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ARTICLE

Stock-Specific Size and Migration of Juvenile Coho Salmon in British Columbia and Southeast Alaska Waters

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Abstract
The variation at 17 microsatellites was analyzed for 5,270 juvenile Coho Salmon *Oncorhynchus kisutch* obtained from coastal British Columbia and Gulf of Alaska surveys during 1998–2012. A 270-population baseline was used to determine the individual identifications of the fish sampled, with individuals being identified to 22 stocks of origin. Columbia River and Washington juveniles were consistently larger than those from British Columbia and Alaska. During June, the larger individuals within a stock were observed in more northerly locations. There was a relationship between the timing of northward migration and juvenile body size, with larger individuals migrating earlier than smaller individuals from the same stocks. Stock composition was more diverse in the northern sampling regions than in those in southern British Columbia. There was only a modest change in stock composition between fall and winter samples in both the Strait of Georgia and west coast of Vancouver Island sampling regions, indicating that juvenile migration had largely been completed by the fall. There was a wide divergence among stocks in juvenile size and dispersion among sampling locations.

Coho Salmon *Oncorhynchus kisutch* juveniles in the southern portion of the species' distribution usually reside in freshwater for a year or more, although some juveniles may rear in estuaries for a portion of their first summer and then move back upstream to overwinter (Miller and Sadro 2003) or migrate to the ocean during their first fall and early winter (Roni et al. 2012; Bennett et al. 2015). If juveniles remain in freshwater until their second spring, most subsequently migrate to the ocean, where they usually spend 6 (for male "jacks") to 18 months rearing before returning to their natal rivers to spawn.

Larger juvenile body size in salmonids in more northern locations has been reported previously (Hartt and Dell 1986; Jaenicke and Celewycz 1994; Farley et al. 2005; Tucker et al. 2009; Burke et al. 2013; Beacham et al. 2014a). Older and larger juvenile salmonids have been reported to migrate to the ocean earlier than other juveniles (Irvine and Ward 1989; Weitkamp et al. 2012). The greater presence of larger juveniles in more northern sampling regions may also reflect differences in juvenile size at the time of smolting and ocean entry, with larger individuals quickly commencing a northward migration while smaller ones rear for a period of time in local waters (Beacham et al. 2014a; Freshwater et al., in press). Even so, this does not preclude the possibilities that larger smolts swim faster or that juveniles encounter better growing conditions as they move farther north (Tucker et al. 2009). Thus, the occurrence of larger body sizes in northern

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locations may simply reflect larger individuals' ability to swim faster than smaller ones. Alternatively, it may be influenced by the higher-quality prey available in more northern areas (Mackas et al. 2004), resulting in higher growth rates for individuals in those areas.

The size of juveniles has been observed to influence the timing of northward migration (Beacham et al. 2014a; Freshwater et al., in press), and the wide variance in juvenile size among stocks may lead to diversity in the rates and times at which individual stocks undertake their general northward migrations. Size-selective mortality is thought to occur during the period of early marine residence, and juveniles must grow quickly to avoid such mortality (Beamish and Mahnken 2001; Hurst 2007; MacFarlane 2010; Duffy and Beauchamp 2011; Tomaro et al. 2012). Body size during the first year in the ocean can thus be an important factor in determining subsequent juvenile survival, and an evaluation of body size in different marine environments may provide some insight into early marine survival. Identification of the relative seasonal abundance of specific stocks in specific marine habitats will aid in evaluating the importance of mortality agents in shaping cohort abundance.

Previous assessments of the pattern of juvenile salmonid migration have indicated that juveniles move primarily northward upon ocean entry, following the continental shelf in a northwesterly direction (Hartt and Dell 1986; Fisher et al. 2007; Tucker et al. 2009, 2012). The reported migration patterns of juvenile Coho Salmon generally reflect this tendency (Morris et al. 2007), but Chittenden et al. (2009) reported some southerly movement upon exiting the Strait of Georgia. Morris et al. (2007) indicated that Coho Salmon stocks are composed of two components: a fast component that undertakes a rapid and direct northwesterly migration route upon entering the ocean and a slow component that migrates a relatively short distance from their natal rivers and resides over the continental shelf during the winter. Based on interceptions of coded-wire-tagged individuals in coastal fisheries, Weitkamp and Neely (2002) reported that Coho Salmon from different freshwater regions inhabited different areas of the coastal ocean. Although the fisheries occurred during the last few months of an 18-month ocean residence, these authors suggested that the differences begin earlier in the ocean residence period and that differences in ocean distribution have a large genetic component (Weitkamp and Neely 2002; Weitkamp 2011).

The routes and timing of juvenile Coho Salmon migrations have largely been inferred through the use of coded wire tags (CWTs) and are based on relatively few individuals. For example, Morris et al. (2007) reported on juvenile Coho Salmon migration based on the recovery of 914 CWTs spread over six large basins, with about half of the tags originating from hatcheries in Puget Sound, Washington. Stock-specific migration patterns in juvenile Chinook Salmon *O. tshawytscha* have also been reconstructed from 1,862 recovered CWTs by Trudel et al. (2009). With the increasing use of genetic stock identification techniques, however (Van Doornik et al. 2007; Tucker et al. 2011; Beacham et al. 2014a, 2014b; Weitkamp et al. 2015), individuals identified through genetic analysis can provide insights into the migration routes and timing of juvenile Coho Salmon.

It is important to determine the exact timing and direction of the general northward migration of juveniles because there may be links between both marine growth (Mueter et al. 2002; Quinn et al. 2005) and migratory behavior (Furey et al. 2015) and survival. Early marine conditions have been reported to be particularly important for Coho Salmon in the Salish Sea (Zimmerman et al. 2015) as well as in other local areas and ocean current systems (Hobday and Boehlert 2001; Teo et al. 2009; Kilduff et al. 2015).

The Strait of Georgia (SOG) in southern British Columbia and Puget Sound (PS) in northern Washington (Figure 1) are important rearing areas for juvenile Coho Salmon. Although there is no reported movement of juvenile Coho Salmon from the SOG southward into PS, depending on the year and time of year there is northward movement from PS, with 6–15% of the Coho Salmon in the SOG being reported as having originated in PS (Beamish et al. 2007, 2008). The migration of juveniles from the SOG to the west coast of Vancouver Island (WCVI) has been reported to occur a few months later than that of juveniles from PS to WCVI (Beamish et al. 2008; Chittenden et al. 2009). Beamish et al. (2007) have suggested that most juveniles leave PS in August, as evidenced by a 93% decrease in the catch rate from July to September, whereas Chittenden et al. (2009) have concluded that migration from the SOG occurs mainly in October and November.

Determination of the migratory routes of Coho Salmon requires several pieces of information: estimates of stock composition, catch per unit effort, area, and the rate of travel through the sampling regions, along with the vulnerability of juveniles to capture methods. This information is necessary to determine where most of the members of a stock are located at specific times, which in turn reveals their migration routes. In the current study, information on the stock composition and catch per unit effort was available on a seasonal basis for the sampling regions, but the area of these regions, the average rate of travel through them, and regional differences in gear vulnerability (there were no regional differences in size-dependent capture rates) were either not available or not considered. Thus, determination of the migratory pathways of juvenile Coho Salmon in our study is subject to these limitations.

In this study, we determined the size variation and stock compositions of catches of juvenile Coho Salmon along coastal British Columbia and Southeast Alaska and evaluated the migration paths of these fish. We specifically evaluated whether stocks from the same geographic region display size variation during migration as well as in their

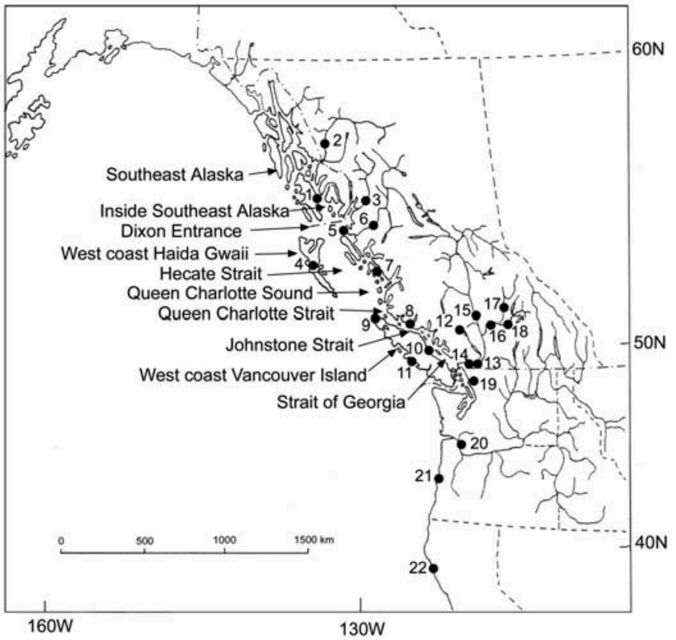

FIGURE 1. Map showing the locations of the 22 stocks of Coho Salmon identified in the study as well as the marine sampling regions. Stock names are listed in Table S.3. Queen Charlotte Strait and Johnstone Strait were combined as a single region, as were Hecate Strait and Dixon Entrance, providing a total of eight marine sampling regions for our analysis.

timing and routes, particularly for stocks from the Fraser River. We also investigated whether juvenile body size during early marine residence influenced the timing of northward migration. The analysis includes a comparison of the seasonal presence and body size of juvenile Coho Salmon in eight marine sampling regions ranging from southern British Columbia to Southeast Alaska. Migration routes and timing of juvenile migration were inferred from the presence or absence of specific stocks in the sampling areas as well as from stock-specific regional and seasonal catch-per-unit-effort indices of juvenile abundance. Seasonal stock compositions and abundance from the marine sampling areas were compared to evaluate the relative importance of different marine habitats during the first year of ocean residence.

METHODS

Sample collection.—In areas outside of the SOG, juvenile Coho Salmon were sampled by means of a midwater trawl during the period 1998–2012 (see Tucker et al. 2009 for the exact sampling locations and other details). Briefly, trawling was conducted between the shelf break and inshore to a minimum depth of 40 m. The trawl net had an opening approximately 30 m wide and 15 m deep, and the net was towed primarily at the surface at an average speed of 2.6 m/s (5 knots). Fork length (FL) was recorded for all of the juvenile salmon caught in a tow. Weight was measured directly on board the ship (to the nearest gram) for up to 30 sampled juveniles per tow. Tissue samples were collected for subsequent DNA analysis from the juveniles that were weighed. Catch per unit effort (CPUE) was determined as outlined by Beamish et al. (2010), where CPUE was defined as the number of juvenile Coho Salmon caught in a tow standardized to 1 h in duration. In the SOG, a similarly modified midwater trawl was the primary gear used to sample juvenile Coho Salmon between 1998 and 2012. Details of the trawl and methods of sampling are given in Beamish et al. (2000) and Sweeting et al. (2003). The net was towed at an average speed of 2.6 m/s at 15-m depth intervals, with the headrope at the surface, 15 m, and 30 m, resulting in fishing depths from the surface to 45 m. Only catches in tows conducted at the surface were included in the estimation of CPUE so that these data would be comparable to those from other regions of the coast. The catch from one tow during winter 2010 in which an unusually large number of Coho Salmon (over 15,000) were caught was not included in the estimation of seasonal CPUE. Catches were standardized as outlined previously. A sample of the Coho Salmon caught were measured (FL) and weighed (g), and tissue samples were collected from a portion of the juveniles sampled between 2005 and 2012 for DNA analysis.

