grouping.

3.2.4. Growth

A total of 458 scale impressions from 247 juvenile Chinook Salmon were measured, and 450 of these from 243 fish met quality control criteria. For individual Chinook Salmon with usable scale data a mean of 1.85 scales per fish were analyzed. Circulus spacing decreased linearly over the study period (P < 0.001) and was significantly different between sites (P = 0.030), being lowest in Maple Bay (Fig. 12). Circulus spacing did not differ significantly among coarse diet groupings for juvenile Chinook Salmon (Pacific Herring, other items, or empty stomachs; P = 0.212). A term for fork length was also highly significant in the model relating circulus spacing to site and DOY (P < 0.001). A smooth term for stratification and site-specific smooth terms for day of the year were all non-significant and were not included in the final model.

3.2.5. CPUE with respect to location, date, depth, time, and tide

Preliminary GAMMs fit to the 1350 fishing events for which speed through water data were available and 1430 fishing events for which stratification data were available, suggested weak, linear, positive relationships between both of these variables and CPUE. However, neither relationship was significant (P = 0.12 and P = 0.07 respectively) and we therefore omitted these variables and fit the model to all fishing events. Overall, this GAMM explained 8% of the deviance in juvenile Chinook Salmon CPUE. We did not detect significant overall effects of site or hour of the day on Chinook Salmon CPUE (Table 4). Chinook Salmon CPUE

was lowest at 5 m and significantly elevated from 15 m to 25 m (Fig. 13). Only Sansum Narrows differed significantly from the global trend, exhibiting lower CPUE for hooks less than 15 m and higher CPUE for hooks deeper than 20 m. The global relationship between day of the year and CPUE was dome shaped, with significantly lower CPUE at the end of the sampling period and a peak in the middle of August. Relative to the global relationship Saanich Inlet had lower CPUE during the middle of the sampling period (late August and early September) and higher CPUE from late September into October. At Sansum Narrows CPUE was slightly elevated late in the sampling period relative to the global trend. We detected significant effects of stage of the tide on Chinook Salmon CPUE only at Sansum Narrows and Maple Bay (Table 4, Fig. 13). At Maple Bay, CPUE was elevated from the late flood tide through most of the ebb but declined to a minimum in the two hours after low slack. At Sansum Narrows CPUE was elevated during the middle of the flood tide and reached a minimum during the late ebb.

4. Discussion

We characterized spatial and temporal variation in water column stratification; zooplankton composition and abundance; and the diet, size, growth, temperature experience and CPUE of juvenile ocean-type Chinook Salmon within a small (<25 km × 10 km; Fig. 1) area of the Southern Gulf Islands in the Salish Sea in late summer and fall. We found little evidence that juvenile Chinook Salmon size, growth, and diet was directly related to local water column properties or zooplankton composition or availability. Nevertheless, our results suggested that individual fish were exhibiting different patterns of foraging behavior, with diet, size and growth varying at a fine spatial scale. Larger juvenile Chinook Salmon were able to transition from a diet of crustacean zooplankton to age-0 Pacific Herring. Forage fish distribution may play an important and size-dependent role in structuring the trophic ecology of juvenile Chinook Salmon in space and time.

