Seasonal Stock-Specific Migrations of Juvenile Sockeye Salmon along the West Coast of North America: Implications for Growth

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Abstract.—Knowledge of the migratory habits of juvenile Pacific salmon *Oncorhynchus* spp. is required to test the hypothesis that ocean food resources are a limiting factor in their production. Using DNA stock identification techniques, we reconstructed the regional and seasonal changes in the stock composition of juvenile sockeye salmon *O. nerka* ($n = 4,062$) collected from coastal Washington to the Alaska Peninsula in coastal trawl surveys from May to February 1996–2007. Individuals were allocated to 14 regional populations. The majority were allocated to stocks from the Fraser River system (42%), while west coast Vancouver Island stocks accounted for 15% of the total catch; Nass and Skeena River sockeye salmon constituted 14% and Rivers Inlet 6% of the total. The remainder of the stocks identified individually contributed less than 5% of the sockeye salmon analyzed. These proportions generally reflected the abundance of those populations. In spring and summer, the majority of fish were caught in close proximity to their rivers of origin, lending further support to the allocations. By fall, sockeye salmon were caught as far north and west as the Alaska Peninsula, the majority being caught from central British Columbia to Southeast Alaska. Juvenile sockeye salmon generally disappeared from the coast by winter, suggesting dispersion into the Gulf of Alaska. Within each region, the proportional stock composition changed as the seasons progressed, with northward (and in some cases, rapid) migration along the coast. We also demonstrated stock-specific differences in migration patterns. For each stock identified, body size and energy density were higher at northern latitudes, suggesting that there is an environmental or food web influence on growth or that faster growing fish initiated their northward migration earlier.

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Pacific salmon *Oncorhynchus* spp. have a complex life cycle that typically involves both freshwater and marine phases, though it is in the marine environment that they spend the greater part of their lives and gain the bulk of their mass and energy for subsequent use in reproduction (Burgner 1991; Bigler et al. 1996). The ocean feeding grounds of Pacific salmon extend over several thousand kilometers of highly variable physical conditions, prey quality and abundance, and predator assemblages. Therefore, the fate of individual stocks may depend on where they migrate and how much time they spend in different regions.

Climate and ocean conditions generally have opposite effects on southern and northern salmon populations in the Pacific Northwest (Hare et al. 1999; Mueter et al. 2002a). In contrast, the response of salmon populations to climate and ocean conditions is generally positively correlated over several hundreds of kilometers, suggesting that production is regulated by local and regional conditions during early marine life (Mueter et al. 2002a, 2002b). However, the correlation among demographic parameters of Pacific salmon is highly variable even among neighboring populations (Mueter et al. 2002b). Hence, an understanding of stock-specific migration behavior is required to determine how climate and ocean conditions regulate the production of highly migratory animals.

In their seminal work, Hartt and Dell (1986) examined catch per unit effort (CPUE) for juvenile salmon caught in purse seines between April and October 1956–1970 over a wide extent of the Pacific Northwest, ranging from the west coast of Vancouver Island to the Gulf of Alaska (GOA) and the Bering Sea. They identified a counterclockwise shift in abundance between spring and fall along the continental shelf. Similar trends in CPUE have recently been reported by Fisher et al. (2007) from concurrent research programs that have been investigating the early marine life of Pacific salmon on the west coast of North American since the late 1990s. In addition, Hartt and Dell (1986) found that the catches of juvenile salmon in seines held open to the south were five times greater than those of nets held open to the north, suggesting an active northward movement on the part of these fish. Finally, they observed that most of the juvenile salmon tagged in coastal waters of the GOA and the Alaska Peninsula were later caught as adults in a clockwise direction from where they were released. From these three lines of evidence, Hartt and Dell (1986) developed a model of counterclockwise migration along the continental shelf. However, only 41 of the 10,411 individual sockeye salmon *Oncorhynchus nerka* tagged at sea were recovered, which precluded them from comparing stock-specific migration patterns.

Stock-specific migration patterns have only been described for a few stocks of any Pacific salmon species (e.g., Welch et al. 2009) owing to the logistical difficulty of inferring juvenile migration for individual stocks. The ocean migration of juvenile salmon has traditionally been studied using spaghetti or disk tags (Hartt and Dell 1986) and coded wire tags (Pearcy and Fisher 1988; Fisher and Pearcy 1995). Other methods include scale pattern analysis (e.g., Gable and Cox-Rogers 1993) and parasite tags (e.g., Bennett et al. 1998). Additionally, thermally marked otoliths (Carlson et al. 2000) are primarily used to identify hatchery stocks in mixed-stock catches. Although these techniques can usually provide unequivocal assessment of the origin of individual fish, few stocks are tagged or marked relative to the number of spawning populations. Moreover, these methods generally require considerable time, effort, and resources to determine migration timing and routes, as the recovery of tagged and marked fish is generally low (Hartt and Dell 1986). For example, the recovery rate of juvenile sockeye salmon tagged at sea between 1956 and 1968 was 0.4% (Hartt and Dell 1986). The recovery of coded-wire-tagged juvenile salmon at sea is also low: 3 per million releases for coho salmon *O. kisutch* and 6 per million releases for Chinook salmon *O. tshawytscha* (Morris et al. 2007; Trudel et al. 2009). Alternatively, DNA provides a natural marker that can be used to reconstruct the migration routes of juvenile salmon at sea (Teel et al. 2003; Seeb et al. 2004). Genetic stock identification techniques, such as those relying on DNA microsatellite variation, enable us to assign salmon to their population of origin (Nielsen et al. 2001; Wirth and Bernatchez 2001; Beacham et al. 2002, 2004, 2005a, 2006), allowing for the integration of other information pertaining to the growth performance of individual fish.

In this study, we examined the seasonal changes in the stock composition of juvenile sockeye salmon along the west coast of North America from Washington State to the Alaska Peninsula during their first year of marine life. In North America, sockeye salmon are widely distributed, from the Columbia River to northwestern Alaska. However, Asian populations are more restricted in their distribution, most spawning occurring on the Kamchatka Peninsula and the western coast of the Bering Sea. Sockeye salmon typically spawn in tributaries to lakes or along lake shores, and juveniles subsequently rear in these nursery lakes for at least 1 year before migrating to sea (Burgner 1991). The largest spawning population is in Bristol Bay in the Bering Sea (Burgner 1991). The next largest spawning populations are associated with the Fraser River basin. Other major spawning populations are

found on Kodiak Island and in central Alaska (Copper River), northern British Columbia (Nass and Skeena rivers), and the Somass River–Alberni Inlet of western Vancouver Island. Historically, large populations were also found in Owikeno Lake (Rivers Inlet in central British Columbia) and the Columbia River system, but these are now greatly reduced (Burgner 1991; McKinnell et al. 2001). Poor ocean conditions and their impacts on survival are thought to be associated with the decline of some of these populations (McKinnell et al. 2001). However, without knowledge of stock-specific differences in migration behavior, the direct causes for these declines remain uncertain.

Size and age at smolting are variable among sockeye salmon populations. However, there is no evidence for a latitudinal trend in smolt size or age. As summarized in Burgner (1991), the largest sockeye salmon smolts come from Lake Washington (in the south) and Bristol Bay (in the north). Variation in smolt age appears to be more a function of lake characteristics. Furthermore, the annual growth attained by juvenile sockeye salmon and the length of freshwater residence varies greatly among populations from different lake systems and between years within particular systems owing to a number of factors (Burgner 1991). However, Hartt and Dell (1986) observed a general increase in the mean length of juvenile salmon from south to north in coastal waters from Washington to Southeast Alaska. This finding has subsequently been supported by additional studies (i.e., Jaenicke and Celewycz 1994; Farley et al. 2005). Assuming that the fish were roughly similar in size on entering the sea, the traditional interpretation has been that the smaller fish in the southerly locations are recent arrivals from nearby production areas, whereas the larger fish in the northerly locations have been at sea longer and probably migrated from more southerly production areas (Hartt and Dell 1986). However, without explicit knowledge of the stocks of origin and their growth trajectories, this assertion is simply an inference (though a testable hypothesis). Alternatively, the growth conditions for salmon are postulated to improve with increasing latitude (i.e., Peterson and Schwing 2003; Mackas et al. 2004; Trudel et al. 2007a). This is thought to be due in part to improved diet quality (i.e., higher lipid content in zooplankton; Peterson and Schwing 2003; Mackas et al. 2004; Trudel et al. 2007a) that causes growth rates to increase as fish move north.

Using DNA markers, we contrasted the migration trajectories of juvenile sockeye salmon from various production areas. We sought to evaluate whether all stocks displayed a rapid, northward progression, generally affirming the counterclockwise model of migration proposed by Hartt and Dell (1986), or if some had longer residence times on the continental shelf. We subsequently evaluated whether there were stock-specific differences in body size (inferred growth rates) and energy densities within each region to evaluate potential differences in juvenile sockeye salmon growth performance.

Methods

Sample collection.—Juvenile sockeye salmon were collected from southern British Columbia to the Alaska Peninsula from 1996 to 2007 by Fisheries and Oceans Canada (Figure 1). The sampling surveys were conducted in various months from May through February, thus allowing us to reconstruct changes in stock composition for a number of regions along the shelf at different seasons of the year (Figure 2). A midwater rope trawl (~90 m long × 30 m wide × 15 m deep; cod end mesh, 0.6 cm; Cantrawl Pacific Ltd., Richmond, British Columbia) was hauled at the surface (0–20 m) for 15–30 min at 5 knots, primarily by CCGS *W. E. Ricker* but by a chartered fishing vessel when that was unavailable (i.e., the *Ocean Selector* in June 2002 and the *Frosti* in June and October 2005). Sampling was conducted between 0600 and 2000 hours. Up to 30 juvenile sockeye salmon were randomly selected from each net tow. Fork length and mass were determined on board the research vessel. A tissue sample was taken from the operculum with a hole punch and preserved in a 95% solution of ethanol for genetic stock identification. Whole fish were then bagged individually and frozen at $-20°C$ for subsequent analysis. Additional samples ($n = 146$) were obtained from May–June 2007 National Marine Fisheries Service coastal pelagic trawl surveys off the coast of Washington State (Fisher et al. 2007). Juvenile salmon were defined as those caught during their first year of marine life. By convention, all salmon are 1 year older on January 1. The salmon collected in this study between May and November were "juveniles" in their first ocean year (ocean age .0), and salmon collected in February and March were technically "immatures" in their second ocean year (ocean age .1). For the purpose of this study, we refer to fish caught in the winter sampling period as juveniles as well, since they are still within their first year at sea and this avoids any misconception that we are dealing with the second-year spring and summer growth periods. Age separation to exclude second-ocean-year fish was based on an examination of age–size distributions (fork length), which had nonoverlapping size modes for sockeye salmon (Trudel et al. 2007b).