The samples of juvenile Coho Salmon were grouped according to eight principal catch regions (Figure 1): (1) the Straits of Georgia and Juan de Fuca (SOG), (2) WCVI, (3) Johnstone and Queen Charlotte straits (JS–QCS), (4) Queen Charlotte Sound (QCS), including British Columbia mainland inlets south of 52°N, (5) Hecate Strait and Dixon Entrance, including British Columbia mainland inlets north of 52°N (hereafter, "Hecate Strait"), (6) the west coast of Haida Gwaii, (7) the inside waters of Southeast Alaska (hereafter "SEAK inside"), and (8) outside waters of Southeast Alaska east of 138°W ("SEAK outside"). The samples were also grouped by four principal seasons: spring (April–May), summer (June–August), fall (September–November), and winter (December–March). The number of samples analyzed for DNA variation is reported by catch region, season, and year of sampling in Table 1. The number of tows conducted in each region and season is shown in Supplementary Table S.1 available separately online, and the catch in each region and season is shown in Table S.2. For the analyses of the variation in length, the samples were grouped by month of capture, with June and October being chosen as the key months for this analysis. Movements from the SOG were evaluated by comparing the seasonal CPUE of all stocks in the SOG with that of stocks in the other catch regions.

In this study, juvenile Coho Salmon were defined as those caught during their first complete year of ocean residence.

TABLE 1. Annual number of juvenile Coho Salmon identified to population or stock for individuals sampled in eight geographic regions and four seasons. The regions were the Straits of Georgia and Juan de Fuca (SOG), west coast of Vancouver Island (WCVI), Johnstone Strait and Queen Charlotte Strait (JS–QCS), Queen Charlotte Sound (QCS), Hecate Strait (Hecate), west coast of Haida Gwaii (HG), inside waters of Southeast Alaska (SEAK inside), and outside waters of Southeast Alaska (SEAK outside).

Year	SOG	WCVI	JS–CS	QCS	Hecate	HG	SEAK inside	SEAK outside
Spring								
1999					1		21	
2009	35							
Total	35				1		21	
Summer								
1998		27	3	8			91	2
1999		86		4				
2000		154		2	14			3
2001		156		42	8	2		65
2002	1	72			3		1	
2003		92						4
2004		97			16			42
2005		64			38			14
2006	86	159		19	78	12		72
2007	83	13			5			3
2008	76	40		5	40	5		
2009	384	57	10		24	7		
2010	9	47	11	5	32	1		
2011	5	47	11	10	34	5		
Total	644	1111	35	95	292	32	92	205
Fall								
1998		75		2	35			26
1999		71						91
2000		60		32	94		27	25
2001		53	4	48	49		32	28
2002		74			25		12	25
2003		1		2	1		1	
2004		59			39		4	18
2005		19			73		2	6
2006	73				0			1
2007	47	1		1	1			
2008	93	17		8	46		18	46
2009	377	46	12	2	37		1	
2010	20	42		2	5		5	
2011		6	2		5			
2012	8	25	9		4			
Total	618	549	27	97	414		102	266
Winter								
2001		125						
2002	59	44	3					
2003		69						
2004		48						
2005		42			1			
2006		40			9		1	
2007	28	4						
2008	10							
2009	9	1						
2010	112	19						
2011	1	8	1					
Total	219	400	4	0	10	0	1	0

Samples collected from June through October may contain two year-classes of Coho Salmon. For example, during June in the SOG, individuals that had entered the ocean in the current year (having spent one winter in freshwater, i.e., of age 1.0) were defined as those with fork lengths ≤320 mm, whereas individuals that had already spent one winter in the ocean (age 1.1) were defined as those with fork lengths >320 mm (Figure 2A). In July, a fork length of 330 mm was used to separate Coho Salmon in their first ocean year from those that were in their second ocean year (Figure 2B), with the value revised to 400 mm for September samples (Figure 2C) and 420 mm for October samples (Figure 2D). The age-classes were separated in the analyses of the variation in size and stock composition.

Stock identification.—The genetic markers surveyed depended on the year in which the samples were received. Samples received between 1999 and 2001 were analyzed with a suite of eight microsatellite loci and two linked exons (α1 and α2) of major histocompatibility complex (MHC) loci as outlined by Beacham et al. (2001). Samples received from 2002 onward were analyzed with a suite of 17 microsatellite loci (Beacham et al. 2012). Microsatellites were surveyed with either an ABI 377 gel DNA sequencer (prior to 2005) or an ABI 3730 capillary DNA sequencer (2005 and after), and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, California) using an internal lane sizing standard, as outlined by Beacham et al. (2012). Allele identifications between the two sequencers were standardized by analyzing approximately 600 individuals on both platforms and converting the sizing from the gel-based ABI 377 platform to match that obtained from the capillary-based ABI 3730 platform, as outlined by Beacham et al. (2012).

The microsatellite baseline used for estimating stock compositions was derived from a survey of about 49,125 Coho Salmon from 270 populations arranged into 22 reporting groups or stocks from Southeast Alaska, British Columbia,

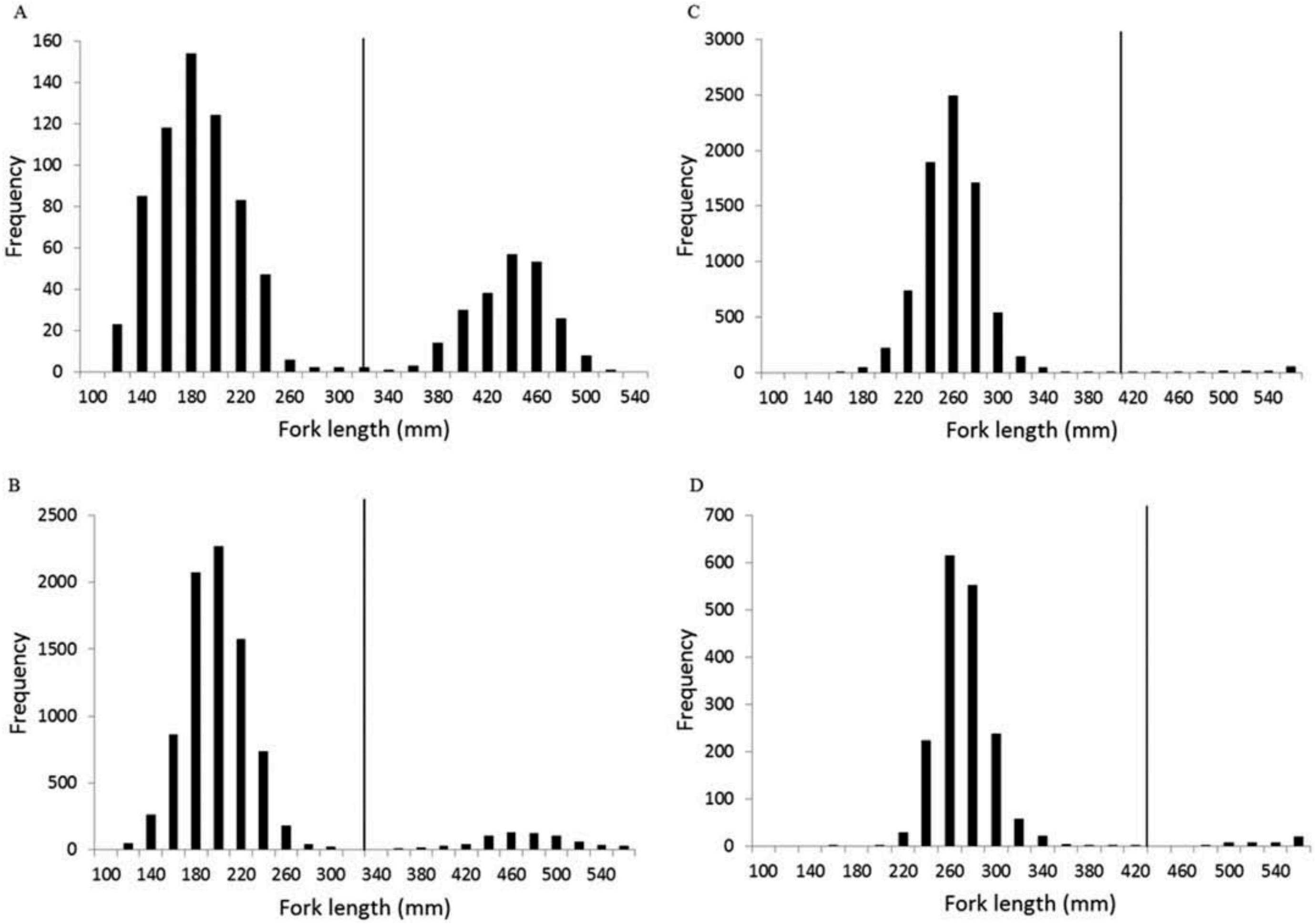

FIGURE 2. Observed fork length frequencies for Coho Salmon sampled in the Strait of Georgia during **(A)** June, **(B)** July, **(C)** September, and **(D)** October. Lengths of 320, 330, 400, and 420 mm, respectively, in the four months (vertical lines) were deemed to distinguish individuals in their first year of ocean rearing from those in their second year.

Washington, the Columbia River, Oregon, and California, as shown in Table S.3. All of the Coho Salmon originating from California were defined as a single stock, as were those from Oregon and the Columbia River. For Washington, the Coho Salmon originating from PS were combined with those from coastal Washington into a single stock. The specific populations assigned to the 22 stocks are shown Table S.3. MHC α1 allele frequencies were not available for one population from Oregon (Alsea River), and MHC α2 allele frequencies were not available from three Oregon populations (Alsea River, Siltcoos Lake, and Yaquina River). Weighted (by sample size) mean regional allele frequencies for the Oregon populations were determined for the α1 and α2 exons, and imputed allele frequencies for the three populations were scaled to a sample size observed at the microsatellites. The baseline population allele frequencies and mixed-stock juvenile multilocus genotypes are listed by Fisheries and Oceans Canada's Molecular Genetics Laboratory at http://www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.html.

Analysis of the samples was conducted by means of a Bayesian procedure (BAYES) outlined by Pella and Masuda (2001) with a modified version of the program developed as a C-based program (http://www.pac.dfo-mpo.gc.ca/sci/mgl/Cbayes_e.htm). In the analysis, eight 20,000-iteration Monte Carlo–Markov chains of estimated stock compositions were produced, with the initial values for each chain being set at 0.90 for a particular population (which was different for each chain). Estimated stock compositions were considered to have converged when the shrink factor was <1.2 for the eight chains (Pella and Masuda 2001). The last 1,000 iterations from each of the eight chains were then combined, and the probability of each fish's originating from each population in the baseline was determined. Each individual was assigned to the population for which we estimated that it had the highest probability of correct assignment. We used a probability of 50% as the lower limit in assigning individuals to a specific reporting group or population (Tucker et al. 2009; Beacham et al. 2014a). The specific populations incorporated in each of the reporting groups are shown in Table S.3. Additional details on the accuracy of the stock identification analysis are outlined for a pooled group of population samples not included in the baseline (Table S.4) and a sample of coded-wire-tagged Coho Salmon derived from both fishery sampling (Beacham et al. 2001) and marine juvenile sampling (Table S.5).

Mean juvenile fork lengths and SDs were determined for the 22 reporting groups or stocks by sampling month and region. Monthly information on the mean lengths of juveniles from the stocks in the eight principal catch regions provided indications of the ocean distributions of different-sized individuals from the same cohort. The migration patterns of specific stocks were inferred from the presence or absence of juveniles in the available samples from the catch regions as well as the stock-specific CPUEs in those regions. Correlation (Microsoft Office Excel) and chi-square analysis were used to test for nonrandom geographic distributions of the captured fish.

Mean fork length was compared among regions using a generalized linear model (GLM) (McCullagh and Nelder 1983). Regions were nested within reporting groups to account for size differences among the reporting groups and entered into the regression models as a series of dummy variables, with QCS serving as the reference region in the analysis. In this analysis, regions were treated as fixed effects and reporting groups were treated as random effects. The variance was modeled using the Gaussian family distribution with the identity link function. Regions were deemed significant when P-values were less than 0.05. These analyses were carried out in R using the lmerTest package (R version 3.1.2).