4.1. Seasonal changes

Near surface water temperature, density stratification and abundance of zooplankton prey of juvenile Chinook Salmon all declined over the study period (Figs. 2 and 4), with densities of zooplankton prey reaching very low levels by October. The temperatures experienced by juvenile Chinook Salmon at depth of capture decreased with date and increased with density stratification. Mean monthly capture temperatures (range = 12.3–14 °C) were very close to optimal growth
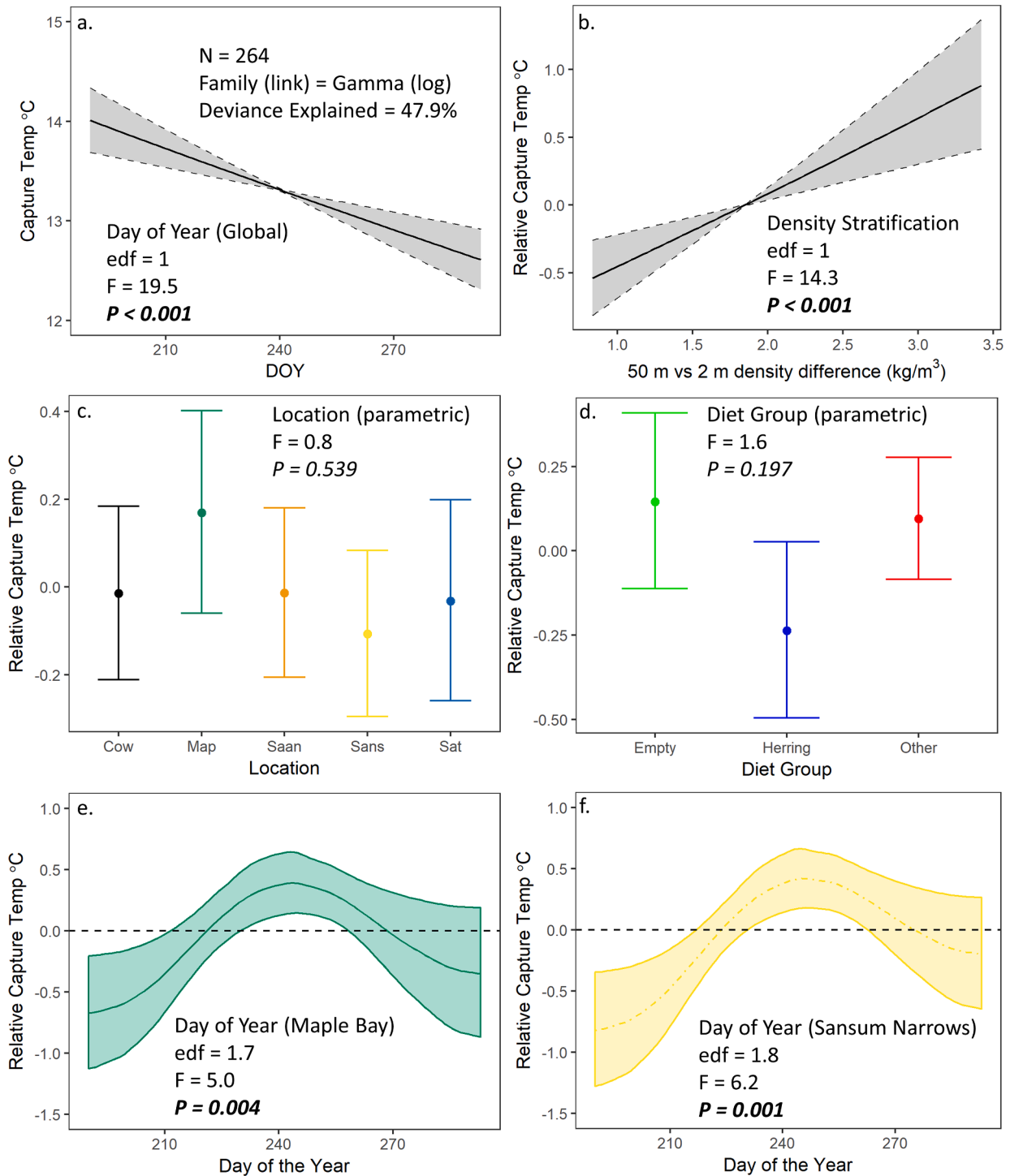
Fig. 11. Effects plots for a generalized additive model relating (a) day of the year (DOY), (b) density stratification, (c) sampling site, and (d) diet grouping to juvenile Chinook Salmon capture temperature measured by thermistors deployed on leaders during fishing. The relationship between capture temperature and DOY differed significantly from the global linear trend (a) only at Maple Bay (e) and Sansum Narrows (f); non-significant site-specific smoothers are not shown. Regression statistics and the error distribution and link function are reported in the panels; significant terms (P < 0.05) are indicated in bold italics. Site names are defined in Table 1 and mapped in Fig. 1.

temperatures for first ocean year Chinook Salmon feeding at 50–100% of C_{max} (Myers et al., 2010). Our results suggest that juvenile Chinook Salmon growth rates decreased over the study period. Plateauing of the non-linear relationship between fork length and date (Fig. 7) could also have been a consequence of size selective mortality (Thomas et al., 2017; Gamble et al., 2018; Nelson et al., 2019) or emigration (Neville et al., 2015); however, circulus spacing also decreased with date

(Fig. 12), suggesting that the decline in growth rate was genuine. One possible explanation for decreasing growth was a shift in energy budget from somatic growth to lipid storage, a common phenomenon in temperate fish prior to winter (reviewed by Martin et al., 2017). Alternatively, if the decline in growth rate was due to physiological limitation, it was more likely a consequence of decreasing food availability than decreasing temperature. This interpretation was supported by
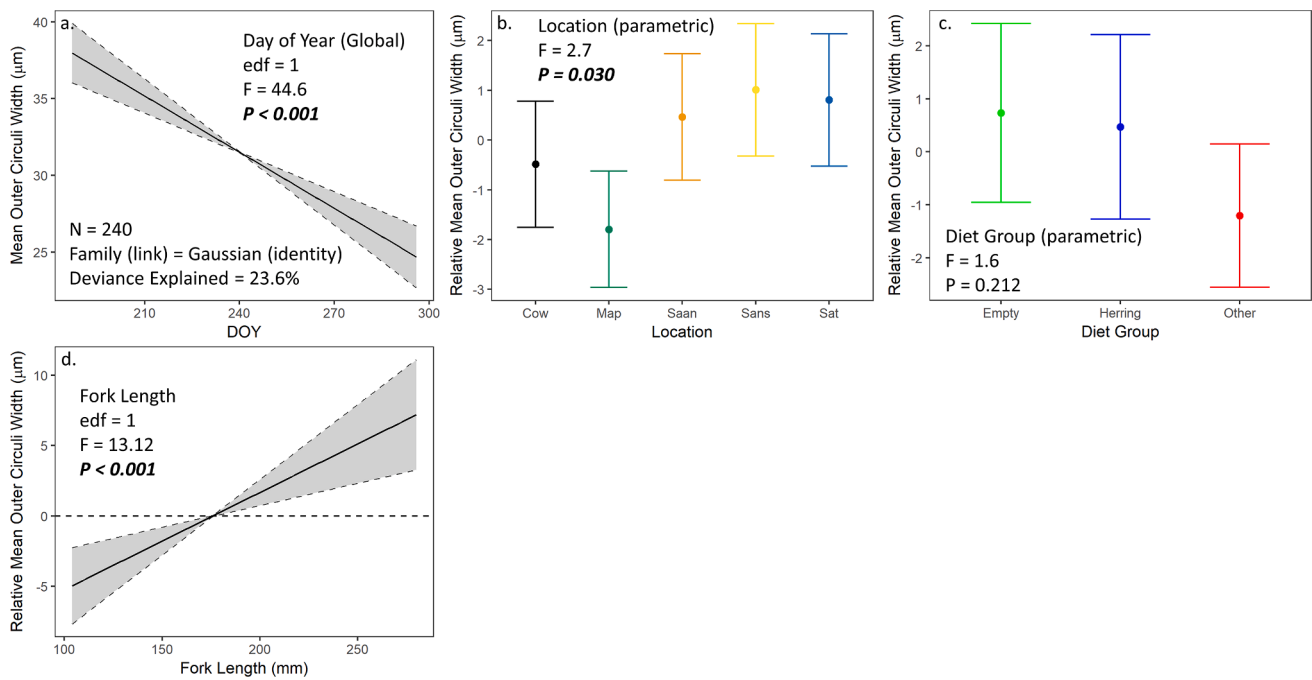
Fig. 12. Effects plots for a generalized additive model relating day of the year (DOY) (a), sampling site (b), diet grouping (c), and nose fork length (d) to mean spacing of the second and third to outermost scale circuli, an index of recent growth in juvenile Chinook Salmon. Regression statistics and the error distribution and link function are reported in the panels; significant terms (P < 0.05) are indicated in bold italics. Site names are defined in Table 1 and mapped in Fig. 1.