In the laboratory, a subsample of fish ($n = 1,890$) were dried at 60°C to constant weight to determine their water content. A subsample of these fish ($n = 75$)
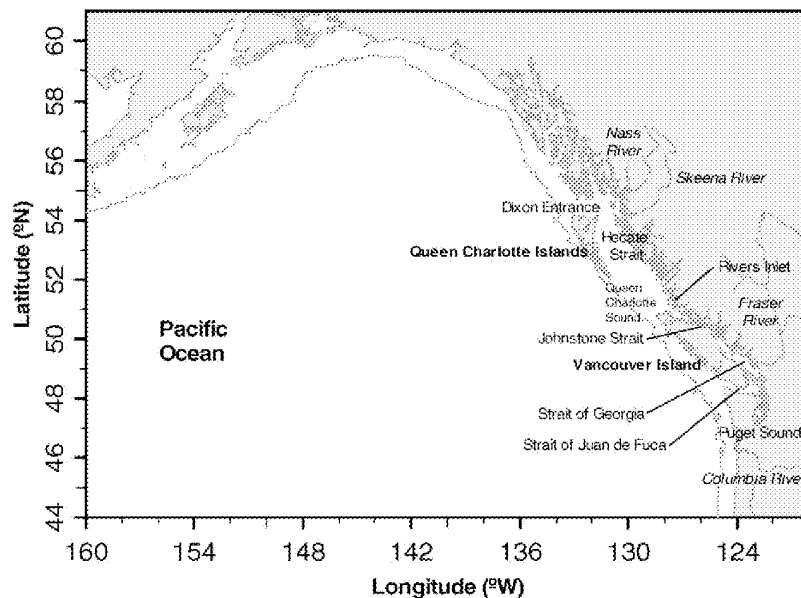
FIGURE 1.—Regional map of study area. The shelf-break was operationally defined as the 1,000 m contour depth in this study and is represented by the solid line beyond the margin of the continent.

were measured by bomb calorimetry (as per Trudel et al. 2005). The energy content of all fish was then determined by means of an empirical model relating energy content and water content that was specific to juvenile sockeye salmon, that is,

$$\text{energy content (J/g)} = 44.09 - 0.29 \cdot \text{water (\%)},$$
$$(F_{1,72} = 111.6, P < 0.001, r^2 = 0.60, SE = 214).$$

To evaluate the spatial changes in stock composition, we divided our sampling locations into seven principal catch regions (Figure 2): coastal Washington (WA), the west coast of Vancouver Island (WCVI), central British Columbia (CBC), the west coast of the Queen Charlotte Islands (QCI), northern British Columbia (NBC), Southeast Alaska (SEAK), and the Gulf of Alaska (GOA). The CPUE for each fishing event in DFO cruises was calculated as per Fisher et al. (2007). Briefly, CPUE was defined as the number of juvenile sockeye salmon caught per tow length of 1.5 nautical miles (2.8 km), that is,

$$\text{CPUE} = \left[\frac{\text{sockeye salmon/tow duration (h)}}{\text{tow speed (nautical miles/h)}} \right]$$
$$\times 1.5 \text{ nautical miles}.$$

To reduce the influence of large catches from individual tows, we $\log_{10}$ transformed the CPUE

estimate for each haul (Fisher et al. 2007). The CPUEs were subsequently pooled for each region and season. The CPUE for Washington conducted by NMFS is from Fisher et al. (2007).

DNA extraction and laboratory analyses.—DNA was extracted from the samples as described by Withler et al. (2000). Briefly, juvenile sockeye salmon ($n = 4,156$) were surveyed for 14 microsatellite loci and a major histocompatibility complex locus. Further details on the loci surveyed as well as the laboratory equipment used are outlined in Beacham et al. (2004, 2005a). A minimum of 10 loci was scored for each fish retained for analysis.

Data analyses.—Analysis of mixed-stock samples of juveniles was conducted using a modified C-based version (cBAYES; Neaves et al. 2005) of the original Bayesian procedure outlined by Pella and Masuda (2001). Samples were pooled per catch region for each season: spring (May–June 20), summer (June 21–August), fall (September–December), and winter (February–March). Uneven sample sizes precluded an evaluation of the interannual variation in regional stock composition. A 359-population baseline (299 populations as in Beacham et al. 2005a, unpublished data on 60 populations [allele frequencies available from T. D. Beacham on request]) comprising approximately 60,000 individuals from Japan, Russia, Alaska, British
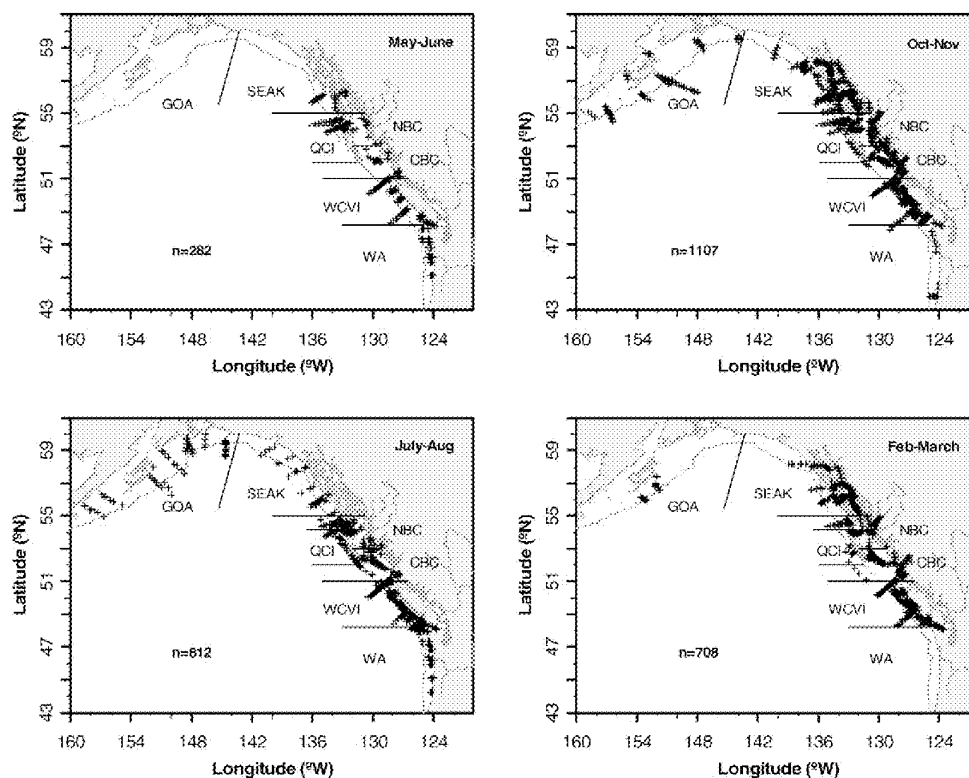
FIGURE 2.—Division of sampling area into 7 main catch regions and sampling locations in each season (crosses and sample sizes represent individual fishing events).The solid line beyond the margin of the continent represents the 1000 m contour depth. WA - Washington; WCVI - west coast of Vancouver Island; CBC - central British Columbia; QCI - west coast of the Queen Charlotte Islands; NBC - northern British Columbia; SEAK - south east Alaska; GOA - Gulf of Alaska.

Columbia, and Washington was used to estimate mixed-stock compositions for each season and catch region. In the mixed-stock analysis, we assigned fish to one of 16 regional populations on the basis of genetic structure (Beacham et al. 2005a). A regional population structure was observed in the Pacific Rim analysis of microsatellite variation (Beacham et al. 2005a), such that the populations within lakes and river drainages were more similar to each other than to the populations in other lakes or river drainages. Given that the regional genetic variation far exceeds the annual effects (Beacham et al. 2004, 2005a), annual updating of the baseline populations is not required. Regional population structure allows correct assignment to region even for those portions of the mixed-population sample that are not explicitly represented in the baseline (Beacham et al. 2005a). In the analysis, eight 20,000-iteration Markov chain–Monte Carlo simulations were run using an uninformative prior with a value of 0.90 for a

randomly picked population (Pella and Masuda 2001). The estimated stock compositions were considered to have converged when the shrink factor was less than 1.2 for the eight chains (Pella and Masuda 2001), and thus the starting values were considered irrelevant. The posterior distributions from the last 1,000 iterations for all chains were combined to estimate the mean stock composition and variance.

In mixed-stock analysis, cBAYES provides the population of origin for each fish together with a probability of assignment. Individual fish were assigned to the baseline population of origin with the highest probability. For individual allocations, we used a probability of 50% as a lower limit (Beacham et al. 2005a). Although the regional genetic differences are large overall (Beacham et al. 2005a), smaller-scale population structuring within large regional populations (e.g., the Fraser River, Nass and Skeena rivers, and WCVI) is evident and well defined (Beacham et al.

TABLE 1.—Allocation of juvenile sockeye salmon to regional populations.