We employed complementary multivariate techniques to explore the variation in the seasonal and regional stock compositions for the eight catch regions. Eight summer, seven fall, and two winter estimates of stock composition were available from the eight regions. The estimates for the California coastal and Oregon coastal stocks were combined for the analysis, as were those for the North Thompson, South Thompson, and Lower Thompson River stocks (the "Thompson River" stock), those for the lower Fraser, Birkenhead, and Chilliwack River stocks (the "lower Fraser River" stock), and those for the north coast and Nass River stocks. Hierarchical agglomerative clustering based on Ward's linkages was used to examine which mixed-stock regional and seasonal compositions most closely resembled each other. Ward's method joins cases into clusters such that the variance within a cluster is minimized. Nonmetric multidimensional scaling (MDS) and analysis of variance using distance matrices (adonis function; Vegan Community Ecology Package version 2.0–5; Vegan Community Ecology Package, R package version 1.17–8; http://CRAN.R-project.org/package=vegan) were used to test for temporal and spatial differences in mixed-stock composition. These analyses all employed resemblance matrices constructed using pairwise Bray–Curtis similarities (S). In this application, Bray–Curtis similarity ranges from 0 (no overlap in mixed-stock composition) to 1 (identical mixed-stock composition). Nonmetric MDS is a ranking technique based on a set of similarity coefficients, which places points in two-dimensional MDS space in relation to their similarity (i.e., points farther apart are less similar than those closer together). The nonmetric MDS uses an iterative process to find the best (minimum) solution; each run consisted of 50 iterations with random starting locations. Minimum stress (a measure of agreement between the ranks of similarities and distances in two-dimensional MDS space) was attained in multiple iterations of each run, while multiple runs of each data set produced similar configurations, suggesting that the true global minimum solutions were attained. Analysis of variance using distance matrices was employed to test for regional and seasonal differences in the mixed-stock compositions. The function adonis can handle both continuous and factor predictors and uses permutation tests with pseudo *F*-ratios to determine the significance of those partitions; we used 10,000 permutations. All analyses were done in R version 3.1.2.

RESULTS

Body Size

The earliest month of sample collection after juveniles migrated to the ocean was May, but sampling during this period was limited and SOG samples were derived from a regional purse seine survey (Table 1). The individuals in these samples reflected recent entry into the ocean from local stocks. For example, in the SOG most of the individuals sampled were from the east coast of Vancouver Island (ECVI; *n* = 33, FL = 122.8 mm [SD = 13.1]), though single individuals of Chilliwack River (111 mm) and lower Fraser River origin (113 mm) were also observed. In inside Southeast Alaska waters, individuals from Southeast Alaska were the predominant ones observed (*n* = 19, FL = 135.8 mm [10.4]), with Skeena River individuals also being observed (*n* = 2, FL = 137.0 mm [17.0]).

A north–south gradient was apparent in mean juvenile FL, with larger Coho Salmon being caught in northern regions (Figure 3). The GLM indicated that in June the mean FL (relative to that of QCS fish) within reporting groups was significantly lower for juvenile Coho Salmon caught in the SOG ($t = -6.3$, $P < 0.0001$) and off WCVI ($t = -2.1$, $P < 0.05$) and significantly higher for those caught in SEAK outside ($t = 4.2$, $P < 0.0001$). The mean FL of Washington-origin juveniles sampled during June in the SOG (likely fish of PS origin; Beamish et al. 2007, 2008) was 177 mm, while those of fish sampled from WCVI, QCS, Hecate Strait, and SEAK outside were 196, 203, 224, and 232 mm, respectively (Table 2). Of the 18 stocks observed in the June sampling, individuals from 11 of these stocks were observed off Southeast Alaska, and the mean FL of these individuals was typically the largest for each stock over the sampling regions in which individuals from that stock were observed. In northern sampling areas such as Hecate Strait, larger FLs were observed in individuals that originated from populations or stocks in more southern latitudes, with smaller body sizes usually being observed in proximate local stocks (Table 2).

However, not all juveniles may migrate in a northerly direction during their first summer of marine residence. In June, juveniles from the central coast of British Columbia were observed off WCVI with a mean FL (*n* = 42, FL = 167.0 mm) almost identical to that of fish in the more proximate QCS (*n* = 5, FL = 167.6 mm) (Table 2), which suggests an initially southern migration route for a component of the stock. That same month, juveniles from the central coast stock were also observed farther north in the Hecate Strait (*n* = 113, FL = 201.4 mm) and Southeast Alaska (*n* = 54, FL = 202.7 mm) sampling regions, but these individuals were larger than those observed in the WCVI region.

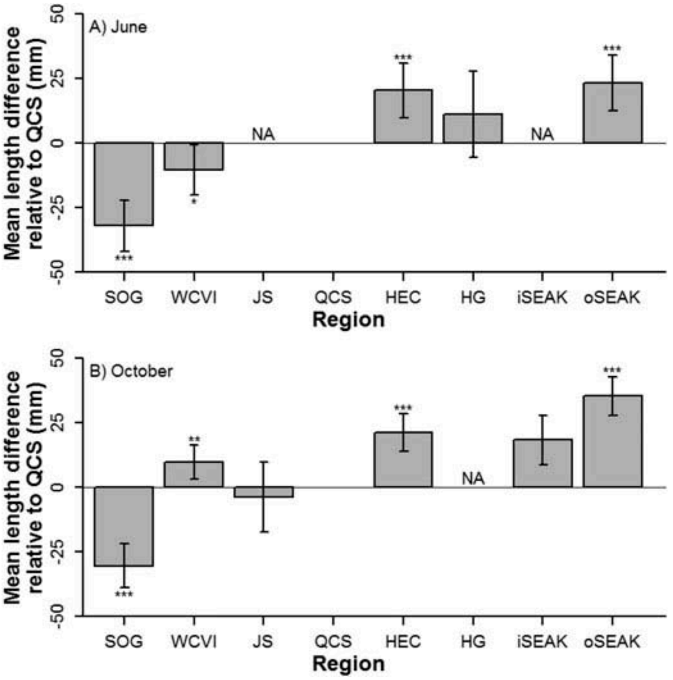

FIGURE 3. Mean differences in fork length between juvenile Coho Salmon caught in different regions relative to those caught in Queen Charlotte Sound in **(A)** June and **(B)** October. Abbreviations are as follows: SOG = Strait of Georgia, WCVI = west coast of Vancouver Island, JS = Johnstone Strait, QCS = Queen Charlotte Strait, HEC = Hecate Strait, HG = Haida Gwaii, iSEAK = inside waters of Southeast Alaska, and oSEAK = outside waters of Southeast Alaska. Regions geographically south of QCS are to the left of QCS on the *x*-axis, regions to the north are on the right. Some differences were significant at varying levels: $P < 0.05$*, $P < 0.005$**, $P < 0.0005$***.

Within sampling regions, juveniles increased in body size during the summer. For example, in the WCVI region, juveniles from the Columbia River increased in both length and weight from June (*n* = 227; FL = 203.3 mm [SD = 26.0], weight = 100.8 g [34.9]) to July (*n* = 72; FL = 211.8 mm [21.7], weight = 114.5 g [37.0]) and August (*n* = 26; FL = 242.1 mm [24.5], weight = 174.6 g [50.3]). Similarly, juveniles from Washington increased from June (*n* = 233; FL = 195.8 mm [30.2], weight = 95.0 g [48.5]) to July (*n* = 61; FL = 201.2 mm [38.1], weight = 110.3 g [72.3]) and August (*n* = 57; FL = 250.1 mm [37.7], weight = 203.8 g [86.1]). Similar trends were also observed in the northern sampling regions. For example, in SEAK outside, juveniles from the Columbia River increased from June (*n* = 19; FL = 224.4 mm [17.4], weight = 132.9 g [39.2]) to August (*n* = 7; FL = 276.2 mm [16.9], weight = 262.1 g [15.5]). The same was true for juveniles from Washington, which increased from June (*n* = 18; FL = 231.6 mm [13.8], weight = 149.3 g [30.1]) to August (*n* = 6; FL = 271.2 mm [11.6], weight = 250.7 g [30.5]). In June, the differentials in size between the SEAK and WCVI

TABLE 2. Regional sample size (*N*) and mean FL (mm; SDs in parentheses) for 22 stocks of Coho Salmon sampled in June 1998–2011. The regional sampling locations were the Strait of Georgia (SOG), west coast Vancouver Island (WCVI), Queen Charlotte Sound (QCS), Hecate Strait (Hecate), and Southeast Alaska (SEAK) outside waters. Stocks with no estimated presence of juveniles are not listed. Dashes indicate that it was not possible to compute an SD because only one fish was sampled.

	SOG		WCVI		QCS		Hecate		SEAK outside	
Stock	*N*	FL	*N*	FL	*N*	FL	*N*	FL	*N*	FL
Oregon coastal			29	198.6 (26.0)			5	233.8 (31.0)	23	236.0 (21.5)
Columbia River			227	203.3 (21.8)			10	229.9 (24.4)	19	224.4 (17.4)
Washington	74	176.9 (26.7)	233	195.8 (30.2)	4	202.8 (21.1)	15	223.9 (26.6)	18	231.6 (13.8)
South Thompson River	4	158.8 (20.5)								
North Thompson River	1	179.0 (-)								
Lower Thompson River	1	141.0 (-)								
Fraser River, lower	98	168.2 (31.3)	2	156.5 (2.1)	2	183.5 (16.3)			1	223.0 (-)
Fraser River, middle	3	163.7 (37.1)								
Chilliwack River	21	172.8 (24.6)								
Birkenhead River	9	161.0 (33.9)								
West coast Vancouver Island	9	141.0 (23.2)	152	176.9 (31.4)	2	186.5 (0.7)	3	196.0 (22.1)	7	223.0 (20.0)
East coast Vancouver Island	132	160.4 (36.9)	6	197.0 (41.4)	2	190.5 (12.0)	6	213.2 (13.2)		
North coast Vancouver Island			89	169.1 (26.6)	2	153.5 (16.3)	8	216.0 (35.6)	3	212.0 (15.7)
South coast	22	170.2 (28.7)	16	184.4 (38.9)	4	182.0 (6.2)	23	202.1 (28.7)	9	209.6 (30.9)
Central coast			42	167.0 (31.3)	5	167.6 (11.5)	113	201.4 (32.2)	54	202.7 (21.6)
Skeena River							7	178.9 (46.7)	1	227.0 (-)
Haida Gwaii							37	191.8 (30.3)	1	207.0 (-)
Southeast Alaska							4	197.3 (11.8)	4	227.3 (13.0)

sampling regions were 21.1 mm and 32.1 g for the Columbia River stock, with larger individuals being observed in SEAK. The differentials for the Washington stock between the two regions were 35.8 mm and 54.3 g, with larger individuals again being observed in the northern region. In August, the differentials between the two regions were 34.1 mm and 87.5 g for the Columbia River stock and 21.1 mm and 46.9 g for the Washington stock. Thus, in August, the size difference between juvenile Coho Salmon from the Columbia River and Washington persisted in both the northern and southern sampling regions. The size differentials between the two regions were observed in other stocks with similar regional trends.

In October, the trend of increasing juvenile Coho Salmon body size from southern to northern sampling regions was still observed (Table 3; Figure 3B). The mean FL (relative to that in QCS) within reporting groups was significantly lower for juvenile Coho Salmon caught in the SOG (t = –5.0, P < 0.0001) but significantly larger for those caught off WCVI (t = –2.1, P < 0.05), in Hecate Strait (t = 5.7, P < 0.0001), in SEAK inside (t = 4.9, P < 0.0005), and in SEAK outside (t = 9.2, P < 0.0001). For example, the body size differentials between the WCVI and SEAK outside sampling regions were 8.3 mm and 11.1 g for the Columbia River stock, 24.6 mm and 22.3 g for the Washington stock, 15.5 mm and 38.3 g for the WCVI stock, 31.8 mm and 92.4 g for the south coast stock, and 28.9 mm and 73.8 g for the central coast stock. Generally, body size increased over time, and within sampling months larger juveniles were typically found in more northern locations; this trend continued until at least March of the year following initial ocean entry (Table 4). However, by March, there was little geographic variation in juvenile body size, with the mean FL of most individuals falling between 300 and 350 mm.