Table 4

Regression statistics for a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, hour of the day, day of the year, depth, and stage of the tide. Depth and day of the year are included in the model both as both a global smooth term and site-specific smooth terms. Stage of the tide is included just as site specific smooth terms and hour of the day just as a global smooth term. Site is also included in the model as a parametric fixed effect and fishing event is included in the model as a random effect. Terms which are significant based on approximate P-values are indicated in bold. Plots of all significant smoothers are provided in Fig. 13.

Type of Term	Variable	Level	Coefficient	Std. Error	z	est. df	Chi.sq	P-value
Parametric Factor								
	Site	Cowichan Bay	0.05	0.13	0.37			0.711
	Site	Maple Bay	0.15	0.12	1.25			0.209
	Site	Saanich Inlet	0.04	0.14	0.25			0.800
	Site	Sansum Narrows	−0.09	0.15	−0.61			0.540
	Site	Satellite Channel	−0.15	0.14	−1.067			0.286
Smoothers								
	Hour of Day	Global				1.00	1.794	0.181
	DOY	**Global**				**2.71**	**20.032**	**<0.001**
	DOY	Cowichan Bay				0.06	0.068	0.260
	DOY	Maple Bay				0.00	0.002	0.665
	DOY	**Saanich Inlet**				**3.40**	**24.865**	**<0.001**
	DOY	**Sansum Narrows**				**1.63**	**5.868**	**0.012**
	DOY	Satellite Channel				0.50	0.730	0.199
	Depth	**Global**				**1.89**	**10.616**	**0.003**
	Depth	Cowichan Bay				0.00	0.005	0.321
	Depth	Maple Bay				0.00	0.000	0.828
	Depth	Saanich Inlet				0.00	0.001	0.446
	Depth	**Sansum Narrows**				**1.55**	**9.481**	**0.002**
	Depth	Satellite Channel				0.00	0.001	1.000
	Tide	Cowichan Bay				0.40	0.530	0.276
	Tide	**Maple Bay**				**1.86**	**10.656**	**0.003**
	Tide	Saanich Inlet				0.01	0.003	0.506
	Tide	**Sansum Narrows**				**1.86**	**9.856**	**0.004**
	Tide	Satellite Channel				0.90	1.700	0.162
	Fishing Event (RE)					51.80	55.037	0.059

decreasing stomach fullness and increased occurrence of empty stomachs over the study period (Fig. 7; but see discussion of link between empty stomachs and piscivory under 4.3). The decrease in crustacean zooplankton abundance (Fig. 4) was mirrored by a decrease in the importance of crustacean zooplankton in the diet of juvenile Chinook Salmon (Figs. 8 and 9). It is important to note that our zooplankton tows represented just an index of zooplankton community composition and