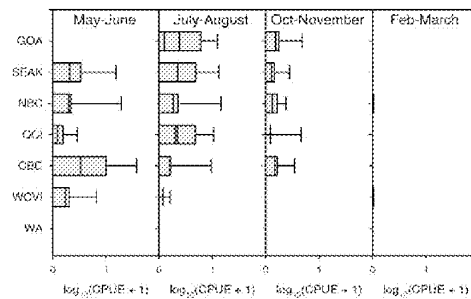| Region	Allocation (%)
Columbia River	4.3
Coastal Washington/Puget Sound	3.1
South coast of British Columbia	0.2
Fraser River	42.0
West coast of Vancouver Island	15.1
East coast of Vancouver Island	0.5
Central coast of British Columbia	5.0
Queen Charlotte Islands	0.6
Rivers Inlet	5.9
Nass and Skeena rivers	14.4
Transboundary region	3.8
Southeast Alaska	4.2
Central Alaska	0.5
Bristol Bay	0.2
Russia	0.1
Japan	0

FIGURE 3.—Box plots of log seasonal Catch per Unit Effort (CPUE) of juvenile sockeye salmon for various catch regions. The ends of the boxes define the 25th and 75th percentiles, with a line at the median and error bars defining the 10th and 90th percentiles.

2002, 2004, 2005a, 2005b). For those regional populations, this allowed for allocation to individual stocks with high certainty, permitting a further level of differentiation.

To describe the migration patterns, we proceeded in the following multi-step manner. First, we considered the seasonal change in the mixed-stock composition (16 regional populations) for each catch region. Subsequently, we looked at the individual fish allocations to map and describe the potential variation in migration patterns between regional populations. Finally, for those regional populations found in high proportions (Table 1; i.e., the Nass and Skeena rivers, the Fraser River, and WCVI), we mapped and examined the potential differences in individual stock migration patterns. For the sake of brevity, we report only stock-specific differences. The survey and stock-specific distributional maps were generated using an R-based (version 2.6.2; R Development Core Team 2008) package (PBS mapping 2.55; Schnute et al. 2008).

General linear model (GLM) analysis of covariance (ANCOVA) was used to investigate the effects of regional population of origin and catch region as main effects and day of capture (day of the year) as a covariate on fish body length (SPSS version 11.5; SPSS 2002). We ran another GLM to evaluate the same main effects on fish energy density. All possible models with two-way interactions were examined, and the residuals were examined for lack of fit.

Results

Overall, a total of 2,909 fishing events contributed to the current data set. On a seasonal basis, effort was highest in summer and fall and lowest in winter and spring. On average, effort was highest from the WCVI to SEAK and lowest for the GOA. Catch per unit effort

was highest in CBC in spring and the northern regions in summer (Figure 3), declined in all regions in fall, and was nominal by winter.

Of the 4,156 juvenile sockeye salmon analyzed, 4,062 were allocated to regional populations for which 85% of the fish had a probability of assignment of more than 90%; only 1% of the fish had a probability of assignment of less than 50%. The majority of the fish (42%) were allocated to the Fraser River system (Table 1). Fish from the WCVI accounted for about 15% of the total catch, while Nass and Skeena River fish accounted for about 14%, Rivers Inlet fish for about 6%, and Columbia River fish for about 4%; the rest of the individual populations each comprised 5% or less of the total. Three fish caught in the GOA and SEAK in summer and fall were from Russian stocks. However, these allocations are within the estimation error of the mixed-stock compositions (Figure 4). None of the sockeye salmon analyzed were allocated to Japan.

Regional Distribution of Juvenile Sockeye Salmon

Washington.—Spring catches (Figure 4A) of sockeye salmon off the coast of Washington (n = 76) were primarily composed of Columbia River fish (86%). The remainder were allocated to coastal Washington or Puget Sound (13%). Interestingly, the sockeye salmon allocated to coastal Washington or Puget Sound and caught in the southern transects were smaller (99–110 mm; n = 4) than those caught in the northern transects (150–168 mm; n = 6). Summer catches (n = 69) were again dominated by Columbia River fish (80%); the remainder of the catch was comprised of Washington or Puget Sound (8.5%), Fraser River (6%), CBC (4%), or WCVI fish (2%). No surveys were conducted in this region during fall and winter.
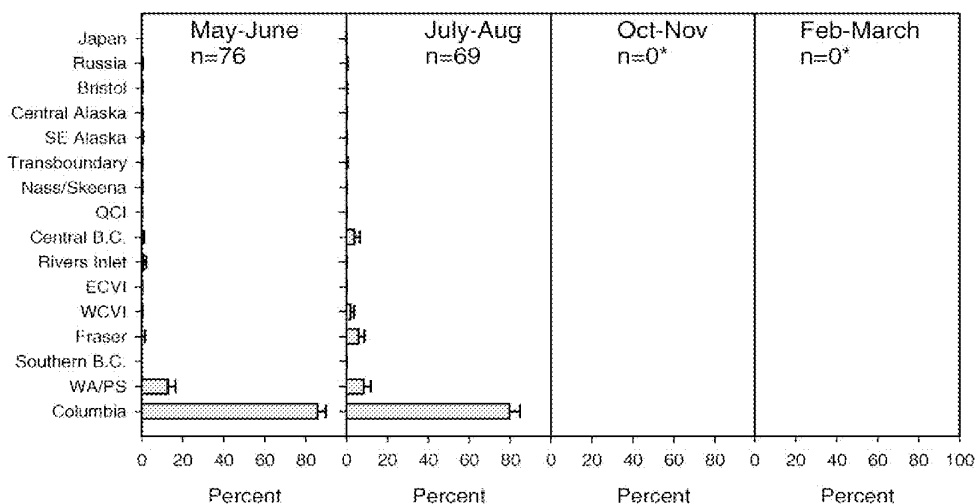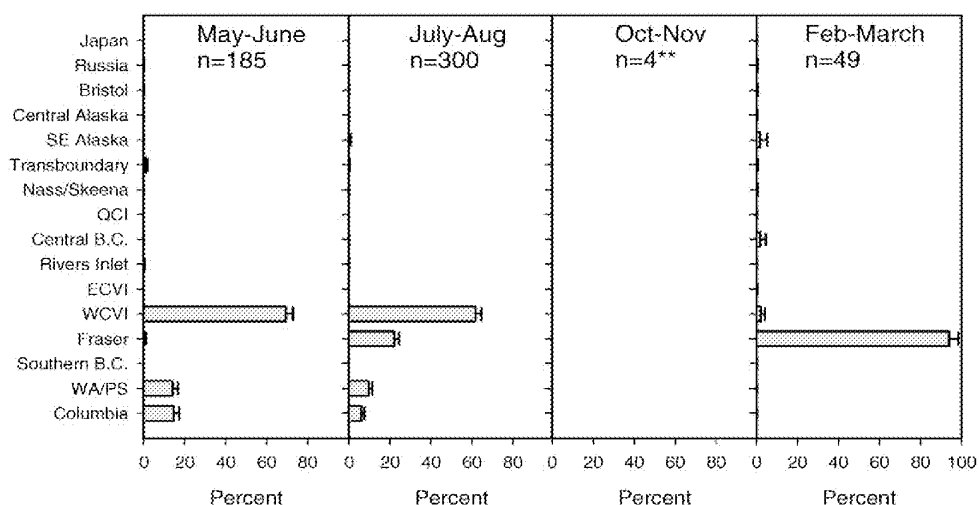
A: Coastal Washington

B: West Coast Vancouver Island

FIGURE 4.—Estimated proportional seasonal stock composition (%) for 7 catch regions (coastal Washington, west coast of Vancouver Island, central British Columbia, west coast of the Queen Charlotte Islands, northern British Columbia, south east Alaska and Gulf of Alaska). Error bars represent 1 standard error; * denotes very low to no sampling effort resulting in zero catch; ** denotes proportional stock composition not estimated due to low sample size.

WCVI.—Spring catches of sockeye salmon ($n = 185$) off the WCVI were predominantly from the WCVI (69.4%), the remainder being composed of Columbia River (15%) and coastal Washington or Puget Sound

fish (14%) (Figure 4B). In summer ($n = 300$), WCVI fish constituted 62% of the catch while 22% were from the Fraser River, 9.5% were from coastal Washington or Puget Sound, and 6% were from the Columbia River
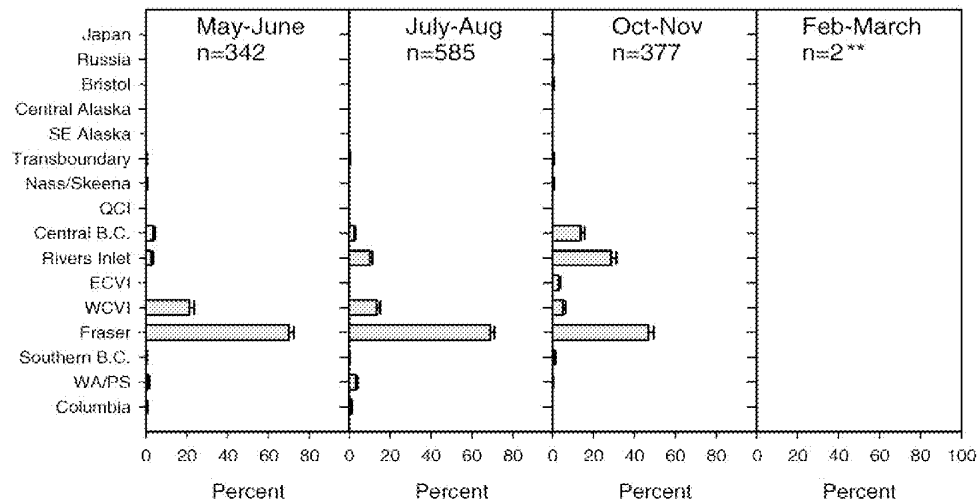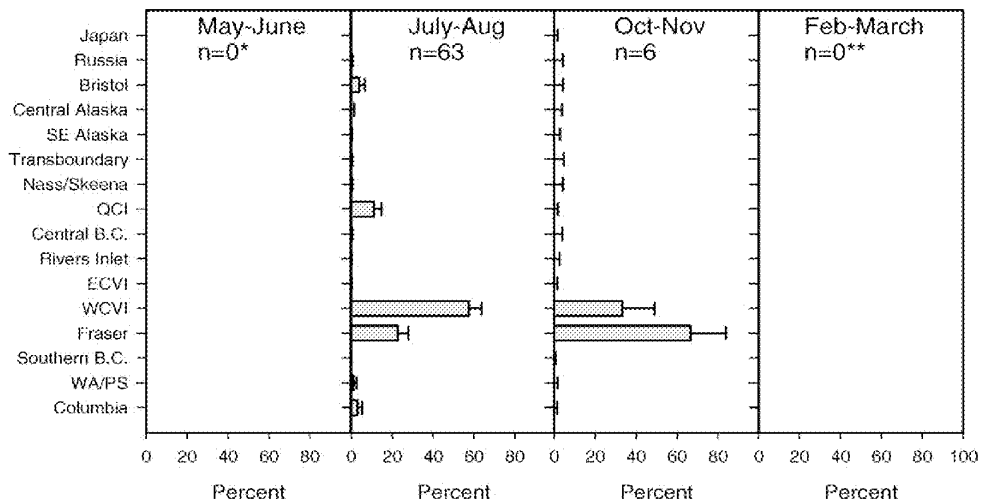
C: Central British Columbia