Seasonal and Regional Stock Compositions

In the spring sampling period, juvenile Coho Salmon were only caught in two sampling regions: the SOG and SEAK inside. In the SOG, individuals of ECVI origin dominated the catch during May (n = 35), with 94% being of ECVI origin, 3% of Chilliwack River origin, and 3% from the lower Fraser River, but as these samples were derived from a regional purse seine survey they may not be representative of the entire SOG. In SEAK inside (n = 21), the May catch was exclusively of individuals of Southeast Alaska (91%) and Skeena River (9%) origin. As expected, juveniles originated from areas proximate to the sampling regions.

In summer sampling in the SOG, all of the stocks observed in appreciable quantities originated from areas proximate to the SOG. For example, the ECVI stock comprised 27.1% of the 644 juveniles analyzed for DNA variation, while the lower Fraser River stock comprised 26.7%, the Washington stock 18.4%, the south coast stock 8.6%, the Chilliwack River stock 7.7%, and the three stocks from the Thompson River 4.6% (Table 5). However, nonlocal stocks were present in the WCVI region, as the summer catch of 1,111 juveniles was comprised of 30.8% Washington stock, 29.9% Columbia River stock, and 4.4% of Oregon stock. Local stocks, such the WCVI (17.2%) and north coast of Vancouver Island (10.2%) stocks were also present, along with a small number from the central coast stock (3.8%). There was little evidence of any juveniles from the seven stocks in the Fraser River drainage having moved to the WCVI region in the summer (0.2% contribution), but a small contribution from the ECVI stock was observed (1.1%). However, there was evidence that juveniles from the ECVI stock had moved into the JS–QCS sampling region (33.3% of the 35 juveniles sampled) along with Fraser River stocks, primarily the Chilliwack River (12.4%) and lower Fraser River (7.9%) stocks (Table 5). Juveniles from Washington comprised 10.4% of those sampled, likely having migrated north through Johnstone Strait. Fish from the Columbia River stock (1.9%) that were present in this region were concentrated in the Queen Charlotte Strait samples (adjacent to Queen Charlotte Sound at the northern end of Vancouver Island; Figure 1). The main components of the catch (n = 95) in QCS were the local central coast stock (15.0%), the WCVI stock (11.3%), and the ECVI stock (16.9%), the latter likely having moved into the region through Johnstone Strait. Juveniles of Fraser River origin were also present, primarily the lower Fraser (9.7%) and Chilliwack River (2.6%) stocks, as was observed in JS–QCS. Washington (7.8%), Columbia River (13.7%), and Oregon coastal (5.0%) stocks were also estimated to be present, with juveniles of U.S. origin comprising 26.5% of those identified in the sampling region.

Stock composition was more diverse in the northern sampling regions than in southern British Columbia. For example, off the west coast of Haida Gwaii the local-origin stock dominated the catch sample (n = 32 [44.7%]), not having previously been observed in more southern sampling regions. Juveniles from the south coast (21.0%) and WCVI stocks (13.9%) were also present (Table 5). In the more coastal Hecate Strait sampling region, the local central coast (n = 292 [40.4%]) and Haida Gwaii stocks (22.9%) were the main components of the catch, with some contributions from the south coast (11.9%), Washington (4.8%), Columbia River (4.1%), and Oregon coastal (2.4%) stocks. In the Southeast Alaska sampling regions, there was a clear difference in stock composition between the inside waters and the offshore waters. The Skeena River stock (n = 92 [10.4%]) and the Alsek–Stikine River stock (11.9%) were present in higher proportions in inside waters than in offshore waters (n = 205 [2.5% and 0.0%, respectively]). Conversely, the Washington (12.5%), and Oregon coastal (12.9%) stocks were present in higher proportions in offshore waters (2.4 and 1.3%, respectively). The central coast stock dominated both the inside (37.8%) and offshore sampling regions (34.3%) (Table 5).

As with the summer sampling, fall sampling in the SOG (n = 618) revealed that all of the stocks observed in appreciable quantities originated from areas proximate to the SOG, with the lower Fraser River (24.4%), Washington (19.5%), south coast (16.5%), and ECVI stocks (13.1%) being the main

TABLE 3. Regional sample size (*N*) and mean FL (mm; SDs in parentheses) for 22 stocks of Coho Salmon sampled in October 1998–2011. See the caption to Table 2 for additional information.

	SOG		WCVI		Hecate		SEAK inside		SEAK outside	
Stock	*N*	FL	*N*	FL	*N*	FL	*N*	FL	*N*	FL
Oregon coastal			16	308.3 (32.4)					3	326.0 (26.2)
Columbia River			25	308.3 (33.7)	7	321.6 (19.6)	1	344.0 (-)	8	316.6 (21.2)
Washington	47	250.5 (24.1)	159	292.0 (29.0)	13	298.1 (28.9)	3	305.0 (34.6)	8	316.6 (17.7)
North Thompson River			1	288.0 (-)						
Lower Thompson River									1	313.0 (-)
Fraser River, middle			1	320.0 (-)	1	306.0 (-)				
Fraser River, lower	7	249.4 (35.9)	19	286.6 (37.7)						
Chilliwack River			2	286.0 (8.5)	4	286.3 (16.2)				
Birkenhead River	2	264.5 (7.8)	2	285.5 (34.6)						
West coast Vancouver Island	1	311.0 (-)	99	286.3 (28.8)	8	306.4 (17.9)	2	286.5 (6.4)	10	301.8 (24.7)
East coast Vancouver Island	5	231.4 (25.1)	53	292.0 (30.8)	10	300.4 (25.9)	1	309.0 (-)	2	338.5 (20.5)
North coast Vancouver Island			81	270.3 (36.8)	6	291.7 (25.2)			6	320.2 (36.0)
South coast	9	250.9 (28.6)	30	281.6 (33.7)	21	299.3 (21.5)	4	296.5 (45.6)	20	313.4 (25.9)
Central coast			10	284.7 (34.8)	57	296.0 (30.0)	14	283.2 (40.7)	55	313.6 (21.0)
Skeena River			1	264.0 (-)	51	291.2 (22.2)	5	307.6 (39.4)	33	301.1 (22.6)
Nass River					23	291.7 (18.3)	13	293.4 (30.2)	11	314.4 (28.0)
Alsek–Stikine River					8	281.3 (26.3)	13	293.4 (31.0)	30	315.7 (24.8)
Haida Gwaii					42	309.3 (22.0)			9	303.9 (18.3)
Southeast Alaska					4	266.5 (44.3)	10	302.4 (23.1)	32	307.4 (21.3)

TABLE 4. Estimated fork length (SDs in parentheses) for juvenile Coho Salmon sampled during November, February, and March in seven geographic regions. See the captions to Tables 1 and 2 for additional information.

Stock	Region	*N*	November	*N*	February	*N*	March
California coastal	SOG			1	411.0 (-)		
Oregon coastal	SOG			5	350.8 (33.5)		
	WCVI	1	305.0 (-)	2	330.0 (5.7)		
	Hecate	1	284.0 (-)			1	410.0 (-)
	SEAK	1	323.0 (-)				
Columbia River	SOG			1	311.0 (-)		
	WCVI			2	326.0 (26.9)	4	359.5 (5.4)
	Hecate	2	382.5 (43.1)				
	Inside	1	384.0 (-)				
	SEAK	2	342.0 (18.4)				
Washington	SOG	4	263.0 (40.3)	53	319.5 (24.9)	8	306.0 (20.5)
	WCVI	6	320.7 (30.6)	46	322.6 (33.7)	46	343.8 932.8)
	Hecate	5	330.2 (49.6)				
	SEAK	1	330.0 (-)				
North Thompson River	SOG			2	310.0 (22.6)		
South Thompson River	SOG			1	326.0 (-)		
Lower Thompson River	SOG			2	311.5 (3.5)		
	JS/QCS	1	294.0 (-)				
	WCVI			1	330.0 (-)	1	297.0 (-)
Fraser River, middle	SOG			1	329.0 (-)		
Fraser River, lower	SOG		314.0 (-)	46	327.8 (16.2)	1	339.0 (-)
	JS/QCS			1	267.0 (-)	1	323.0 (-)
	WCVI	1	323.0 (-)	11	318.7 (35.5)	13	329.4 (24.6)
Chilliwack River	SOG	1	287.0 (-)	23	325.5 (15.0)		
	WCVI	1	328.0 (-)			3	308.7 (34.8)
	Hecate	1	302.0 (-)				
Birkenhead River	SOG			8	325.6 (25.4)	1	291.0 (-)
	WCVI			2	307.0 (35.4)		
	JS/QCS	2	270.0 (36.8)				
West coast Vancouver Island	WCVI	2	305.0 (26.9)	11	322.3 (31.8)	19	345.5 (21.3)
	Hecate	4	318.8 (35.6)				
	Inside	1	285.0 (-)				
	SEAK	1	347.0 (-)				
East coast Vancouver Island	SOG	2	251.5 (23.3)	21	319.6 (14.2)	1	314.0 (-)
	WCVI	1	335.0 (-)	23	322.9 928.0)	34	346.0 (26.4)
	Hecate	3	337.3 (25.3)				
North coast Vancouver Island	SOG			2	300.5 (55.9)		
	WCVI	19	231.8 (31.9)	46	310.2 (34.3)	41	321.2 (30.6)
	Hecate	3	328.3 (29.0)				
	SEAK	1	330.0 (-)				
South coast	SOG	1	266.0 (-)	17	324.5 (27.6)	1	340.0 (-)
	WCVI	2	267.5 (30.4)	15	322.8 (34,7)	36	321.5 (50.2)
	JS/QCS	1	251.0 (-)			1	314.0 (-)
	Hecate	6	326.8 (48.0)			2	331.0 (52.3)
	SEAK	1	300.0 (-)				
Central coast	WCVI			21	307.0 (24.2)	17	321.9 (39.6)
	Hecate	40	329.4 (39.5)			2	391.0 (26.9)
	Inside	5	311.4 (12.6)				
	SEAK	10	334.8 (18.6)				

TABLE 4. Continued.

Stock	Region	*N*	November	*N*	February	*N*	March
Skeena River	Hecate	35	318.4 (35.1)				
	Inside	2	293.0 (52.3)				
	SEAK	2	319.5 920.5)				
Nass River	WCVI			1	321.0 (-)	1	333.0 (-)
	Hecate	13	317.7 (27.1)			1	405.0 (-)
	Inside	3	290.7 (29.1)				
	SEAK	2	335.0 (38.2)				
Haida Gwaii	Hecate	36	332.5 (28.1)				
	SEAK	1	360.0 (-)				
Alsek–Stikine River	Hecate	9	306.6 (27.1)				
	Inside	6	292.8 (22.8)				
	SEAK	2	302.0 (35.4)				
Southeast Alaska	WCVI			2	329.0 (72.1)	1	302.0 (-)
	Hecate	1	253.0 (-)				
	Inside	6	313.0 (54.8)				
	SEAK	1	325.0 (-)				

contributors to the catch (Table 6). Fall sampling in the WCVI region (n = 549) revealed that the Washington stock was the most abundant (28.8%), but unlike in the summer sampling the ECVI stock (10.6%; $\chi^2 = 79.6$, df = 1, $P < 0.01$) and the three lower Fraser River stocks (the Birkenhead, Chilliwack, and lower Fraser river; 4.5%; $\chi^2 = 42.7$, df = 1, $P < 0.01$) were more abundant in this sampling region. In JS–QCS (n = 27), the central coast (25.3%), ECVI (18.3%), and lower Fraser River stocks (12.8%) were the most abundant ones, though the three Thompson River stocks comprised 7.8% of the catch. In the QCS region (n = 97), the ECVI (27.7%) and south coast stocks (25.7%) comprised the majority of the catch, but the central coast (15.1%), Chilliwack River (8.3%), and lower Fraser River stocks (7.7%) were also present, as were the Washington (5.0%) and Oregon coastal stocks (1.5%).