abundance rather than a representative sampling of zooplankton prey available to juvenile Chinook Salmon. The limitations of plankton nets for representative sampling of juvenile salmon prey has been documented (Brodeur et al., 2011) and was demonstrated in the present study by the absence or near absence from plankton tows of some zooplankton prey which were frequently encountered in juvenile Chinook Salmon stomachs (e.g. adult euphausiids and *Hyperia medusarum*;
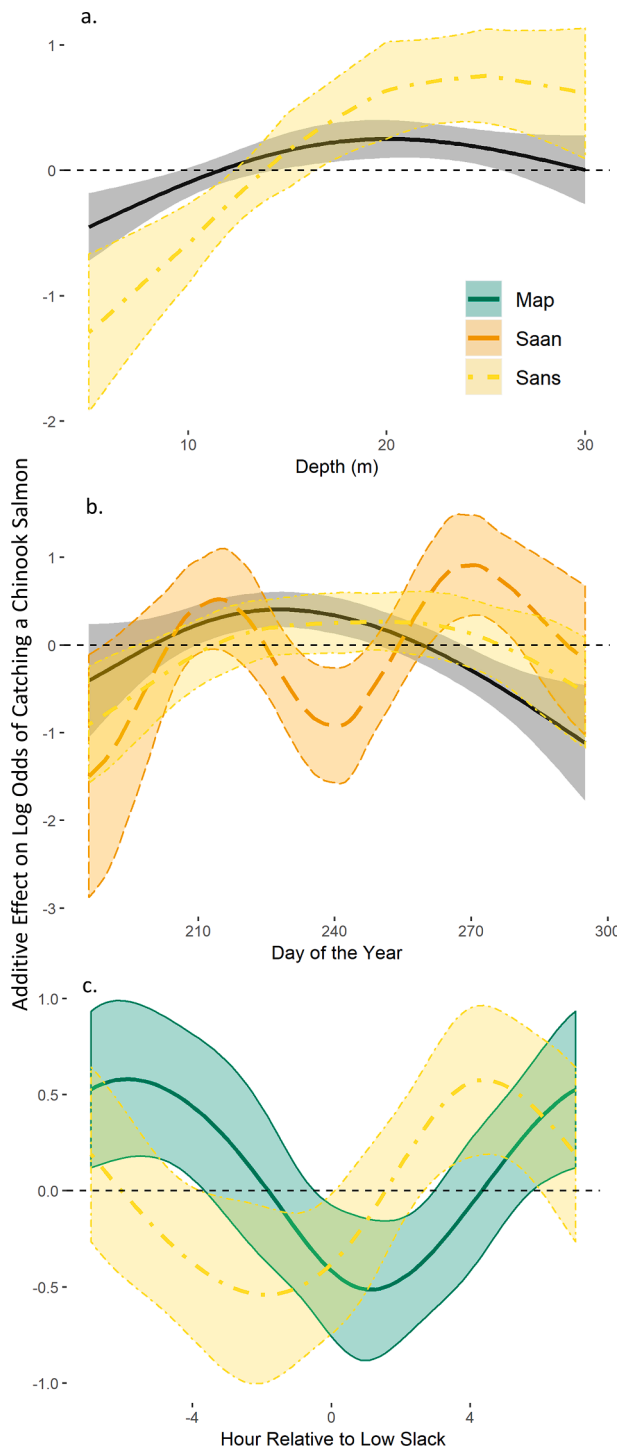
Fig. 13. Plots for all significant (p < 0.05) smooth terms in a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, hour of the day, day of the year, depth, and stage of the tide (see Table 4 for all regression statistics). Significant smooth terms were a. global and site-specific (Sansum Narrows) effects of depth, b. global and site-specific (Sansum Narrows and Saanich Inlet) effects of day of the year, and c. site-specific (Sansum Narrows and Maple Bay) effects of stage of the tide. Global smoothers are plotted as a solid black line. In the presence of a global smoother, site-specific smoothers include the global smoother. Shaded regions indicate 2 × the standard error of the estimated effect, in the case of site-specific smooths, only the error of the site-specific smoother is illustrated. Site names are defined in Table 1 and mapped in Fig. 1.

Tables 2 and 3). Nevertheless, our zooplankton sampling detected a dramatic decline in biomass density of decapod larvae through the study period (Fig. 4, Supporting Table S3). These larval forms collectively represented 29.5% of juvenile Chinook Salmon diets by mass (Table 3). Previous work has found that decapod larvae are at times an important summer diet component for juvenile Chinook Salmon in the Strait of Georgia (Riddell et al., 2018) and on the continental shelf (Brodeur et al., 2007). Decapod larvae are particularly important in some regions of Puget Sound, where they are thought to drive increased growth of juvenile Chinook Salmon as they move offshore (Duffy et al., 2010; Davis et al., 2020). The declining abundance of decapod larvae that we observed in autumn was expected given the strong seasonal links between phytoplankton and meroplankton production in high latitude oceans (Thorson, 1946; Highfield et al., 2010). The biomass of euphausiids within the Strait of Georgia peaks in late fall (Heath, 1977), while biomass of predatory amphipods (including hyperiids and the gammarid *Cyphocaris challengerii*) is highest during spring and summer (Harrison et al., 1983). Declining partial fullness scores for crustacean zooplankton from July to September indicate that euphausiids were not able to compensate for declining abundance of decapod larvae and other small crustacean zooplankton in Chinook Salmon diets. Partial fullness scores for fish, primarily driven by Pacific Herring, also increased after July but were not able to compensate for decreased meroplankton abundance (discussed further in Section 4.3). The planktonic larval duration of decapods and other meroplankton is strongly inversely linked to water temperature (Lindley, 1998; O'Connor et al., 2007). This relationship has the potential to curtail the availability of meroplankton earlier in the season during warmer years when food demands of juvenile salmon may be higher (Daly and Brodeur, 2015).

The dome shaped relationship that we observed between CPUE and date (Fig. 13) likely resulted from increasing catchability of juvenile Chinook Salmon from July to August followed by emigration and mortality between August and October. Chinook Salmon below approximately 150 mm fork length are less vulnerable to microtrolling than larger fish (Duguid and Juanes, 2017) which may have lowered July CPUE. Some mortality will also have occurred throughout the study period. Beamish et al. (2012) attributed ~80% July to September declines in swept volume-based abundance estimates for Cowichan River Chinook Salmon in the Southern Gulf Islands in 2008 to mortality. The modest decline in CPUE that we observed was inconsistent with mortality on this scale. Preliminary results for Cowichan River Chinook Salmon PIT-tagged in May-June (collected via purse seine) and August-September (microtrolling) show only 3–4 fold greater survival for the latter group (Kevin Pellett, DFO, unpublished data), suggesting a lower summer mortality rate than inferred by Beamish et al. (2012). Consistent with Beamish et al. (2012) we did not detect a decline in the proportion of hatchery origin Cowichan River Chinook Salmon from July to October (Figure S1), suggesting that any differential survival of hatchery and natural origin fish occurs outside of this period. The results of Beamish et al. (2012) suggest dramatically lower survival of hatchery origin Chinook Salmon prior to July, while recent results based on PIT tagging suggest that much lower survival of hatchery fish occurs after September (Kevin Pellett, DFO, unpublished data). As discussed above for seasonal changes in length, it is also possible that differential emigration of hatchery and wild-origin fish may confound inferences of differential mortality (or lack-thereof) from changes in hatchery and wild catch proportions.