D: Queen Charlotte Islands

FIGURE 4.—Continued.

system. Only 4 sockeye salmon were caught off the WCVI in fall. However, 49 were caught in winter; 94% of these fish were allocated to the Harrison River in the Fraser River drainage.

CBC.—In spring, 342 sockeye salmon were caught in CBC, 70% from the Fraser River, 21% from the WCVI, 4% from CBC, and 3% from Rivers Inlet

(Figure 4C). By summer, Fraser River stocks comprised 69% of the catch ($n = 585$), while the proportion of Rivers Inlet stocks increased to 10%. The proportions of Rivers Inlet and CBC sockeye salmon increased to 29% and 14%, respectively, in the fall ($n = 377$), while those of Fraser River and WCVI fish dropped to 47% and 5%. Thus, sockeye salmon from

E: Northern British Columbia
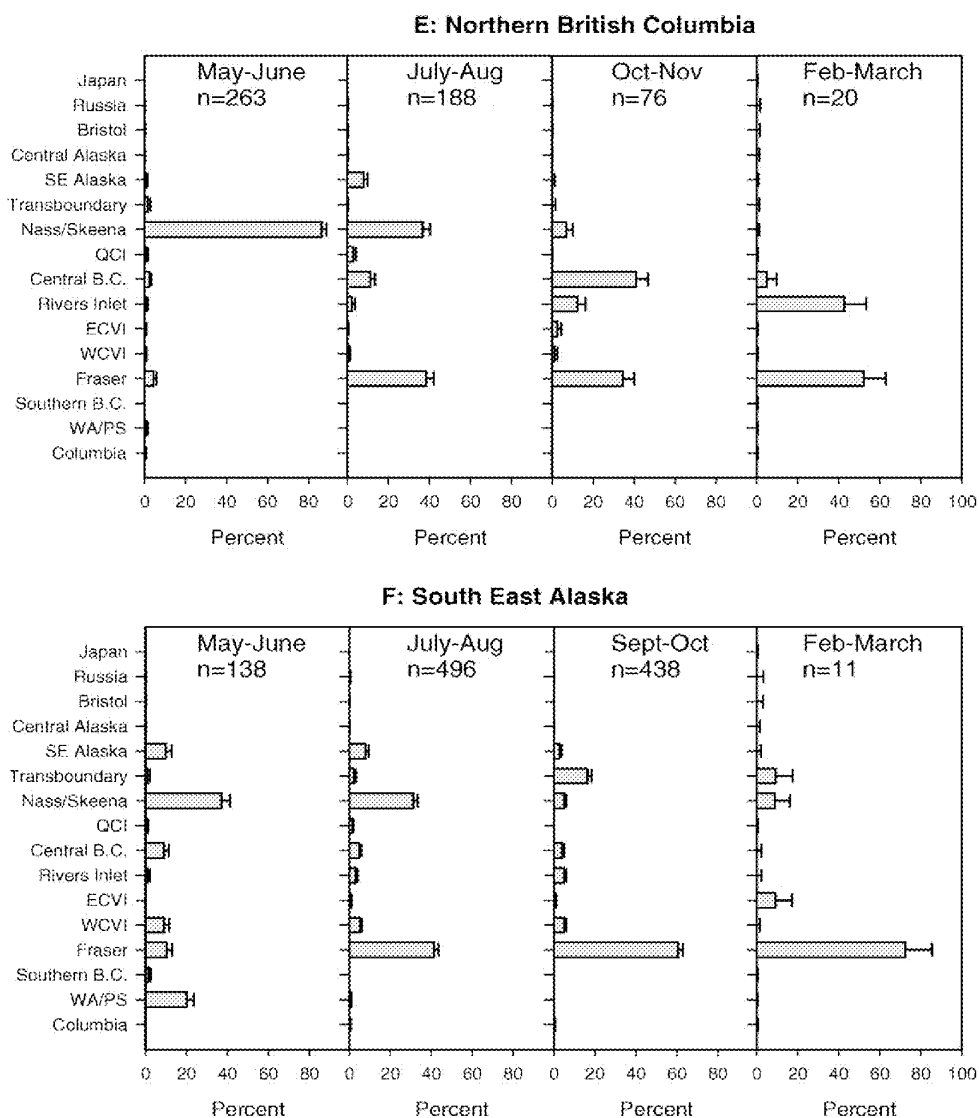

F: South East Alaska

FIGURE 4.—Continued.

Rivers Inlet constituted an increasing proportion of the catch from the spring through fall whereas the proportion of Fraser River fish decreased over this time period. Only 2 fish were caught in winter, both from the Fraser River.

QCI.—Fishing effort was relatively low in the QCI (Figure 2). No sampling was conducted in this area in the spring. In summer, catches were small ($n = 63$) and

composed predominantly of WCVI (58%), Fraser River (23%), and QCI fish (11%) (Figure 4D). Catches declined dramatically in fall ($n = 6$) and winter ($n = 0$), though sampling effort was low during these seasons.

NBC.—In spring, the vast majority of fish caught in NBC ($n = 263$) were from the Nass and Skeena rivers (87%) (Figure 4E). By summer ($n = 188$), the proportion of fish from the Nass and Skeena Rivers
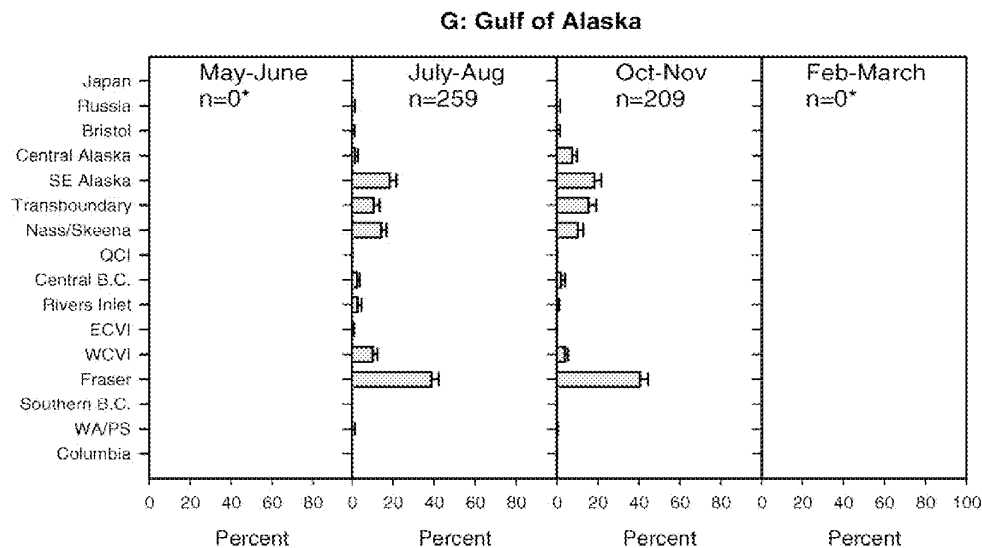
G: Gulf of Alaska

FIGURE 4.—Continued.

declined to 37%, while those from the Fraser River and CBC represented 39% and 11%, respectively. In fall, the sample size dropped considerably ($n = 76$), as did the proportion of Nass and Skeena River fish (7%). Sockeye salmon from CBC then comprised the majority of fish (41%), while Fraser River and Rivers Inlet fish represented 35% and 12% of the total catch, respectively. Catches continued to decline in winter ($n = 20$), the majority of the fish being from the Fraser River (52%) but the proportion of Rivers Inlet fish increased to 43% of the total catch.

SEAK.—The majority of spring catches ($n = 138$) were composed of northern stocks (37% Nass and Skeena rivers, 10% SEAK; Figure 4F). However, fish from the southern stocks (WCVI, Fraser River, and coastal Washington/Puget Sound) made up 40% of those caught. By summer ($n = 496$), the proportion of fish from the northern stocks remained the same while that of Fraser River sockeye salmon increased to 41%. Catches remained high ($n = 438$) in fall, suggesting that there was a high relative abundance of sockeye salmon in the region at this time. Fraser River (61%) and transboundary stocks (16%) constituted the majority of individual stocks. It is interesting to note that in fall the majority of sockeye salmon from the southern stocks were caught in the sheltered inside waters and not on the open shelf. However, we did not sample the inside waters in spring and summer (Figure 2) and so do not know whether these are important areas for these

populations at these times. In winter ($n = 11$), the majority of fish were from the Fraser River system (73%).

GOA.—No surveys were conducted in this region until summer ($n = 259$), when Fraser River stocks represented 39% of the total, WCVI, Nass and Skeena River, transboundary, and SEAK stocks constituting 10, 14, 11, and 18%, respectively (Figure 4G). Catches ($n = 209$) and proportional stock composition were approximately equivalent in the fall. Few surveys were conducted in this region during winter, and no juvenile sockeye salmon were caught.