As in the summer, the fall stock compositions were more diverse in the northern sampling regions (Hecate Strait, SEAK inside, and SEAK outside) than in the southern regions. Northern stocks (Southeast Alaska to Skeena River) were only observed in the northern sampling regions (Table 6). By way of example, the Skeena River ($\chi^2 = 207.8$, df = 1, $P < 0.01$) and Nass River stocks ($\chi^2 = 108.4$, df = 1, $P < 0.01$) were significantly more prevalent in northern sampling regions.

In winter sampling, the largest contributors to the catch in the WCVI region (n = 400) were the southern-origin Washington (22.1%), north coast of Vancouver Island (20.3%), ECVI (14.3%), south coast (13.4%), and WCVI (8.8%) stocks (Table 7). When Coho Salmon were available in the SOG (n = 222), the Washington stock was again the most dominant (29.7%), followed by the lower Fraser River (24.1%), Chilliwack River (12.0%), ECVI (10.6%), south coast (10.2%), and Birkenhead River stocks (5.7%). Stock composition was similar between the fall and winter sampling periods in the two regions, with the fall and winter WCVI estimates of stock composition clustering together, as did the fall and winter estimates from the SOG (Figure 4). For example, for the more abundant stocks in the WCVI region, there was no significant difference in the proportions of the EVCI (10.6% in fall versus 14.3% in winter; $\chi^2 = 3.0$, df = 1, $P > 0.05$) and north coast Vancouver Island stocks (18.7% versus 20.3%; $\chi^2 = 0.3$, df = 1, $P > 0.05$), limited differences for the Washington (28.8% versus 22.1%; $\chi^2 = 5.3$, df = 1, $0.01 < P < 0.05$) and Columbia River stocks (4.6% versus 1.4%; $\chi^2 = 5.6$, df = 1, $0.01 < P < 0.05$), and somewhat greater differences for the south coast (6.7% versus 13.4%; $\chi^2 = 5.6$, df = 1, $P < 0.01$) and WCVI stocks (18.7% versus 8.8%; $\chi^2 = 5.6$, df = 1, $P < 0.01$). In the SOG, there were no significant seasonal differences between the fall and winter proportions among the ECVI (13.1% versus 10.6%; $\chi^2 = 0.8$, df = 1, $P > 0.05$), lower Fraser River (24.4% versus 24.1%; $\chi^2 = 0.0$, df = 1, $P > 0.05$), Birkenhead River (5.1% versus 5.7%; $\chi^2 = 0.1$, df = 1, $P > 0.05$), and South Thompson River stocks (2.3% versus 1.0%; $\chi^2 = 0.1$, df = 1, $P > 0.05$), limited differences for the south coast (16.5% versus 10.2%; $\chi^2 = 4.8$, df = 1, $0.01 < P < 0.05$) and Chilliwack River stocks (5.5% versus 12.0%; $\chi^2 = 6.2$, df = 1, $0.01 < P < 0.05$), and somewhat greater differences for the Washington (19.5% versus 29.7%; $\chi^2 = 6.2$, df = 1, $P < 0.01$) and middle Fraser River stocks (4.2% versus 0.4%; $\chi^2 = 7.4$, df = 1, $P < 0.01$) stocks.

TABLE 5. Estimated percentages by stock for juvenile Coho Salmon sampled during June, July, and August in eight geographic regions. The values in parentheses immediately below the region acronyms are sample sizes; the values in parentheses within the body of the table are SDs. The acronym WCHG stands for the west coast of Haida Gwaii; other abbreviations are as in previous tables.

Stock	SEAK (205)	SEAK inside (92)	Hecate (292)	WCHG (32)	QCS (95)	JS–QCS (35)	WCVI (1,111)	SOG (644)
Southeast Alaska	2.8 (2.4)	14.2 (4.0)	1.6 (1.0)	8.3 (6.0)	0.0 (0.3)	0.4 (1.4)	0.0 (0.0)	0.0 (0.0)
Alsek–Stikine River	0.0 (0.2)	11.9 (4.6)	0.0 (0.2)	0.0 (0.4)	0.0 (0.2)	0.0 (0.2)	0.0 (0.0)	0.1 (0.2)
Nass River	0.1 (0.4)	1.5 (3.4)	0.0 (0.1)	0.0 (0.3)	0.0 (0.3)	0.0 (0.5)	0.1 (0.1)	0.0 (0.0)
Haida Gwaii	1.9 (1.2)	0.6 (1.3)	22.9 (2.6)	44.7 (9.1)	0.0 (0.4)	0.1 (1.0)	0.0 (0.0)	0.1 (0.2)
North coast	0.0 (0.1)	0.0 (0.1)	0.5 (0.5)	0.0 (0.2)	0.0 (0.1)	0.0 (0.4)	0.0 (0.0)	0.0 (0.2)
Skeena River	2.5 (1.9)	10.4 (3.8)	2.7 (1.1)	0.0 (1.1)	0.1 (0.5)	0.0 (0.9)	0.1 (0.1)	0.0 (0.0)
Central coast	34.3 (4.2)	37.8 (7.3)	40.4 (3.5)	3.6 (4.9)	15.0 (4.5)	0.1 (1.1)	3.8 (2.0)	0.5 (0.5)
South coast	8.7 (2.8)	7.1 (3.4)	11.9 (2.7)	21.0 (8.6)	11.6 (4.5)	23.7 (7.6)	2.2 (0.8)	8.6 (1.3)
North coast Vancouver Island	1.9 (1.5)	3.1 (3.4)	3.7 (1.4)	0.2 (1.3)	5.2 (2.8)	7.0 (4.7)	10.2 (2.5)	0.0 (0.2)
East coast Vancouver Island	0.3 (0.7)	3.0 (2.7)	3.7 (1.4)	0.5 (1.8)	16.9 (4.5)	33.3 (8.2)	1.1 (0.6)	27.1 (2.0)
West coast Vancouver Island	6.5 (2.1)	6.6 (3.2)	1.3 (0.9)	13.9 (8.8)	11.3 (3.8)	0.1 (1.2)	17.2 (1.9)	1.9 (0.7)
Fraser River–Birkenhead River	0.0 (0.1)	0.0 (0.1)	0.0 (0.0)	0.0 (0.3)	0.0 (0.1)	0.0 (0.4)	0.0 (0.0)	3.0 (0.7)
Fraser River–Chilliwack River	0.0 (0.1)	0.0 (0.1)	0.0 (0.0)	0.3 (1.4)	2.6 (1.9)	12.4 (5.9)	0.0 (0.0)	7.7 (1.2)
Fraser River, lower drainage	1.5 (1.9)	0.1 (0.5)	0.0 (0.2)	5.2 (4.5)	9.7 (3.4)	7.9 (7.0)	0.2 (0.3)	26.7 (2.1)
Fraser River, middle drainage	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.0 (0.5)	0.0 (0.1)	0.1 (0.8)	0.0 (0.0)	1.2 (0.4)
Lower Thompson River	0.0 (0.1)	0.0 (0.3)	0.0 (0.1)	0.0 (0.8)	0.0 (0.1)	0.6 (1.7)	0.0 (0.0)	1.4 (0.6)
North Thompson River	0.0 (0.1)	0.0 (0.2)	0.0 (0.0)	0.0 (0.4)	1.1 (1.1)	0.1 (0.8)	0.0 (0.0)	1.9 (0.5)
South Thompson River	0.0 (0.1)	0.0 (0.3)	0.0 (0.1)	0.0 (0.6)	0.0 (0.2)	2.1 (2.8)	0.0 (0.0)	1.3 (0.6)
Washington	12.5 (2.6)	2.4 (2.6)	4.8 (1.6)	1.2 (2.8)	7.8 (2.9)	10.4 (6.5)	30.8 (2.1)	18.4 (1.9)
Columbia River	14.2 (2.6)	0.0 (0.2)	4.1 (1.2)	0.6 (1.8)	13.7 (3.5)	1.9 (2.7)	29.9 (1.5)	0.0 (0.0)
Oregon coastal	12.9 (2.7)	1.3 (1.2)	2.4 (1.2)	0.6 (1.8)	5.0 (2.9)	0.0 (0.5)	4.4 (0.9)	0.3 (0.4)
California coastal	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)	0.0 (0.5)	0.0 (0.1)	0.0 (0.4)	0.0 (0.0)	0.0 (0.0)

TABLE 6. Estimated percentages by stock for juvenile Coho Salmon sampled during September, October, and November in seven geographic regions. See the caption to Table 5 for additional information.

Stock	SEAK (264)	SEAK inside (102)	Hecate (414)	QCS (97)	JS–QCS (27)	WCVI (549)	SOG (618)
Southeast Alaska	14.2 (2.7)	16.9 (4.8)	1.6 (1.1)	0.0 (0.2)	0.6 (1.6)	0.1 (0.2)	0.0 (0.0)
Alsek–Stikine River	13.3 (3.1)	28.2 (5.7)	4.3 (1.3)	0.0 (0.1)	5.7 (5.4)	0.2 (0.5)	0.1 (0.1)
Nass River	6.0 (2.7)	12.6 (4.1)	8.9 (1.6)	0.2 (0.7)	0.0 (0.3)	0.1 (0.2)	0.0 (0.0)
Haida Gwaii	3.7 (1.3)	0.9 (1.3)	18.1 (2.0)	0.0 (0.2)	0.0 (0.5)	0.0 (0.1)	0.0 (0.1)
North coast	0.0 (0.0)	0.0 (0.1)	0.0 (0.0)	0.0 (0.1)	0.0 (0.2)	0.0 (0.0)	0.0 (0.0)
Skeena River	12.8 (3.0)	7.2 (4.2)	19.9 (2.4)	0.0 (0.3)	0.1 (0.8)	0.2 (0.2)	0.0 (0.1)
Central coast	22.8 (3.8)	17.7 (5.0)	21.4 (2.7)	15.1 (4.9)	25.3 (8.1)	2.8 (1.3)	0.3 (0.4)
South coast	9.1 (2.9)	5.0 (4.0)	8.5 (1.9)	25.7 (5.6)	11.2 (6.4)	6.7 (1.5)	16.5 (1.7)
North coast Vancouver Island	3.1 (1.2)	0.1 (0.7)	2.7 (1.3)	6.2 (2.8)	0.1 (0.9)	18.7 (2.2)	0.1 (0.3)
East coast Vancouver Island	1.5 (1.4)	2.0 (2.8)	3.9 (1.3)	27.7 (4.9)	18.3 (6.8)	10.6 (1.7)	13.1 (1.6)
West coast Vancouver Island	4.5 (1.6)	3.0 (1.8)	2.6 (0.9)	1.4 (1.4)	3.3 (3.0)	18.7 (2.2)	0.2 (0.2)
Fraser River–Birkenhead River	0.0 (0.0)	0.0 (0.1)	0.0 (0.0)	0.0 (0.2)	7.3 (3.9)	0.4 (0.3)	5.1 (0.9)
Fraser River–Chilliwack River	0.1 (0.3)	0.0 (0.1)	1.1 (0.7)	8.3 (3.1)	0.2 (1.0)	0.7 (0.4)	5.5 (1.0)
Fraser River, lower drainage	0.2 (0.6)	0.3 (0.8)	0.1 (0.3)	7.7 (3.2)	12.8 (5.6)	3.4 (1.1)	24.4 (2.0)
Fraser River, middle drainage	0.0 (0.1)	0.0 (0.1)	0.2 (0.3)	0.0 (0.1)	1.9 (2.4)	0.2 (0.2)	4.2 (0.8)
Lower Thompson River	0.4 (0.4)	0.0 (0.3)	0.1 (0.2)	1.0 (1.0)	2.5 (2.5)	0.0 (0.1)	2.6 (0.7)
North Thompson River	0.0 (0.0)	0.0 (0.1)	0.0 (0.0)	0.0 (0.1)	0.1 (0.8)	0.2 (0.2)	6.0 (1.0)
South Thompson River	0.0 (0.1)	0.0 (0.2)	0.0 (0.1)	0.2 (0.7)	5.2 (3.6)	0.0 (0.1)	2.3 (0.6)
Washington	2.9 (2.2)	4.9 (3.5)	4.1 (1.4)	5.0 (3.1)	2.4 (4.1)	28.8 (2.6)	19.5 (1.9)
Columbia River	3.8 (1.3)	1.0 (1.3)	2.4 (0.8)	0.0 (0.2)	2.9 (2.7)	4.6 (1.0)	0.2 (0.2)
Oregon coastal	1.4 (0.9)	0.3 (0.7)	0.4 (0.3)	1.5 (1.6)	0.0 (0.5)	3.5 (0.9)	0.1 (0.2)
California coastal	0.0 (0.1)	0.0 (0.1)	0.0 (0.0)	0.0 (0.2)	0.0 (0.3)	0.0 (0.0)	0.0 (0.0)

TABLE 7. Estimated percentages by stock for juvenile Coho Salmon sampled during December, January, February, and March off the west coast of Vancouver Island (WCVI) and in the Strait of Georgia (SOG).