Many juvenile ocean-type Chinook Salmon are thought to migrate out of the Salish Sea and onto the continental shelf in autumn of their first year at sea (Neville et al., 2015), although some also exhibit residence through at least part of their life history (Chamberlin and Quinn, 2014; Rechisky et al., 2019). Healey (1982) suggested that some distributional shifts of juvenile Pacific Salmon at sea may be linked to foraging success. Our results suggest that declining meroplankton availability in fall may decrease the value of the Southern Gulf Islands as rearing habitat. Unfortunately, few data are available on diets of first

ocean year Chinook Salmon after October. On the West Coast of Vancouver Island, Hertz et al. (2017) found that euphausiids, amphipods and fish were important diet components in autumn (October-November) and winter (February-March), with stomach fullness higher in winter. Future work on summer to winter shifts in prey availability and diet of juvenile Pacific Salmon may clarify mechanisms driving migration phenology.

4.2. Distribution, size and growth in relation to physical and biological oceanography

Our results did not provide support for the hypothesis that juvenile Chinook Salmon abundance (as reflected by CPUE) was directly related to local scale water column stratification or zooplankton composition and abundance. Stratification and zooplankton abundance differed significantly between sites (Fig. 4), as did zooplankton composition (Fig. 5). However, we did not detect significant differences in mean catch per unit effort with stratification or between sites, although Saanich Inlet and Sansum Narrows had relatively higher CPUE at the end of the sampling period. Consistent tidal patterns in density stratification were detected only at Satellite Channel and Cowichan Bay (more and less stratified during flood respectively; Figs. 3 and 4), while significant tidal patterns in CPUE were detected only at Sansum Narrows and Maple Bay (Fig. 13). Only Sansum Narrows exhibited a significant relationship between zooplankton biomass density and stage of the tide (Fig. 4) with biomass density counterintuitively lower on the flood tide when Chinook Salmon CPUE was elevated.

Our failure to detect strong spatial patterns in CPUE suggest that juvenile Chinook Salmon were broadly distributed in epipelagic habitats within the Southern Gulf Islands. Despite this, we feel our results are inconsistent with random distribution of juvenile Chinook Salmon through the study area. Juvenile Pacific Salmon are highly mobile and are capable of rapid directed migrations, although Chinook Salmon exhibit more milling and consequently lower migration rates than other species (Welch et al., 2011). The shortest distance between our two most separate sites (Saanich Inlet and Maple Bay) was approximately 24 km. At the travel speed reported by Welch et al. (2011; 0.33 body lengths per second) it would take a 176 mm juvenile Chinook Salmon (the overall mean for the present study) 4.8 days to cover this distance. This is lower than the median local movement rate of 18.9 km/day reported by Rechisky et al. (2019) for juvenile Chinook Salmon tagged in September 2017 in the same region as the present study. Given these movement rates, some mixing of juvenile Chinook Salmon among the sites in our study region almost certainly occurred. Nevertheless, capture site was associated with significant variation in juvenile Chinook Salmon size (Fig. 7), growth (Fig. 12), and diets (Fig. 8), suggesting that individual juvenile salmon were using the seascape in ways which influenced their likelihood of being caught at a given site.

While characteristics of juvenile Chinook Salmon differed between sites, clear cut linkages to local scale physical and biological oceanography were not evident. We detected no evidence that water column stratification significantly structured Chinook Salmon diets. We also found no support for the hypothesis that juvenile Chinook Salmon captured at sites with greater water column stratification experienced faster growth. This was exemplified by Maple Bay and Sansum Narrows, which had warmer near-surface temperatures (Fig. 2) and significantly greater density stratification (Fig. 4) than the global mean. These two sites also had similar zooplankton composition (Fig. 5). Despite these similarities and their physical adjacency, characteristics of juvenile Chinook Salmon differed more between Sansum Narrows and Maple Bay than between other sites. Diets at Maple Bay were dominated by small crustacean zooplankton (Figs. 8 and 9) while diets at Sansum Narrows contained more Pacific Herring, euphausiids, and cephalopods. Sansum Narrows had the largest (Fig. 7) and fastest growing (Fig. 12) juvenile salmon of any site, while Maple Bay had smaller fish which were the slowest growing of any site. These results were surprising given that

Sansum Narrows also had the lowest zooplankton biomass density of any site (see Section 4.4). Sansum Narrows was also the only site to differ from the global relationship between depth and CPUE; the deeper distribution of juvenile Chinook Salmon at Sansum Narrows (Fig. 13) may explain why capture temperature was lower (although not significantly so) for fish at Sansum Narrows than Maple Bay (Fig. 11) despite similar thermal stratification (Fig. 2). The low growth rate of juvenile Chinook Salmon at Maple Bay was inconsistent with the hypothesis that stratification promotes higher growth rates by allowing selection of optimal temperatures (Burke et al., 2013). Our failure to detect a clear link between local-scale variability in water column stratification and juvenile Chinook Salmon abundance, size or growth does not contradict evidence for the importance of stratification to juvenile Chinook Salmon growth at larger spatial scales (Burke et al., 2013; Journey et al., 2020).