Seasonal Distribution of Regional Populations

Examples of seasonal distributions of individuals from specific regional populations are presented in Figure 5. All stocks displayed northward migration: by May–June individuals were found adjacent to or north of their respective rivers of origin. For example, we caught individuals from the southern stocks (Columbia, Washington/Puget Sound, Fraser River, WCVI) north of Vancouver Island in May–June. By late summer and fall, individuals from the majority of stocks were caught in NBC, SEAK and/or GOA. The exception to this rapid northward trajectory was sockeye salmon from Rivers Inlet, as these individuals appeared to remain close to their river of origin through October–November (Figure 5E). In addition, fish originating from the Columbia River and Wash-
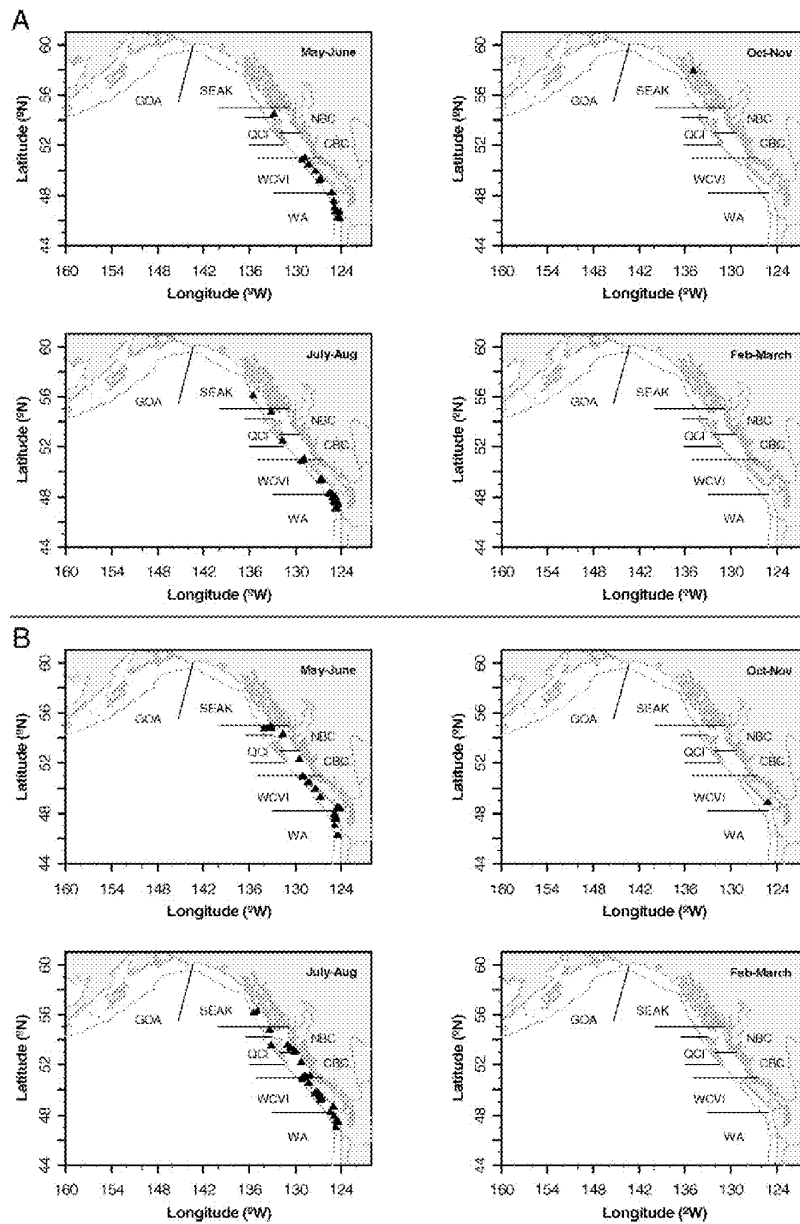
Figure 5.—Seasonal distribution of individual sockeye salmon (triangles) originating from representative stocks Panel A: Columbia River; Panel B: Washington and Puget Sound; Panel C: Fraser River; Panel D: West Coast Vancouver Island; Panel E: Rivers Inlet; Panel F: Nass and Skeena Rivers.
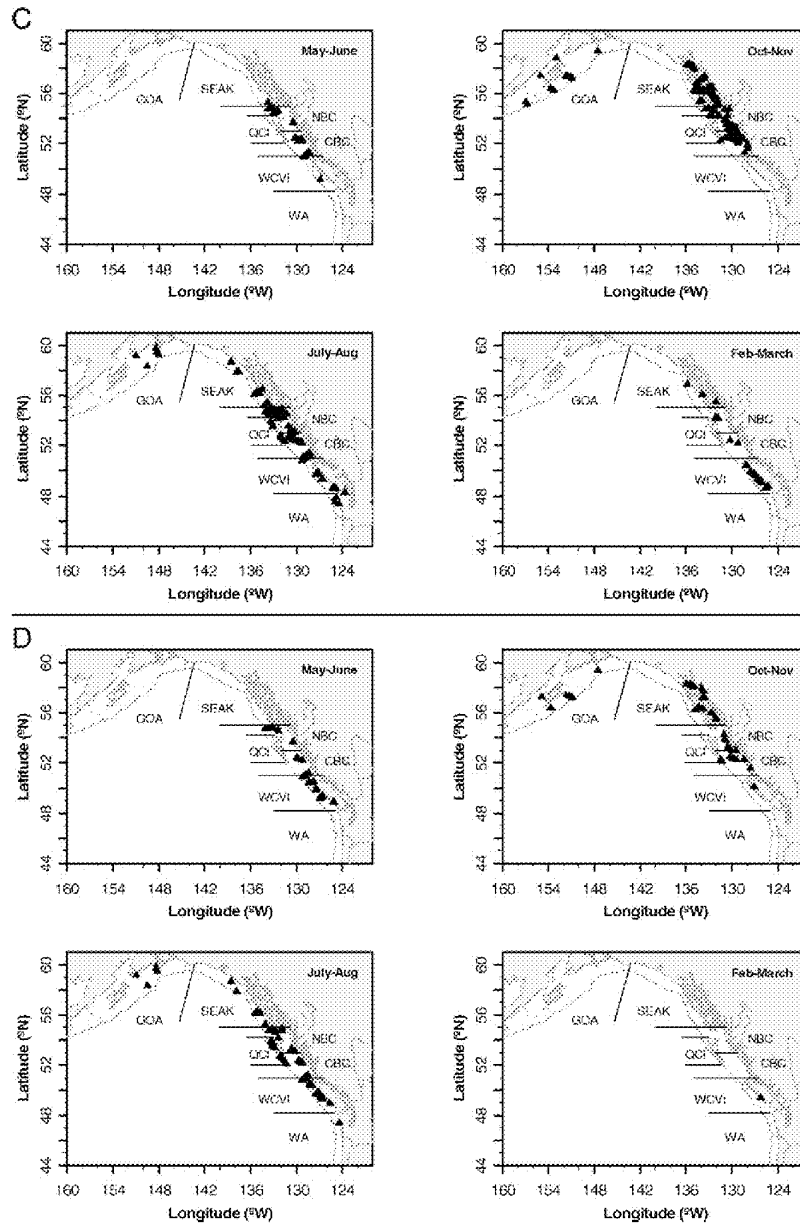
FIGURE 5.—Continued.

ington/Puget Sound stocks did not display the same northwest extent in distribution (Figure 5A, B) as we did not catch any individuals from these stocks beyond SEAK and in fact, few individuals were caught in fall.

In winter, catches were low as most sockeye salmon appeared to have moved away from coastal shelf areas or further north. However effort was low in the GOA at this time.
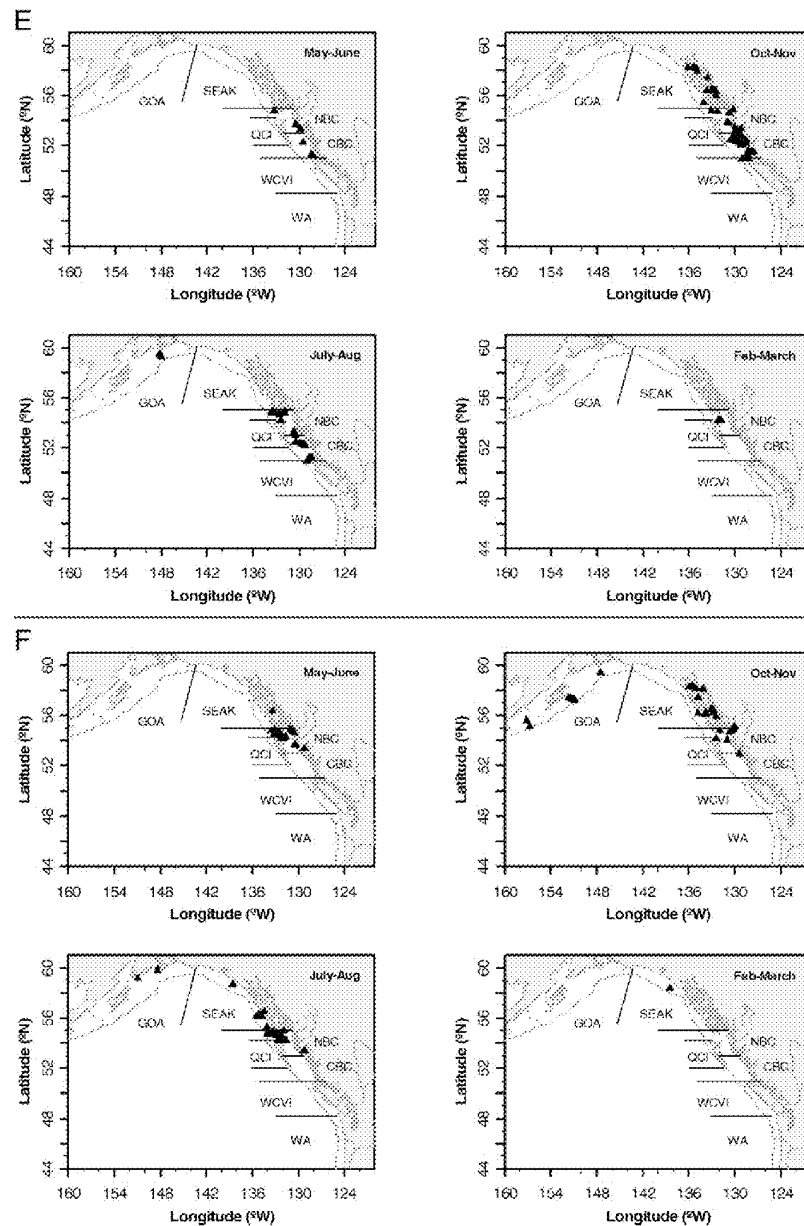
FIGURE 5.—Continued.