Stock	WCVI (400)	SOG (222)
Southeast Alaska	0.7 (0.6)	0.0 (0.1)
Alsek–Stikine River	0.0 (0.1)	0.0 (0.0)
Nass River	0.4 (0.4)	0.0 (0.)0
Haida Gwaii	0.1 (0.2)	0.0 (0.1)
North coast	0.0 (0.0)	0.0 (0.0)
Skeena River	0.2 (0.5)	0.0 (0.2)
Central coast	9.1 (1.9)	0.4 (0.7)
South coast	13.4 (2.2)	10.2 (2.4)
North coast Vancouver Island	20.3 (2.6)	0.5 (0.6)
East coast Vancouver Island	14.3 (2.1)	10.6 (2.3)
West coast Vancouver Island	8.8 (1.7)	0.2 (0.5)
Fraser River–Birkenhead River	0.6 (0.4)	5.7 (1.6)
Fraser River–Chilliwack River	1.0 (0.7)	12.0 (2.4)
Fraser River, lower drainage	6.1 (1.5)	24.1 (3.3)
Fraser River, middle drainage	0.0 (0.0)	0.4 (0.5)
Lower Thompson River	0.5 (0.4)	0.5 (0.6)
North Thompson River	0.0 (0.0)	0.8 (0.8)
South Thompson River	0.0 (0.1)	1.0 (0.7)
Washington	22.1 (2.5)	29.7 (3.7)
Columbia River	1.4 (0.6)	0.5 (0.5)
Oregon coastal	1.0 (0.7)	3.0 (1.6)
California coastal	0.0 (0.0)	0.5 (0.5)

The hierarchical cluster analysis of the seasonal and regional mixed-stock compositions yielded three distinct clusters having a strong correspondence with catch region. The stock compositions from northern regions like Southeast Alaska (both inside and outside waters), Hecate Strait, and Haida Gwaii clustered together regardless of the season, as did those from WCVI and QCS in summer and those from the SOG, JS–QCS, and QCS in fall (Figure 4). In particular, the seasonal SOG estimates of stock composition all clustered together and were most closely related to the summer and fall estimates of stock composition in JS–QCS and the fall estimates in QCS. The variation in mixed-stock composition was also explored by ordination with nonmetric MDS, which confirmed the patterns observed in the cluster analysis. The nonmetric MDS analysis of mixed-stock compositions represented the data reasonably well in two dimensions (two-dimensional stress = 0.11), in which samples from common catch regions tend to be closer. The fit was better in three dimensions (three-dimensional stress = 0.05). In Figure 5, we have superimposed the resultant cluster configuration (above) on the nonmetric MDS plot. Group delineation proved to be congruent between the two techniques, with non-overlapping groups of mixed stocks in common catch regions. By examining the regional and seasonal mixed-stock compositions with a permutation analysis of variance using Bray–Curtis distance matrices, we found significant differences between catch regions ($P < 0.001$) but none between seasons ($P = 0.32$).

Migration Routes and Speed

The Oregon coastal and Columbia River stocks were observed in the WCVI region in June. Coho Salmon from these stocks migrated along the WCVI and reached the northern tip of Vancouver Island, whence it appears that the majority migrated into the more coastal QCS waters rather than continuing along the west coast of Haida Gwaii (Figure 6, Table 8). However, once the fish were in Alaska waters, the stock-specific CPUE of both stocks was higher in offshore waters than in inshore ones, suggesting that the preferred migration route was through Hecate Strait and Dixon Entrance.

Coho Salmon juveniles from Washington moved into both the SOG and JS–QCS during summer as well as along the WCVI and further north into QCS, Hecate Strait, and Alaska waters, both inshore and offshore (Figure 6). Although some juvenile Coho Salmon from Washington (probably originating from PS) were observed in the SOG and likely migrated northward through Johnstone Strait to QCS, the majority from PS migrated through the Strait of Juan de Fuca to the WCVI sampling region. Juveniles from coastal Washington moved northward off WCVI, as juveniles from both PS and coastal Washington constituted 31% of those sampled in the region (Table 5). Once at the northern tip of Vancouver Island, the majority of the individuals chose a more coastal northward migration route through Hecate Strait (Figure 6). Although the stock remained widely dispersed in the fall, higher CPUEs for

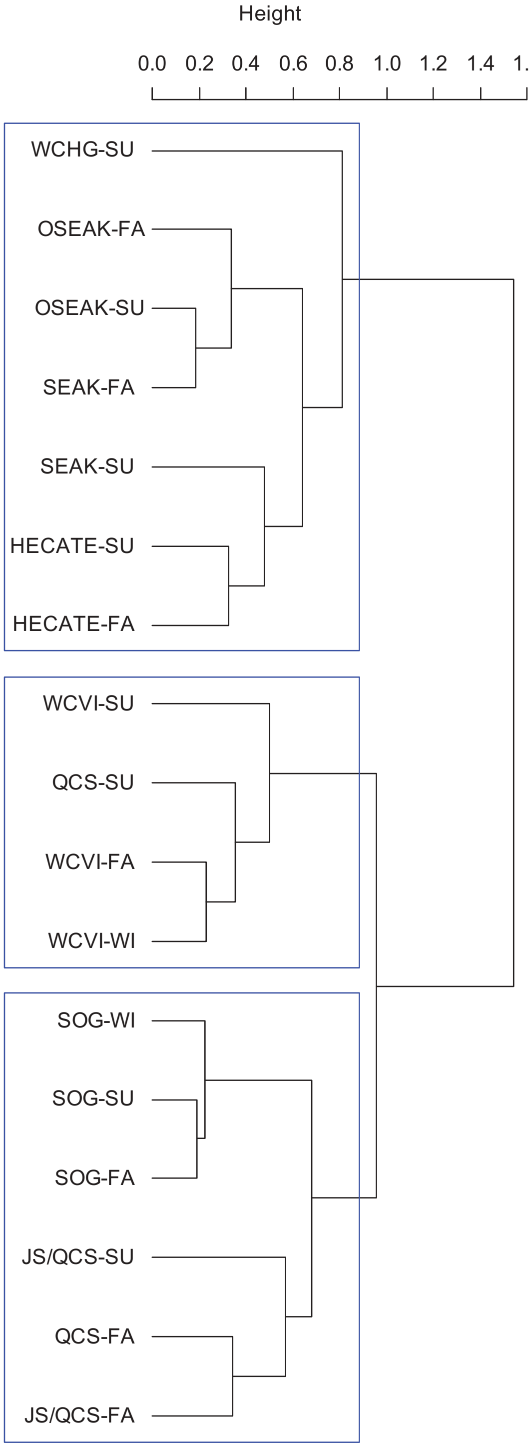

FIGURE 4. Hierarchical cluster dendrogram (Ward's minimum variance method) of regional and seasonal mixed-stock compositions for eight catch regions. Season abbreviations are as follows: SU = summer, FA = fall, and WI = winter; region abbreviations are as follows: SOG = Strait of Georgia, WCVI = west coast of Vancouver Island, JS–QCS = Johnstone Strait and Queen Charlotte Strait, QCS = Queen Charlotte Sound, HECATE = Hecate Strait and Dixon Entrance, WCHG = west coast of Haida Gwaii, ISEAK = inside waters of Southeast Alaska, and OSEAK = outside waters of Southeast Alaska. The blue rectangles highlight the main clusters.

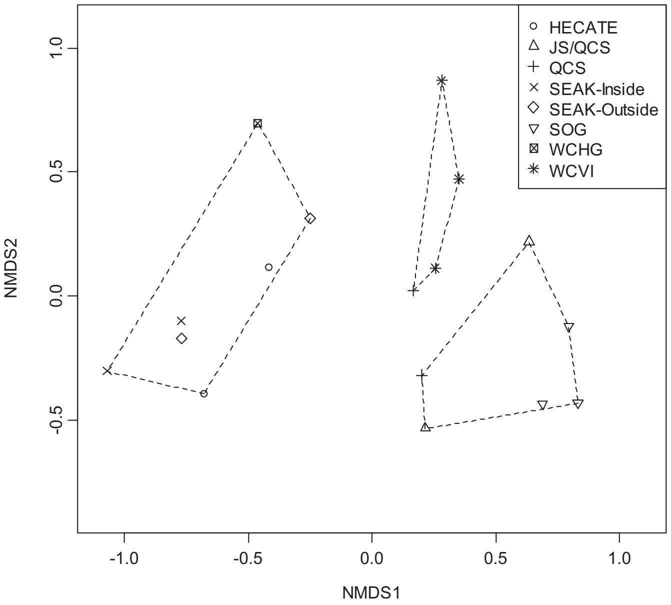

FIGURE 5. Nonmetric multidimensional scaling ordination plot of regional and seasonal mixed stock compositions (two-dimensional stress = 0.11). The seasonal mixed-stock groupings are coded by catch region. The dashed lines represent the resultant cluster groupings from the hierarchical cluster analysis shown in Figure 4.

this stock were observed in the WCVI sampling region than in more northern regions, illustrating the importance of that region for rearing in both fall and winter (Figures 7, 8).

In southern British Columbia, the timing of the northward migration of juveniles once they reached marine waters differed among stocks. For example, Coho Salmon from the ECVI displayed a greater propensity to exit the SOG during the summer than did those from the Fraser River, with 23.2% (49 of the 211 samples processed) of all summer captures of juveniles of EVCI origin being observed outside of the SOG, compared with 7.0% (20 of 287 samples) for juveniles of Fraser River origin ($\chi^2 = 26.9$, df = 1, $P < 0.01$). Once outside of the SOG in summer (with Johnstone Strait serving as the main migration corridor), the ECVI juveniles that exited the SOG moved at least as far north as Southeast Alaska (Figure 6). For stocks originating in the Fraser River drainage, individuals from the three Thompson River stocks were rarely observed outside of the SOG during summer, which suggests an extensive period of initial rearing in the SOG for these stocks. Similar results were also observed for the Birkenhead River stock originating in the lower Fraser River drainage. In contrast, some individuals from the Chilliwack and lower Fraser River stocks exited the SOG through Johnstone Strait in the summer, passed through QCS, and followed the more seaward route north along the west coast of Haida Gwaii (Figure 6).