4.3. Size and growth in relation to diet and the importance of Pacific Herring

While biological characteristics of juvenile Chinook Salmon were not clearly linked to local biological and physical oceanography, linkages to diet were apparent. Juvenile Chinook Salmon which had preyed on Pacific Herring were larger and had greater stomach fullness than those which had not (Fig. 7). Scale circulus spacing based growth rates of Chinook Salmon which had eaten Pacific Herring were also higher than those which had fed on other items, although this difference was not significant (Fig. 12). Juvenile Chinook Salmon size and growth were elevated at sites where fish formed a greater proportion of the diet. The lowest growth rate was observed at Maple Bay (Fig. 12), which had diets dominated by small crustacean zooplankton (Figs. 8 and 9). The largest, fastest growing juvenile Chinook Salmon were captured at Sansum Narrows, where diets included more Pacific Herring, euphausiids and cephalopods. Cowichan Bay, Saanich Inlet and Satellite Channel were intermediate between Maple Bay and Sansum Narrows in Chinook Salmon growth rates (Fig. 12) and the relative importance of crustacean zooplankton and fish in diets (Figs. 8 and 9, Table S4). The smallest juvenile Chinook Salmon were observed at Cowichan Bay, where diets were dominated by small crustacean zooplankton in July and August and mean partial fullness indices were lower than other sites after August despite fish constituting most of the diet. Smaller size of Chinook Salmon in Cowichan Bay may also have been partially due to proximity to the mouth of the Cowichan River, as smaller individuals in a population may disperse more slowly from their point of ocean entry (Freshwater et al., 2016). Our results were consistent with evidence that the transition to piscivory provides an important growth advantage to juvenile fish (Juanes and Conover, 1994; Olson, 1996; Juanes et al., 2002). The growth advantage provided by piscivory has also been demonstrated for juvenile Chinook Salmon in other regions. In the Northern California Current, growth and condition of juvenile Chinook Salmon were elevated during periods when Northern Anchovy were abundant in trawl samples and salmon diets (Litz et al., 2017). In Puget Sound, stomach fullness and growth were greater for piscivorous juvenile Chinook Salmon and growth was higher in regions where fish dominated diets (Davis et al., 2020).

Our growth rate results were likely influenced by the inclusion of fork length as a predictor in the scale circulus spacing model. This conservative approach was based on lab results suggesting that circulus spacing varies with fish size independently of growth rate (Duguid et al., 2018). As pointed out by Ferriss et al. (2014), correcting growth indices for possible independent relationships with fish size can reduce risk of type I error but may increase risk of type II error. Duguid et al. (2018) discuss the possibility that scale circulus spacing becomes independent of length as Chinook Salmon grow, but more work is required to confirm this. Our approach may have underestimated the effect of diet and location on growth as both variables were also strongly related to fish size (Fig. 7).

The strong relationship that we observed between juvenile Chinook

Salmon size and consumption of Pacific Herring may have important implications as Pacific Herring are the dominant forage fish in the Salish Sea (Riddell et al., 2018; Greene et al., 2015). Failure to reach the size threshold necessary to transition to piscivory on a dominant prey species can dramatically reduce growth of juvenile fish (Olson, 1996). Juvenile Chinook Salmon become more piscivorous as they grow but generally consume prey < 40% of their body length (Brodeur, 1991; Daly et al., 2009). In our study region, age-0 Pacific Herring were the primary fish prey of juvenile Chinook Salmon (at least 62.0% of fish prey for focal stocks and 73.4% for all stocks combined). While no individual Pacific Herring were intact enough for accurate measurements, the remains observed typically appeared close to the size threshold for consumption. Chamberlin et al. (2017) found that IGF-1 concentration (a proxy for growth rate) of juvenile Chinook Salmon in Puget Sound was more strongly related to length where small (relative to Chinook Salmon length) Pacific Herring were abundant. These authors concluded that this pattern could result from a size dependent shift to piscivory. The size dependence of juvenile Chinook Salmon predation on Pacific Herring is also evident in the Northern Bering Sea where Pacific Herring outgrow the prey size threshold of Chinook Salmon in their first year at sea and are rarely encountered in diets (Murphy et al., 2014). In the present study Pacific Herring did not become important in diets until August. Working in the same region, Chittenden et al. (2017) reported that fish prey were relatively unimportant in diets of juvenile Chinook Salmon from April to June. These recent results contrast with historical data from the same region which suggest that Pacific Herring were important in diets throughout the late spring and summer (Argue et al., 1986; Healey, 1980).