Within-Regional-Population Variation in Migration

Given the overall high abundance of Fraser River sockeye salmon, we were able to delineate stock-specific patterns in migration behavior for these stocks.

The majority of Fraser River stocks appear to be migrating from their ocean entry point, the Strait of Georgia, through Johnstone Strait into Queen Charlotte Sound as the majority of these fish were caught in

central BC in May-June as opposed to the WCVI (Figure 5C). Subsequently, fish are traveling rapidly north into NBC and SEAK through Hecate Strait; very few were caught on the west side of the Queen Charlotte Islands. In summer months, the majority of Fraser River sockeye salmon were caught in the central BC region though individuals were caught as far as GOA at this time. However, there were exceptions to this general pattern for stocks from the Fraser River drainage (Figure 6) as not all stocks from here exhibited the same migration pattern. Specifically, sockeye salmon originating from both the Stuart and Stellako Rivers (Figure 6A) displayed a pattern somewhat similar to that observed for Columbia River and Washington/Puget Sound fish (Figure 5A, B) in that no individuals from these two stocks were caught in the fall or winter on the continental shelf. Although fish from these stocks displayed rapid, northward movement similar to other Fraser River fish, they are clearly gone from coastal areas months ahead of other Fraser River stocks (Figure 6C). In winter, catches were low for all stocks of sockeye salmon; however we caught a conspicuous group (n = 47) of sockeye salmon off the west coast of Vancouver Island. These were identified as Harrison River origin individuals from the Fraser River drainage (Figure 6B). In fact, this was the only time of year that Harrison River sockeye salmon were caught; a pattern entirely opposite to other Fraser River origin fish. We noted no other stock-specific differences in migration patterns for fish originating from other large drainage systems.

Body Size and Energy Density

Body size increased with increasing latitude as seasons progressed (Figure 7). Body size was equivalent in spring across all regions although there was greater variance in northern regions likely reflecting a greater range in smolt sizes observed in those areas (Burgner 1991). Body size increased as the seasons progressed, reflecting seasonal growth; however body size was progressively larger in northern sampling areas. Specifically, through ANCOVA we found a significant effect of catch region ($F_{(6, 3993)} = 57.99$; $p < 0.001$), day of year ($F_{(1, 3993)} = 6207.7$; $p < 0.001$) and origin ($F_{(13, 3993)} = 11.14$; $p < 0.001$) on body length of sockeye salmon (Figure 7). In addition, there was a significant interaction between catch region and population of origin ($F_{(39, 3993)} = 2.93$; $p < 0.001$) suggesting differential growth between stocks.

Similarly, energy density increased from spring to fall for fish caught in all regions (Figure 8). However, values declined between the fall and winter sampling periods although sample sizes were smaller in winter. Energy density was equivalent in spring across all

regions but became progressively larger in northern sampling areas. Through the fall, there was a significant effect of catch region ($F_{(4, 2007)} = 7.64$; $p < 0.001$), day of year ($F_{(1, 2007)} = 815.71$; $p < 0.001$) and population of origin ($F_{(13, 2007)} = 2.72$; $p = 0.001$) on energy density of fish. In addition, there was a significant interaction between region and origin ($F_{(26, 2006)} = 3.46$; $p < 0.001$) suggesting differential energy gains between stocks.

Discussion

General migration behavior

We applied genetic stock identification to survey the marine distribution of populations of juvenile sockeye salmon over multiple seasons. This allowed us to reconstruct seasonal changes in stock composition for a number of regions along the continental shelf of the Northeast Pacific Ocean and infer their migratory behaviour. Despite substantial fishing effort, sample sizes were often small precluding an analysis of annual variation. We used the entire Pacific Rim baseline (Beacham et al. 2005a) to ensure all populations were represented and avoid any biases based on preconceived notions of migration patterns; populations absent from the baseline will not be identified in the catch. For the most part, but with notable exceptions, identifying fish from regional populations and individual stocks provided support for the longstanding assertion of northward and westward movement of juvenile sockeye salmon; the model of counter-clockwise migration (Hartt and Dell 1986).

In spring/summer, the majority of sockeye salmon were caught in coastal waters either close to their rivers of origin or further north (Figures 4, 6). For example, Columbia River sockeye salmon dominated catches off Washington; west coast of Vancouver Island sockeye salmon initially predominated in catches off the west coast of Vancouver Island and Queen Charlotte Strait, while northern British Columbia stocks dominated the catches made in NBC and SEAK. As the seasons progressed, stocks were found further to the north of their rivers of origin suggesting that the vast majority of fish undertook a northward migration. Furthermore, the seasonal changes in CPUEs reflect this trend of northward displacement. Fisher et al. (2007) report nominal CPUEs of juvenile sockeye salmon off the coast of Washington between June and July, with catches dropping to zero by fall, suggesting sockeye salmon had moved from these areas by summer. Consistent with trends reported in Fisher et al. (2007) as well as Hartt and Dell (1986) and Jaenicke and Celewycz (1994), abundance was highest in CBC in May-June and declined in July-August. This was
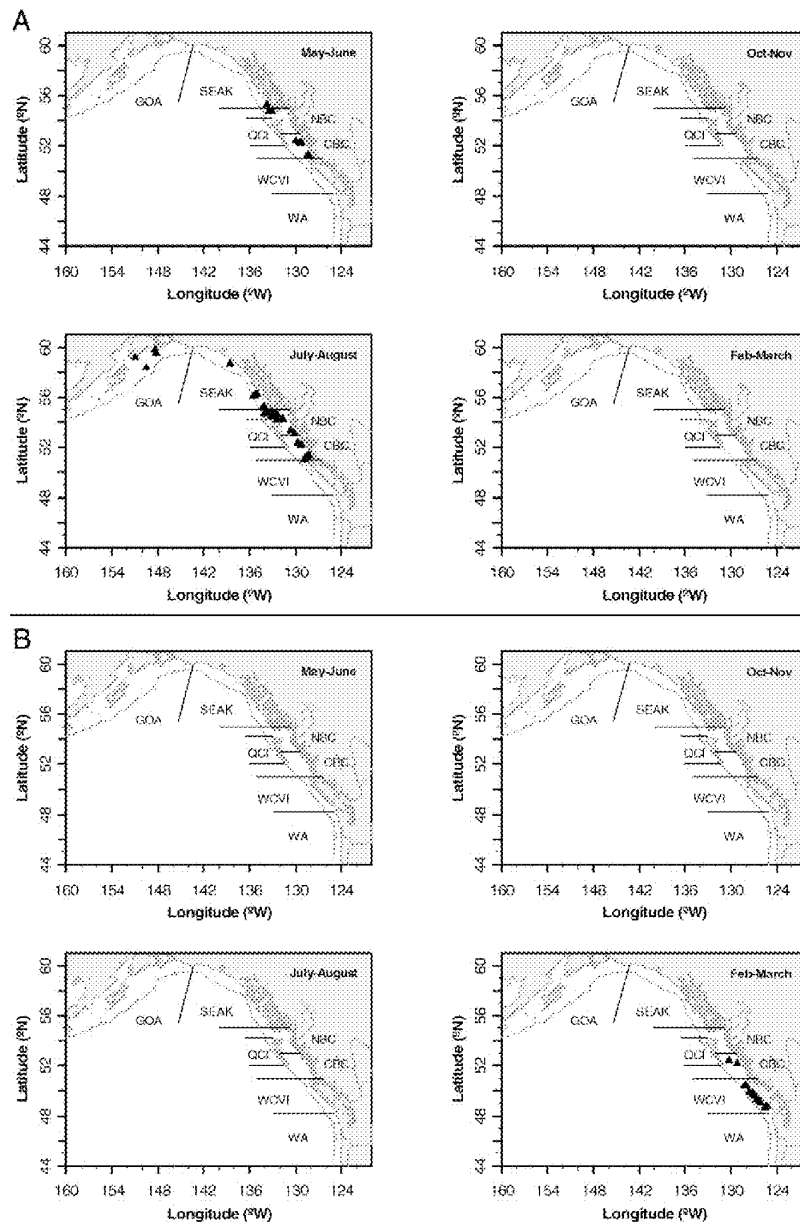
FIGURE 6.—Seasonal distribution of individual sockeye salmon (triangles) originating from the Fraser River drainage. Panel A: Stuart and Stellako Rivers; Panel B: Harrison River; Panel C: Remaining Fraser River stocks include individuals from Birkenhead River, Chilko River, Little River, Adams River, Lower Shuswap River, Middle Shuswap River and Quesnel Lake (Beacham et al. 2005a).
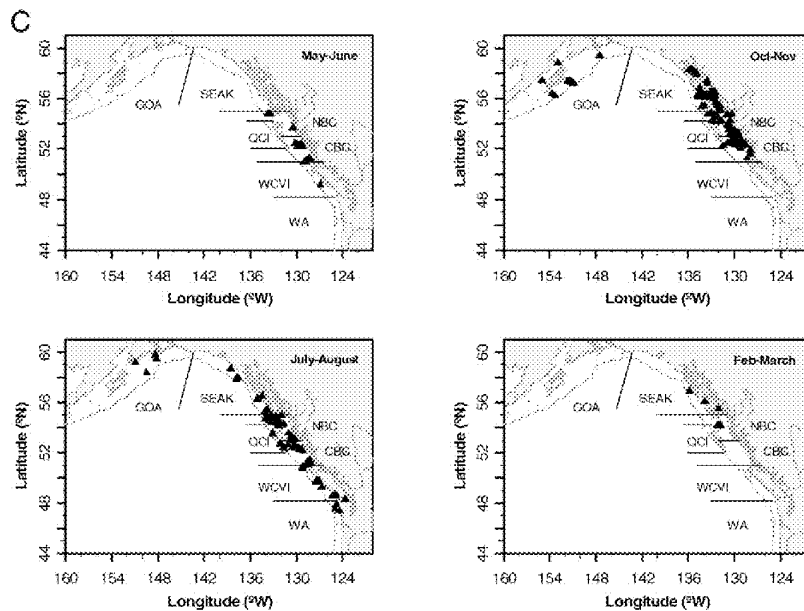
C

FIGURE 6.—Continued.

paralleled by increased CPUEs in northern regions during the summer months.