The WCVI stock migrated along the WCVI and, rather than preferentially moving into the more coastal Hecate Strait sampling region, continued northward along the west coast of Haida Gwaii, as indicated by a stock-specific CPUE over three times as high off the west coast of Haida Gwaii (Figure 6). While a portion of the south coast stock remained in the SOG to rear during the summer, the majority of the stock moved north through Johnstone Strait and into QCS, taking both the more inshore Hecate Strait and the more offshore west coast of Haida Gwaii routes to Southeast Alaska waters (Figure 6; Table 5). While a small portion of the central coast stock moved south to rear off the WCVI, a large majority of individuals from this stock moved north into Southeast Alaska waters, following both the more inshore Hecate Strait and the more offshore west coast of Haida Gwaii routes (Figure 6). The Skeena, Nass, and Alsek–Stikine River stocks were more likely to be located in inshore waters in Southeast Alaska rather than offshore, illustrating the importance of the inshore waters for initial rearing (Figure 6). The SEAK stock was observed in the Haida Gwaii sampling region in

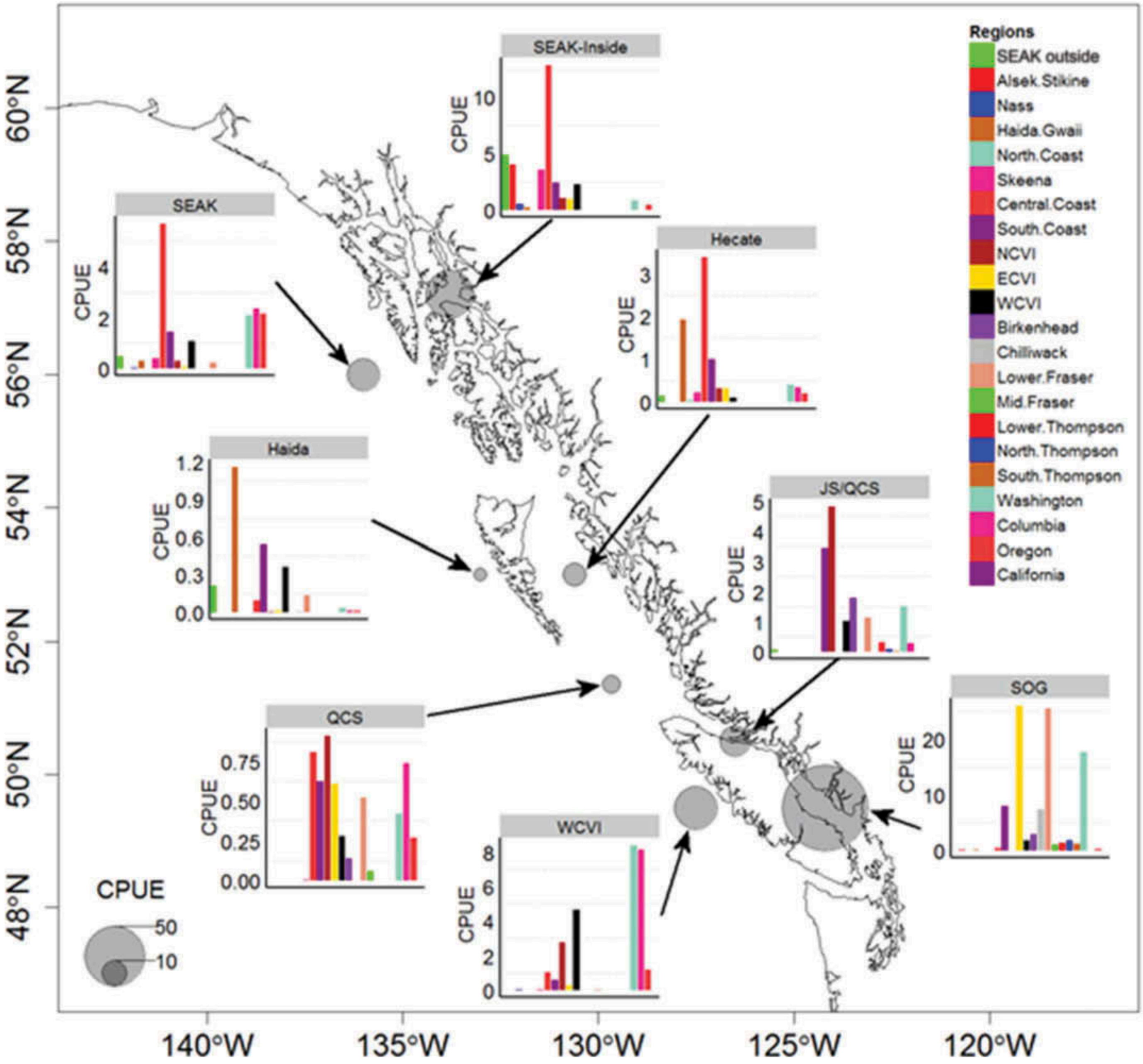

FIGURE 6. Stock-specific catch per unit effort during summer (June–August) of juvenile Coho Salmon in sampling regions in British Columbia and Southeast Alaska.

TABLE 8. Average CPUE in trawl surveys during summer (June–August), fall (September–November), and winter (December–March) in eight regions of British Columbia and Southeast Alaska. CPUE was defined as the average number of juvenile Coho Salmon caught per 60-min tow, with empty sets being included in the estimation. The number of tows associated with each CPUE value is given in parentheses.

Region	Summer	Fall	Winter
Strait of Georgia	95.8 (585)	36.8 (553)	2.1 (218)[a]
WCVI	27.2 (302)	4.6 (610)	3.9 (522)
JS–QCS	14.5 (26)	2.0 (80)	0.2 (42)
QCS	5.4 (103)	4.5 (211)	0.0 (132)
Hecate Strait	8.4 (90)	2.5 (306)	0.00 (122)
Haida Gwaii	2.6 (82)	0.00 (13)	0.00 (7)
SEAK inside	34.0 (7)	1.3 (399)	0.00 (227)
SEAK outside	16.6 (151)	6.0 (240)	0.2 (120)

[a] One tow that netted 15,000 Coho Salmon was omitted from the analysis. If it were included, CPUE would be 70.6 fish/60 min.

summer, indicating an initial southern migration for a small portion of the stock, similar to that of the central coast stock.

DISCUSSION

Body Size

Juveniles of larger body sizes were observed in more northern sampling regions, and this trend was consistent through the summer, fall, and early winter of the first year of marine rearing. However, by March latitudinal variation in the sizes within stocks was largely absent, though the limited sample sizes available from the northern regions during this period limits the inferences that can be drawn. In northern regions, larger FLs were observed in individuals originating from populations or stocks in more southern latitudes, with smaller body sizes typically being observed in local stocks. The larger body sizes observed in more northern sampling locations during the summer and fall reflect the fact that larger individuals from southern populations were present in these regions, and individuals from local stocks were in fact smaller than those from more distant southern locations. While swimming speed and prey quality may contribute to larger juvenile size in more northern regions, it is likely that the more important factors are that the larger smolts were larger upon ocean entry and migrated north earlier, while the smaller smolts reared for a longer time in local waters (Freshwater et al., in press). It is possible that some portion of the larger juvenile body sizes in northern areas stems from the earlier migration of freshwater age-2 Coho Salmon than of freshwater age-1 ones.

Seasonal and Regional Stock Composition

The results from our study illustrate the importance of separating out identifiable stocks of Coho Salmon when the migration characteristics of juveniles are considered. For example, seven stocks were identified within the Fraser River drainage, and the results of our study indicate that there were differences in migration behavior between the Thompson River stocks and those in the lower Fraser River drainage. The Thompson River stocks were observed in the SOG during the summer (5.6% of the catch), but there was little evidence of any movement outside of the SOG. Conversely, the lower Fraser River and Chilliwack River stocks were observed in the JS–QCS region as well as the SOG in summer, indicating that a portion of those stocks left the SOG during the summer. However, by the fall the three Thompson River stocks comprised 7.8% of the catch in JS–QCS but were essentially absent from the WCVI and regions north of JS–QCS. The lower Fraser and Chilliwack River stocks comprised 7.7% and 8.3%, respectively, of the fall catch in QCS, perhaps indicating a more extensive northern migration than that of the Thompson River stocks. In similar fashion, the Birkenhead River stock, which is situated in the lower Fraser River drainage, was essentially observed only in the SOG in the summer (3.0% of the summer catch) and only in the SOG (5.1%) and JS–QCS (7.3%) in the fall.

Migration Routes and Speed

In an analysis of juvenile migration based on CWTs, Morris et al. (2007) found that Coho Salmon stocks were composed of a fast component that undertakes a rapid and direct northwest migration upon entering the ocean and a slow component that migrates a relatively short distance from their natal rivers and resides over the continental shelf during the winter. Their fall sampling of juveniles showed that juveniles originating from Oregon to the WCVI (including the SOG) resided off the WCVI, which would place them in the slow-migrating component. The fast-migrating component was sampled in more

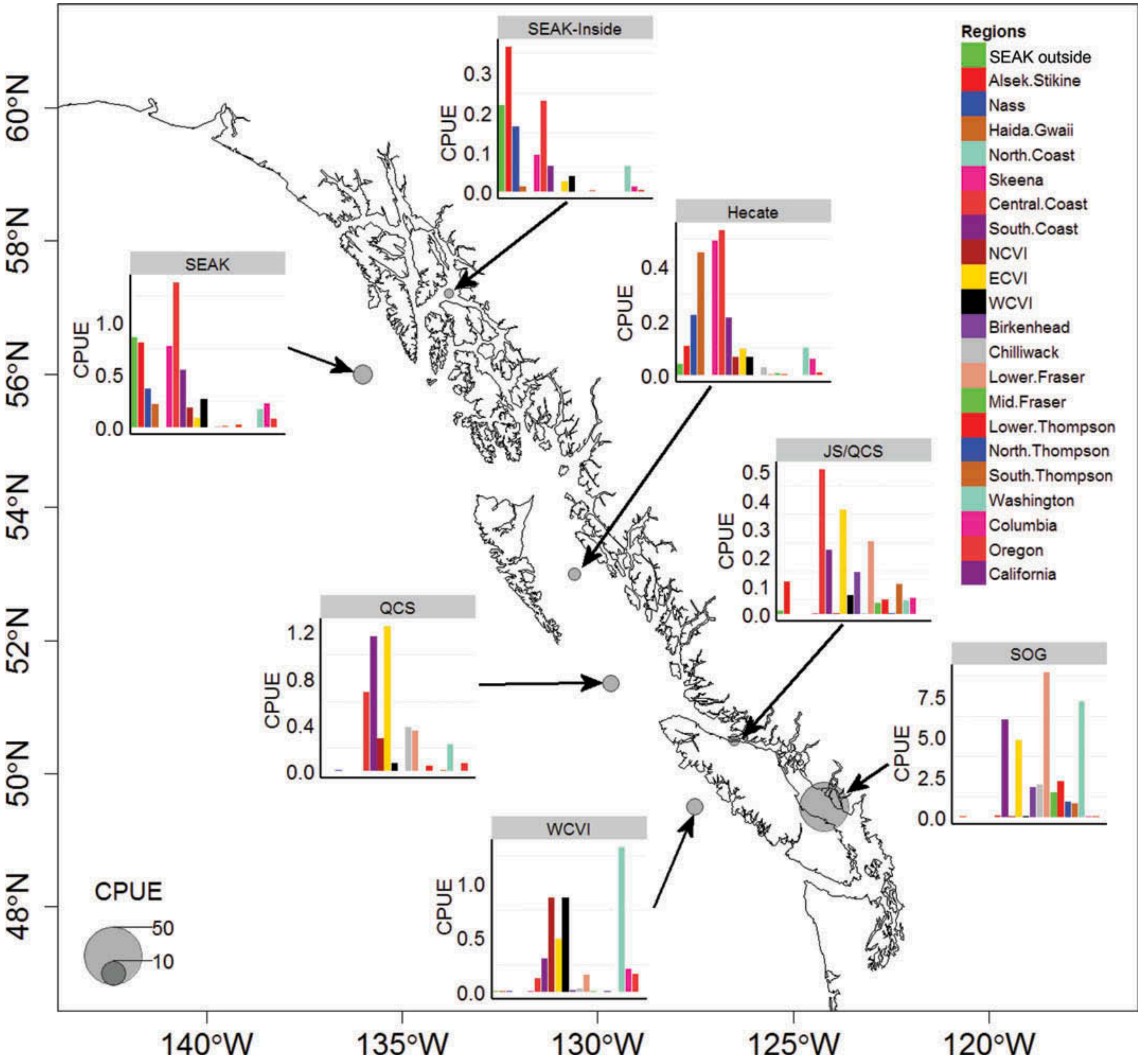

FIGURE 7. Stock-specific catch per unit effort during fall (September–November) of juvenile Coho Salmon in sampling regions in British Columbia and Southeast Alaska.

northern regions. Similar results were obtained in our study, with juveniles of Washington and Columbia River origin being observed in Southeast Alaska in June, along with stocks from southern British Columbia. However, individuals from these same stocks were also observed in southern sampling regions in June and throughout the fall and winter, which would place them in the slow-migrating component.