Could changes in the predator-prey size ratio over time explain this apparent shift from consumption of Pacific Herring throughout the first summer at sea to a late season, size dependent shift to piscivory? Pacific Herring in the Northeast Pacific primarily spawn in March and early April, although genetically distinct late and early spawning populations also occur (Beacham et al., 2008; Petrou, 2019). Chamberlin et al. (2017) hypothesized that late (April to June) spawning Pacific Herring could be particularly important as prey to juvenile Chinook Salmon due to their presumed smaller size. The primary late spawning population in the Salish Sea (Cherry Point) was historically the largest stock within the inside waters of Washington State but has declined precipitously since the, 1990s (Sandell et al., 2019). Interannual changes in temperature and density dependence can also influence the size of age-0 Pacific Herring in the Salish Sea (Reum et al., 2013). The Strait of Georgia is warming (Chandler, 2019) and warm spring temperatures may result in relatively larger age-0 Pacific Herring in summer (Reum et al., 2013). Density dependent growth also plays a role in the size and condition achieved by age-0 Pacific Herring by fall (Reum et al., 2013; Boldt et al., 2018). It is likely that Pacific Herring population diversity, cohort abundance, and environmental conditions are all interacting with juvenile Chinook Salmon size to regulate predator-prey dynamics, potentially at multiple spatial and temporal scales. Given the importance of piscivory to growth (Litz et al., 2017; Davis et al., 2020) and growth to survival (Moss et al., 2005; Duffy and Beauchamp, 2011), changes in the predator to prey size ratios of Pacific Herring and Chinook Salmon may explain part of both interannual variability and long term trends in Salish Sea Chinook Salmon survival. One caveat to this hypothesis is that South Thompson ocean-type Chinook Salmon, which enter the ocean later than other ocean-type stocks and are therefore smaller in late summer and fall, have experienced high survival relative to other Strait of Georgia stocks in recent decades (Beamish and Neville, 2016).

Our results support a defined shift in foraging behaviour of juvenile Chinook Salmon from feeding on a mixed assemblage of zooplankton to targeting age-0 Pacific Herring, with individuals which had consumed Pacific Herring containing a number of other prey taxa significantly less often than would be expected by chance (Fig. 10). Reduced diversity of diet items in juvenile Chinook Salmon which had fed on Pacific Herring

may have been partly a seasonal effect given the observed decline in zooplankton abundance and increase in occurrence of piscivory over the study period. However, it is also likely that Chinook Salmon diets become more specialized as they transition to piscivory, as has been described for other predatory fish (e.g. Sánchez-Hernández et al., 2017). If specialization is occurring, a reduction in occurrence of zooplankton prey could result from piscivorous juvenile Chinook Salmon selecting against these prey when encountered, or from a shift in behaviour and habitat use that increased encounters with Pacific Herring at the expense of encounters with alternative prey. For piscivorous fish, Juanes (1994) suggested that apparent selection of small (relative to the available size distribution) prey was generally a function of prey vulnerability rather than predator selection. One possible explanation for differences in the size and growth of juvenile Chinook Salmon between sites is that larger, piscivorous fish spent more time in areas where age-0 Pacific Herring were abundant. In historical purse seine surveys conducted in the Strait of Georgia, Chinook and Coho Salmon CPUE became correlated with age-0 Pacific Herring CPUE in late summer and fall (Tanasichuk et al., 2008). If larger, faster growing juvenile Chinook Salmon actively associate with age-0 Pacific Herring this could have implications for predation exposure, competition, and the impacts of Pacific Herring recruitment on Chinook Salmon survival.

Interestingly, size and growth of juvenile Chinook Salmon with empty stomachs were more similar to those of individuals containing Pacific Herring than to those of individuals containing other prey (Figs. 7 and 12). While non-significant, the occurrence of empty stomachs was also greater at sites with larger, faster growing juvenile salmon. Empty stomachs occur more frequently in piscivorous fish (particularly those that engulf their prey whole) than in those with other habits (Arrington et al., 2002). It seems likely that fish captured with empty stomachs in the present study were disproportionately those which had transitioned to piscivory. This could be explained by fish maintaining empty stomachs between large, high value meals. Alternatively it is possible that gastric lavage sometimes failed on individuals containing large prey (although we believe that this is unlikely) or that juvenile Chinook Salmon containing age-0 Pacific Herring were more likely to completely regurgitate their stomach contents prior to landing than those containing zooplankton. We did occasionally observe regurgitation of prey, including fish, prior to gastric lavage. Regurgitation of prey poses a challenge for fish diet studies and may be difficult to detect (Bowman, 1986). We are unaware of any research that has investigated frequency of regurgitation of different prey types by salmonids during capture. In Puget Sound, the frequency of empty stomachs and occurrence of fish in diets of juvenile Chinook Salmon was elevated in offshore relative to nearshore habitats (Duffy et al., 2010) and in Southeast Alaska juvenile Chinook Salmon had more empty stomachs and were more piscivorous than juvenile Coho Salmon (Weitkamp and Sturdevant, 2008). Caution should be used when interpreting empty stomachs of juvenile Pacific Salmon as an indicator of unsuccessful feeding (e.g. Brodeur et al., 2007; Weitkamp and Sturdevant, 2008).

4.4. Tidal jets as foraging hotspots

Support for the hypothesis that the tidal jet at Sansum Narrows would represent a foraging and growth hotspot was equivocal. While Sansum Narrows did have the largest, fastest growing juvenile Chinook of any site, CPUE was not significantly higher than the global mean. Size and growth at Sansum Narrows were also very similar to those at Satellite Channel and Saanich Inlet. Pacific Herring were important in Chinook Salmon diets at Sansum Narrows, and qualitative sonar observations suggested elevated occurrence of forage fish schools (Duguid et al., unpubl. data). One striking result was the significantly lower biomass density of crustacean zooplankton at Sansum Narrows relative to other sites, with densities also significantly lower on the flood tide. Satellite Channel, which was upstream of Sansum Narrows on the flood tide, exhibited the opposite pattern of tidal zooplankton abundance,