In July 2007 and again in June 2008, we recovered coded-wire-tagged sockeye salmon: two off the northeast corner of the Queen Charlotte Islands and one off the northern tip of Vancouver Island (Table 2). These were released into Redfish Lake in the Columbia River system in the month of May of respective years (M. Peterson, Idaho Department of Fish and Game, Nampa. personal communication). These fish had thus swum between an estimated 1,800–2,500 km in under two months (estimated travel rate of 40–48 km/d Table 2) supporting the notion of rapid, directed northward movement displayed by these stocks. The relative abundances of sockeye salmon declined in all regions in fall and were minimal to zero by winter, suggesting that juvenile sockeye salmon are leaving coastal shelf areas at some point between these two sampling periods. However, it should be noted that due to severe weather conditions encountered in fall and winter and associated hazards, coastal waters of GOA remain poorly sampled during these time periods. Thus, the winter abundance of juvenile sockeye salmon in these waters will likely continue to remain unclear.

Although most juvenile sockeye salmon migrated north, a small number of fish (n = 11) were recovered south of their region of origin. In particular, west coast

of Vancouver Island, Fraser River, and Puget Sound sockeye salmon were recovered off the coast of Washington during the summer months. These fish may have been transported south by the equatorial flow of the California Current System in the spring and summer (Crawford and Thomson 1991). Similarly, approximately 4% of the juvenile sockeye salmon caught in this region during summer were allocated to Central BC. However, we suspect that these fish were misclassified, as no Central BC juvenile sockeye salmon were recovered off the west coast of Vancouver Island, a region located between Central BC and the coast of Washington. These could merely be errors in allocation due to gaps in the baseline (Beacham et al. 2005a).

Stock-specific migration behavior

Typically, Fraser River sockeye salmon migrate to sea between the months of May and June after one year of freshwater residency. The major exit corridor for salmon emigrating from the Fraser River is thought to be Queen Charlotte Strait rather than Juan de Fuca Strait (Groot and Cooke 1987; Burgner 1991; Welch et al. 2009). Most yearling smolts are thought to leave the Strait of Georgia by June through July (Burgner 1991; Beamish et al. 2001); the same time period when large numbers were caught in central BC. By summer, the
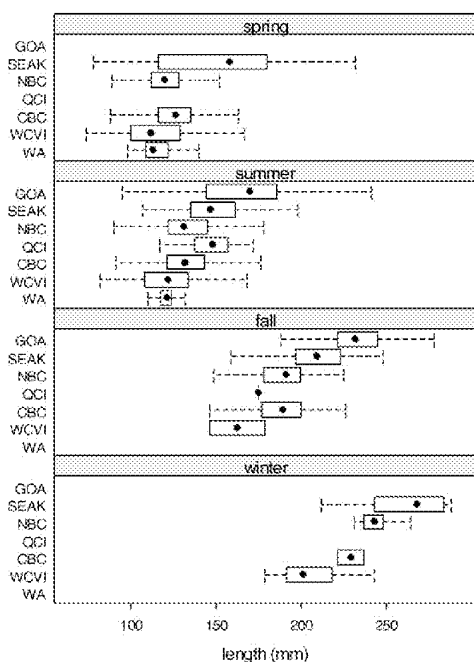
FIGURE 7.—Box plot of body size (mm) for juvenile sockeye salmon caught in different catch regions in each of four seasons.
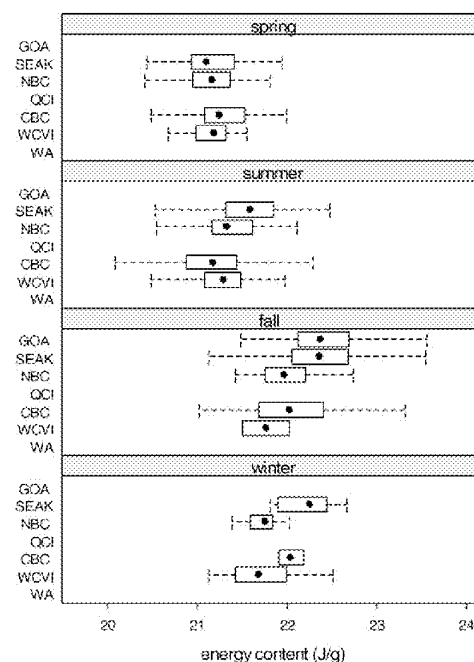
FIGURE 8.—Box plot of energy density (J/g) for juvenile sockeye salmon caught in different catch regions in each of four seasons.

majority of Fraser River sockeye salmon were caught in the central BC region (n = 403) including Queen Charlotte Sound, Hecate Strait, the West Coast of the Queen Charlotte Islands and Dixon Entrance, suggesting rapid northward migration. A small number of Fraser River sockeye salmon (n = 36) were caught off the west coast of Vancouver Island in summer suggesting that at least a portion of the population is leaving the Strait of Georgia south via Juan de Fuca Strait. This is consistent with the pattern of exit seen for a specific Fraser River stock, Cultus Lake, measured using a large-scale telemetry array (Welch et al. 2009). Probably due to the small population size

and thus extreme conservation concern for Cultus Lake sockeye salmon (COSEWIC 2003), we only identified one Cultus Lake fish in our samples. By fall, Fraser River sockeye salmon were caught as far north and west as the Alaska Peninsula with the majority of fish caught in central BC, northern BC and southeast Alaska.

Stock-specific differences in migration patterns were also apparent within the Fraser River system. The Harrison River sockeye salmon population display an "ocean–type" life history pattern: they migrate to sea shortly after emergence from gravel and enter the marine system in spring (Burgner 1991). Therefore,

TABLE 2.—Release and capture information for coded-wire-tagged sockeye salmon. All fish were released into Redfish Lake, Idaho, in the Columbia River system in the spring of the recovery year. The distance traveled consists of an estimated 1,445 km from Redfish Lake to the mouth of the Columbia River and the straight line distance from there to the point of capture.

Tag number	Release date	Capture date	Length at capture (mm)	Capture location	Distance traveled (km)	Speed (km/d)
108277	7 May 2007	1 Jul 2007	162	54°14′49″N, 131°40′44″W	2,508	46
101781	7 May 2008	21 Jun 2008	138	49°2′52″N, 126°6′28″W	1,797	40
094629	7 May 2008	28 Jun 2008	193	54°27′21″N, 131°35′45″W	2,525	48

they are particularly small when they enter the Strait of Georgia relative to other sockeye salmon smolts. It is thought that fry may remain within the Fraser delta for as long as 5 months (Birtwell et al. 1987). Subsequently, they are found well dispersed in the Strait of Georgia by August and September (RJ Beamish, Pacific Biological Station, personal communication) and reach a size similar to yearling smolts by September (Healey 1980). However, it is unknown when they leave the Strait for the exposed shelf waters and by which route (Burgner 1991). In this study, all Harrison River sockeye salmon were caught during the winter following their first year at sea. Considering that only four juvenile sockeye salmon were caught off WCVI during fall with slightly more fishing events than during winter (fall = 323 tows; winter = 271 tows), these winter catches are highly significant. These results also suggest that Harrison River sockeye salmon are migrating through Juan de Fuca Strait, as these fish were primarily recovered off the west coast of Vancouver Island (n = 47) rather than in Queen Charlotte Sound (Figure 6B). The life history of the Harrison River stock puts them in the marine environment almost a full year ahead of their congeners as other Fraser River stocks typically smolt following one year of freshwater residence. In addition, these fish appear to be following a northward trajectory along the shelf months ahead of other southern stocks smolting in May and June. Essentially, no other juvenile sockeye salmon are found off WCVI in winter as fish which smolted in the same year have generally moved north or offshore by this point. Interestingly, Harrison River sockeye salmon marine survival and returns are among the highest within the Fraser River system (Sue Grant, Fisheries and Oceans Canada, personal communication). We therefore hypothesize that this timing of northward migration confers an advantage over other southern stocks with respect to early marine survival and growth since these fish would be able to exploit more favorable feeding conditions earlier or escape potential competition pressure from other juvenile salmonids or a seasonal incursion of pelagic piscivorous fishes into southern BC waters (e.g., Ware and McFarlane 1995; Orsi et al. 2007).

We found additional evidence for stock-specific differences among Fraser origin sockeye salmon. Specifically, sockeye salmon from the Stuart and Stellako Rivers disappeared from coastal regions by fall although they did exhibit the same northward extent in distribution as other Fraser River stocks (Figure 6). Not capturing fish from these stocks due to low stock size and consequent low probability of capture is unlikely, as fishing effort was high in October and November and we identified sockeye salmon from relatively small populations within the Fraser River drainage during this time. Interestingly, escapement trends for these stocks over the time period of our study are different as Stuart River sockeye salmon have been declining in number while escapement for Stellako River sockeye salmon has been consistent and fairly substantial (Stock Assessment, Fisheries and Oceans Canada). Therefore, it is unclear at this point if there is any link between population trends and migration patterns for these stocks.