Morris et al. (2007) reported that the migration speed of juvenile Coho Salmon along the continental shelf slowed considerably in the fall relative to that observed earlier in the year, particularly for the slow-migrating component of the stock. In our study, there was only a modest change in stock composition between fall and winter sampling in both the SOG and WVCI sampling regions, indicating that juvenile migration had largely been completed by the fall.

The use of genetic variation to determine stock-specific migration patterns, as outlined by Tucker et al. (2011, 2012) and Teel et al. (2015) for Chinook Salmon *O. tshawytscha*,

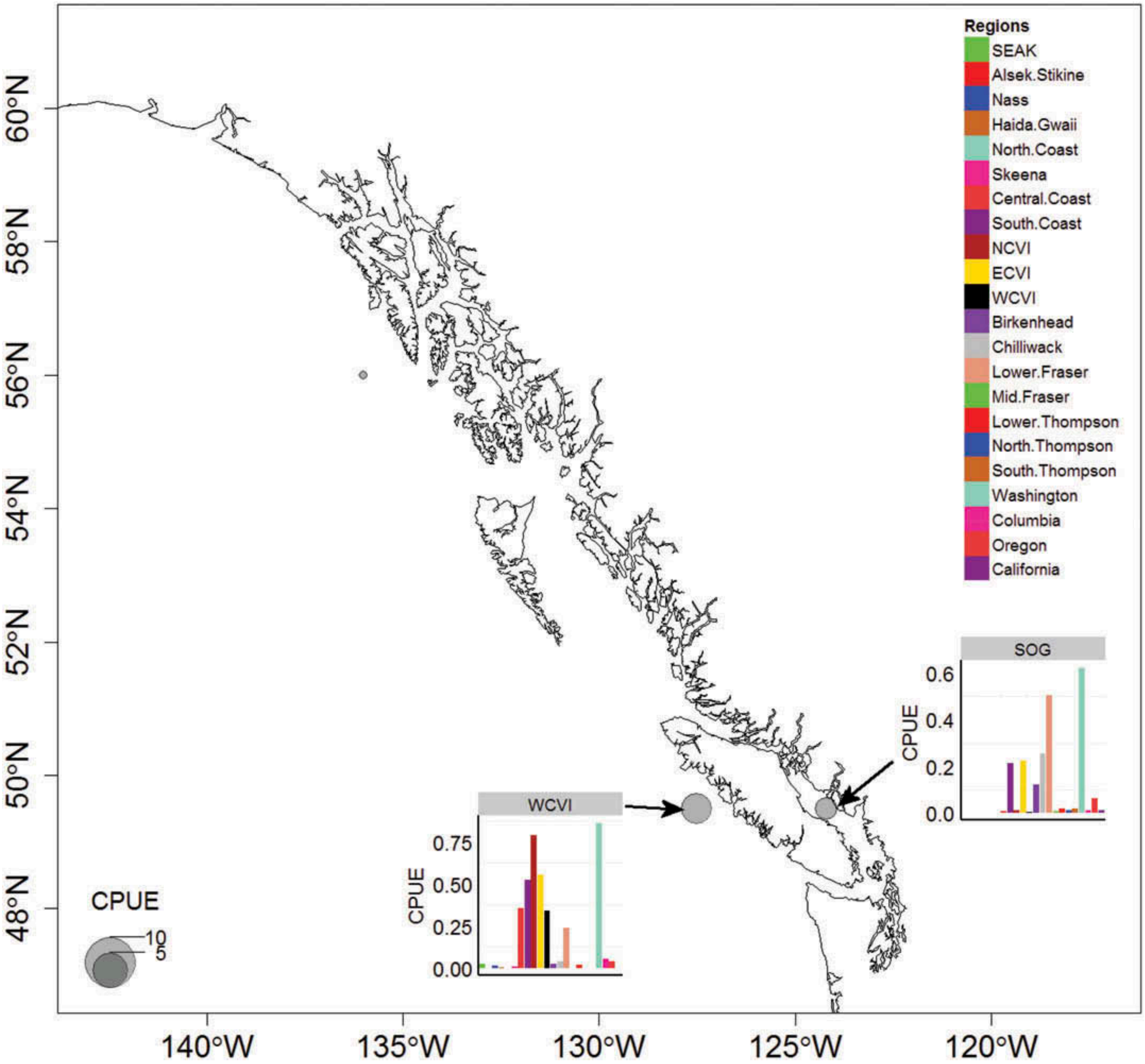

FIGURE 8. Stock-specific catch per unit effort during winter (December–March) of juvenile Coho Salmon in the Strait of Georgia and west coast of Vancouver Island sampling regions.

may provide greater insight than is available from CWTs. For example, Morris et al. (2007) reported that the June limit to the northward migration of juvenile Coho Salmon from Oregon, the Columbia River, and Washington was near the northern tip of Vancouver Island, since no juveniles with CWTs were recovered in surveys farther north. However, the results from our study indicate that individuals from these stocks were to be found as far north as Southeast Alaska during June. Winter sampling of coded-wire-tagged juveniles off WCVI suggests that those from coastal Washington, the Columbia River, and the WCVI stocks that were present on the continental shelf in the fall had migrated farther north or farther offshore (Morris et al. 2007). However, according to our genetic analysis, there was only a modest change in stock composition between the fall and winter sampling periods in the WCVI region, as the stock compositions from both seasons clustered together in the cluster analysis, with the Washington, Columbia River, and WCVI stocks still being present in the region.

The SOG was an important rearing area for juvenile Coho Salmon during the summer and into the fall of the first year of ocean residence, according to the CPUE values obtained during the study (Table 8). Based on an analysis of CWT recoveries, Beamish et al. (2008) concluded that the movement of juvenile Coho Salmon out of the SOG occurred after September, as most of them remained in the SOG through October and November of their first marine year (Chittenden et al. 2009; Beamish et al. 2010). Beamish et al. (2010) reported that of the 1,269 juveniles caught in the SOG in September cruises between 2007 and 2009, 22 had CWTs (1.7% of all juveniles sampled), and as only 1 individual of Canadian origin from the 954 juveniles sampled in the Strait of Juan de Fuca in September had a CWT, there was little movement out of the SOG prior to September. Even though small numbers of Coho Salmon were detected in an acoustic tagging survey reported by Melnychuk et al. (2010), the predominant early route of exit from the SOG was northward through Johnstone Strait (10 of 11 fish with detected tags). Chittenden et al. (2008) also reported an early northern movement of acoustically tagged juvenile Coho Salmon from the SOG through Johnstone Strait. The results of our study indicate that although the SOG remained a very important summer rearing area, the predominant early exit route was through Johnstone Strait, as was the case for Sockeye Salmon *O. nerka* (Beacham et al. 2014b), and that an unknown proportion (but presumably a relatively small one, based on a comparison of regional and seasonal CPUEs) of juvenile Coho Salmon exited the SOG prior to September. As with Sockeye Salmon, it may be that the initial early-migration route from the SOG is through Johnstone Strait; but it may also be the case that juveniles remaining in the SOG through late summer exit via the Strait of Juan de Fuca instead, as reported by Chittenden et al. (2009). The application of genetic variation to the determination of the routes and timing of migration allows virtually all of the juveniles sampled to be included in the analysis (not just the 1–2% that possess CWTs), thus potentially providing more inclusive results.

If some juvenile Coho Salmon exit the SOG in early summer, their main migration route appears to be northward through JS–QCS into QCS, as evidenced by the presence of the ECVI, Chilliwack River, and lower Fraser River stocks in JS–QCS in the summer coupled with the virtual absence of those stocks off WCVI in the summer. By the fall, when the majority of juvenile Coho Salmon have been reported to have left the SOG (Beamish et al. 2008), the ECVI and lower Fraser River stocks were observed in the WCVI region, indicating migration through the Strait of Juan de Fuca as well as a continuing presence in JS–QCS and QCS. However, the hierarchical cluster analysis showed that the seasonal SOG estimates of stock composition all clustered together and were most closely related to the summer and fall estimates of stock composition in JS–QCS and the fall estimates in QCS, possibly indicating a northern exit from the SOG as well as via the Strait of Juan de Fuca, as reported by Chittenden et al. (2009).

The proportion of the catch consisting of stocks proximate to the SOG (ECVI, Fraser River, and south coast) did increase in the WCVI sampling region from the summer (3.5% of sampled catch) to the fall (19.2%) and winter (22.5%), but the increase did not fully reflect the large decline in CPUE in the SOG from summer (96 juveniles/h) to fall (37 juveniles/h) and winter (2 juveniles/h), with the CPUE in the WCVI declining as well (from 27 to 5 to 4 juveniles/h). Juveniles may have (1) exited the SOG via the Strait of Juan de Fuca and moved south (Chittenden et al. 2009), (2) exited the SOG through the Strait of Juan de Fuca into the WCVI region but resided in deeper waters or more inshore than where the sampling gear was deployed, (3) exited the SOG via Johnstone Strait (SOG stocks present from Southeast Alaska to JS–QCS in the fall), or (4) simply died in the SOG.

Based on an analysis of CWT recoveries in coastal fisheries, Weitkamp and Neely (2002) reported that Coho Salmon from different freshwater regions inhabit different areas of the coastal ocean. They further suggested that differences among stocks in ocean rearing areas begin earlier than in the last few months of an 18-month ocean residence, as variation in body size is correlated with growth rates during the last year in the ocean (Rogers and Ruggerone 1993). Our results support the view that there is segregation of ocean rearing areas among stocks and suggest that stocks are not equally dispersed among sampling areas. For example, some stocks (such as the Thompson River stocks) displayed a much reduced distribution relative to the lower Fraser and Chilliwack River stocks. Stock differences in ocean rearing areas occur during the first year of marine rearing and may reflect the differences in subsequent size and survival observed among stocks. However, local populations in the Salish Sea tend to display strong local correlation in survival (Beamish et al. 2010; Zimmerman et al. 2015), which suggests that divergence in their distributions beyond the first few weeks contributes little to the differences among populations.

While there was a general northward movement of juvenile Coho Salmon during their first year of marine residence, the results from our study suggest that there is a south-migrating component for two northern stocks, namely, the central coast and SEAK stocks. In the case of the central coast stock, the waters adjacent to the north end of Vancouver Island are a transition zone between the Alaska and California currents. Crawford et al. (1985) indicated that during summer the winds are usually from the northwest, resulting in an upwelling along the eastern shore of QCS and the WCVI and a westward movement of water out of QCS toward the continental shelf. Combined with the California Current, which flows south (illustrated by Borstad et al. 2011), this could bring some of the central coast juveniles south off the WCVI to rear during their first marine summer. A southern migratory orientation has also been identified for some Columbia River stocks (Weitkamp and Neely 2002; Van Doornik et al. 2007) and some SOG Coho Salmon (Chittenden et al. 2009), but Morris et al. (2007) were unable to identify any southward movement of coded-wire-tagged juveniles in the spring. However, as there has been very limited use of CWTs with juveniles from the central coast, any southern migration would not be revealed by analysis of CWT capture locations.

Determination of stock–specific areas of ocean residence and the timing of migration by Coho Salmon will be important if the location of presumed early mortality is to be identified and the causal mechanisms evaluated. The examination of juvenile migratory behavior should be conducted at the level of the smallest identifiable unit, as there can be considerable variation in juvenile life histories that will be masked if the unit under evaluation consists of larger units, e.g., populations in the same river drainage or geographic area. In any event, determination of the body size, location, and migratory timing of specific stocks of Coho Salmon may lead to better understanding of their presumed critical sizes and critical periods, which may link natural mortality directly to the productivity of the ocean ecosystem and indirectly to climate and climate change.

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