although this difference was non-significant (Fig. 4). Low zooplankton densities 'downstream' from the constriction of Sansum Narrows could be a consequence of disruption of a concentrated zooplankton layer (possibly at a chlorophyll maximum; Harris, 1988) by turbulent mixing in the narrows and homogenization of zooplankton through the water column. Testing this hypothesis would require depth stratified zooplankton sampling. An alternative explanation for low zooplankton densities at Sansum Narrows in general, and downstream of the narrows in particular, would be that locally abundant forage fish schools, possibly age-0 Pacific Herring, graze down zooplankton as they pass through the tidal passage. Pacific Herring consume many of the zooplankton crustacean taxa that were included in our index of zooplankton biomass density (Kemp, 2014). Local predation pressure has been suggested as a mechanism of reduced zooplankton abundance or altered zooplankton community composition over or downstream of seamounts (Genin et al., 1988; Dower and Mackas, 1996). Why might age-0 Pacific Herring consistently occupy Sansum Narrows? Zamon (2002) demonstrated that flood currents increased copepod densities in near-surface waters in San Juan passage through upwelling of deeper water. This in turn led to changes in the distribution of Pacific Sandlance (*Ammodytes hexapterus*) and Pacific Herring that increased prey encounter probabilities for avian and pinniped predators (Zamon, 2000, 2003). The lower biomass density of zooplankton that we observed in the top 30 m of the water column at Sansum Narrows was inconsistent with advection of a zooplankton subsidy from depth, although it is possible that such an effect could have been masked by intense local predation. Elevated water velocities associated with abrupt topographies can increase flux of prey particles available to waiting predators, providing an energetic advantage even if prey densities in the water column are not elevated (the "feed-rest" hypothesis reviewed by Genin, 2004). Tidal narrows also generate turbulence that may modulate predator-prey interactions. Turbulence reduces the ability of calanoid copepods to evade predation (Clarke et al., 2005; Gilbert and Buskey, 2005) which could provide a foraging advantage to planktivorous Pacific Herring. Turbulence may also impact the ability of fish to detect their own predators or may make prey capture more challenging for predatory fish (Higham et al., 2015). It is possible that turbulent flows influence predatory interactions between age-0 Pacific Herring and juvenile Chinook Salmon, however; it is uncertain whether predator or prey would be at an advantage. Tidal narrows are conspicuous features of the Salish Sea and other coastal areas of the Northeast Pacific. More work is required to understand the role of such sites in the trophic ecology of juvenile Chinook Salmon and their prey.

4.5. Unusual conditions in 2015

The North Pacific experienced an unprecedented heat wave from the winter of 2013–14 until the winter of 2015–16 (Di Lorenzo and Mantua, 2016). Sea surface temperatures in coastal British Columbia in 2015 were the highest of any year between 1935 and 2018 based on time series collected at coastal lighthouses (Chandler, 2019). Juvenile Chinook Salmon (Neville, 2017) and age-0 Pacific Herring (Boldt et al., 2018) were also larger than average in fall surveys conducted by DFO in the Strait of Georgia. Warm ocean conditions in the year of outmigration have been associated with poor smolt to adult survival of Pacific Salmon (Beamish et al., 2009; Sharma et al., 2013). However, escapements of adult Chinook Salmon to the Cowichan River in 2017 and 2018 (the two primary return years for fish sampled in this study) were in the top five returns from 1988 to 2019 (Kevin Pellett, DFO, unpublished data). These exceptional conditions raise questions about the generality of the results reported in the present study. At the scale of the Salish Sea, climate impacts stratification through effects on freshwater inputs, surface warming and wind mixing. The open water of the Strait of Georgia, which can be strongly stratified in summer (Journey et al., 2020), is an important rearing area for juvenile Pacific Salmon (Beamish et al., 2000; Beamish et al., 2011). Our study area in the Southern Gulf Islands was

sheltered from strong wind-driven mixing, and local variation in water column properties was primarily influenced by tidal mixing that would be consistent across interannual variation in ocean temperature. As stated earlier, the lack of a clear relationship between water column stratification and size, diet or growth of juvenile Chinook Salmon in the present study should not be interpreted as evidence that stratification, including climate driven variation in stratification, is not important at other spatial scales (Burke et al., 2013; Journey et al., 2018; Journey et al., 2020). While age-0 Pacific Herring were larger than average in 2015, mean lengths in fall surveys were shorter than in 4 years since 1992 (1998, 2005, 2007, and 2010; Boldt et al., 2018). Our key result of apparent size-dependence of predation by juvenile Chinook Salmon on age-0 Pacific Herring is therefore likely applicable beyond this one study year. Indeed, Chamberlin et al., 2017 hypothesized a link between size mediated foraging on Pacific Herring and growth advantages to large juvenile Chinook Salmon based on sampling conducted in Puget Sound in 2011. The present study is one step in a process of understanding juvenile Pacific Salmon marine ecology that will require the integration of multiple spatial and temporal scales, including interannual variation.

4.6. Conclusion

Juvenile Chinook Salmon are broadly distributed in coastal marine waters. Our results suggest that this distribution is not homogenous, even at fine spatial scales. Our failure to detect clear linkages between CPUE or characteristics of juvenile Chinook Salmon and local water column stratification and zooplankton abundance suggest that other factors may be more important in structuring juvenile Chinook Salmon habitat use at fine scales. Specifically, the importance of Pacific Herring in diets, combined with linkages between size, growth, catch location and piscivory, suggest that the distribution of forage fish may play a size dependent role in structuring how juvenile Chinook Salmon use their environment.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102512.

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