Size and energy density

Growth and energy accumulation are highly variable in fish and influenced by both genetic factors and environmental conditions (Weatherley et al. 1987; Arendt 1997; Trudel et al. 2007a). For each population of sockeye salmon identified here, body size (i.e., fork length) was consistently smaller in southern regions than northern regions within each season and the difference increased over time. In addition, we found higher energy densities in fish caught in northern regions suggesting higher rates of energy deposition. We did not display population specific results given the number of different populations but report a significant statistical effect. We have likely pooled juvenile sockeye salmon across smolt ages. However, our size cut-offs for fish in their first year at sea are within those limits reported for smolt sizes (Burgner 1991) and thus encompasses age 0.0, 1.0 and 2.0 fish. Therefore the range of sizes encompasses all age classes and variation in size. Despite this, the trend is clearly obvious. This latitudinal trend in body size parallels observations from previous studies (e.g., Hartt and Dell 1986; Jaenicke and Celewycz 1994; Farley et al. 2005).

There are several competing, though not mutually exclusive, hypotheses to explain this pattern: 1) fish are encountering better growing conditions as they move north thereby attaining larger sizes, 2) larger fish migrate faster or 3) there is variation in time and size at ocean entry (and thus the initiation of rapid growth). Juvenile sockeye salmon consume a diet composed predominantly of invertebrate prey (Brodeur et al. 2007). As lipid content is generally higher in northern species of copepods than southern copepods (Peterson and Schwing 2003; Mackas et al. 2004) and simulation models have shown that juvenile salmon growth is highly sensitive to small changes in prey energy density (Trudel et al. 2002), juvenile sockeye salmon should be expected to grow faster at higher latitudes. In addition, there is evidence for a decreasing trend in potential competition with other planktivorous species as abundances of clupeids decline approximately tenfold between the California Current System and the Alaska Coastal Current (Orsi et al. 2007). These

observations would lend support to the hypothesis of more favorable growing conditions in northern regions. However, stock-specific smolting times are not typically an abrupt event, and indeed larger sockeye salmon have been reported to smolt earlier (Burgner 1991). Thus, larger fish may simply have been larger smolts or have been at sea for a longer period of time. Clearly this pattern requires further exploration and might be resolved with an examination of individual and stock-specific growth trajectories through an analysis of ageing structures, coupled with detailed estimations of diets and region-specific measurements of prey energy densities.

Migration behavior and marine survival

The diversity and complexity of mechanisms regulating the fluctuations of salmon populations indicate the need to consider: 1) assessment of ecosystem-scale marine environment properties and in turn, 2) the variety of ocean regions that salmon migrate through during their lives. Accurately defining patterns of migration then has broad implications for managing particular salmon populations and for forecasting the effects of climate change on salmon fisheries. In the case of sockeye salmon, this is perhaps best exemplified by recent observations of differential survival of particular BC stocks.

With annual catches often exceeding one million fish until the late 1970s, sockeye salmon stocks from Rivers Inlet in the CBC formed one of the most valuable salmon fisheries in British Columbia (Walters et al. 1993; McKinnell et al. 2001). However, despite prompt action to sharply reduce harvest rates in the early 1980s to compensate for sharply declining recruitment following the 1977 regime shift (Hare et al. 1999), these stocks collapsed over a 20-year period to approximately 0.1% of their initial abundance, and have been closed to commercial fishing since 1996 to protect and rebuild the stocks (Rutherford and Wood 2000; McKinnell et al. 2001). Although the specific cause of the collapse has not been established, it would appear to be due to an extended period of poor marine survival (Rutherford and Wood 2000; McKinnell et al. 2001). The lack of consistent trend in egg-to-smolt survival since 1960 and the parallel collapses of sockeye salmon stocks from nearby watersheds such as Smith Inlet, where freshwater habitat is nearly pristine, further indicate that these declines were likely due to a common cause in the marine environment (Rutherford and Wood 2000; McKinnell et al. 2001). Such drastic declines in marine survival were not observed for other sockeye salmon stocks over the same time period. The cause is particularly interesting when one considers that the primary migration pathway

for the vast majority of juvenile Fraser River sockeye is past the mouth of both Rivers and Smith Inlets.

The summer distribution of juvenile Rivers Inlet sockeye salmon catches was centered in inshore waters of central BC including Queen Charlotte Sound (adjacent to Rivers Inlet), Hecate Strait and Dixon Entrance. Numbers increased by fall (perhaps suggesting a later smolt out-migration) and fish were concentrated in central BC particularly Queen Charlotte Sound, Hecate Strait and inside coastal waters. Overall fall catch rates for sockeye salmon dropped sharply relative to summer, while the proportional abundance of Rivers Inlet sockeye salmon increased. Escapement data collected over the time-period of our study suggests that Fraser River sockeye salmon (3.8 million; Fraser Stock Assessment, Fisheries and Oceans Canada) are on the order of 57 times more abundant than Rivers Inlet sockeye salmon (66000; Stock Assessment, Fisheries and Oceans Canada). However in the CBC catch region in spring, summer, and fall, the proportion of Rivers Inlet fish increased as the seasons progressed while the proportion of Fraser River sockeye salmon decreased and only exceeded Rivers Inlet fish by 27, 7, and twofold respectively. Similarly in NBC, the proportion of Rivers Inlet fish also increased as the seasons progressed and in all seasons the proportion of juvenile Fraser River sockeye salmon only exceeded Rivers Inlet fish by 1.2–17 fold. This suggests that juvenile Rivers Inlet sockeye salmon were disproportionately more abundant in these waters relative to expected stock sizes. We therefore conclude that Fraser River sockeye salmon migrated to the north along the coast while Rivers Inlet sockeye salmon remained resident in the coastal region near their rivers of origin. This is evident in the maps of stock-specific distribution shown in Figure 5.

Given that our analyses showed juvenile sockeye salmon size was higher at northern latitudes along the continental shelf of the west coast of North America, stocks that remain in southern regions for extended periods of time would also be expected to sustain higher mortality because of their smaller attained body size (e.g., McGurk 1996, 1999). For instance, juvenile Rivers Inlet sockeye salmon remain in the Central Coast of British Columbia, an area of low growth, for more than six months and have experienced poor marine survival for at least the last two decades (McKinnell et al. 2001). In contrast, most Fraser River sockeye salmon stocks undertake a rapid northward migration along the continental shelf and have generally maintained high marine survival. However in contrast to Fraser River sockeye salmon, other southern stocks are presently exhibiting poor returns (Good et al. 2005) despite displaying a similar pattern

of northward migration. As mentioned above, potential competition with high abundances of other planktivorous species within the California Current ecosystem may be a contributing factor to poor growth conditions and survival for sockeye salmon (Orsi et al. 2007). Given the ocean entry point of Washington/Puget Sound and Columbia River stocks and their subsequent northward migration path up the west coast of Vancouver Island, this hypothesis may help explain their lower marine survival compared to Fraser River stocks. Thus, the fate of individual stocks may depend on where they migrate to in the ocean and how much time they reside in different areas.

Accuracy of DNA analyses

The validity of these interpretations depends on the accuracy of the DNA analyses performed in this study. Overall, the DNA allocations appear to be reasonable. First, as with previous tagging studies (i.e., Hartt and Dell 1986), the DNA analyses in conjunction with changes in CPUE suggest that juvenile sockeye salmon are generally undertaking a northward migration along the continental shelf. Second, with the exception of Southeast Alaska in spring, the majority of the juvenile sockeye salmon were caught in coastal waters in proximity to their respective rivers of origin. For Southeast Alaska, 40% of the juvenile sockeye salmon caught in the spring were allocated to southern stocks (WCVI, Fraser River and Washington/Puget Sound). A closer inspection of the data revealed that fish that were caught in Southeast Alaska early in the spring (May 23–26) were allocated to the Nass and Skeena Rivers. All the juvenile sockeye salmon caught during spring in Southeast Alaska that were allocated to southern stocks were caught late in the spring (June 17–19). Thus, the high proportion of southern stocks in Southeast Alaska during spring is merely an artifact of requisite categorization of data into temporal and spatial blocks as we used June 21 as a division between spring and summer. Finally, estimates performed on a mixture of known origin fish (from Fraser, Skeena, Nass, Stikine, and Alsek Rivers) indicate that 86–99% of sockeye salmon were correctly allocated to the stock and region of origins with the current DNA baseline used in this study, suggesting that only a small fraction of the fish caught would be misallocated (Beacham et al. 2005a).

Nevertheless, there were likely some misallocations in our dataset, though they likely represented less than 1% of the samples analyzed. Some of these misallocations can be readily identified. For example, three fish from Russia were noted in our results. This level of allocation is within the estimation error of mixed stock compositions. It is likely then that these were misallocations. The juvenile salmon that were allocated to Washington/Puget Sound, specifically to Lake Washington, off the Washington coast during spring were smaller near the Columbia River (99–110 mm; n = 4) than those caught a few 100 km north (150–168 mm; n = 6). Given that the average size for Lake Washington sockeye salmon smolts is around 125 mm (contained in Burgner 1991), it is unlikely that these four fish originated from Lake Washington. These misallocations are likely due to gaps in the baseline of coastal Washington stocks (Beacham et al. 2005a).

This is the first effort to characterize the ocean migration of juvenile sockeye salmon through the application of current DNA-based techniques over the eastern Pacific continental shelf. We also present a preliminary assessment of the implications of regional residency on juvenile sockeye salmon growth performance. The capacity to identify individual fish to stock of origin through genetic analysis coupled with other biochemical tracers (i.e., Tucker and Rasmussen 1999; Trudel et al. 2000, 2001) will likely prove extremely insightful in identifying field-based processes and the subsequent underlying influence of various environmental factors influencing salmonid production.

Acknowledgments

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