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ARTICLE

Life History and Seasonal Stock-Specific Ocean Migration of Juvenile Chinook Salmon

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Abstract

The ocean feeding grounds of juvenile Pacific salmon *Oncorhynchus* spp. range over several thousand kilometers in which ocean conditions, prey quality and abundance, and predator assemblages vary greatly. Therefore, the fate of individual stocks may depend on where they migrate and how much time they spend in different regions. Juvenile ($n = 6,266$) and immature ($n = 659$) Chinook salmon *Oncorhynchus tshawytscha* were collected from coastal Washington to Southeast Alaska in coastal trawl surveys from February to November 1998–2008, which allowed us to reconstruct changes in stock composition for seasons and regions by means of DNA stock identification techniques. Individuals were allocated to 12 regional stocks. The genetic stock assignments were directly validated by showing that 96% of the 339 known-origin, coded-wire-tagged fish were accurately allocated to their region of origin. Overall, the analyses performed in this study support the main findings of previous work based on tagging. However, given that the sample sizes for all stocks were larger and additional stocks were analyzed, we can extend those results; coastal residency of local stocks in their first year at sea with differences between smolt classes for southern stocks. Notably, yearling Chinook salmon moved quickly into waters north of the west coast of Vancouver Island, including Southeast Alaska. Furthermore, subyearling salmon were found over shallower bottom depths than yearling fish. Summer catches in all regions were dominated by Columbia River yearling fish, which suggests a rapid northward migration. In contrast, very few Columbia River subyearling fish were recovered north of Vancouver Island. Columbia River fish were a minor component of the catches in fall and winter, as fish originating from other southern stocks dominated catches off the west coast of Vancouver Island while northern British Columbia and Southeast Alaska stocks dominated northern regions during these time periods. In addition, we found no effect of hatchery origin on the distribution of fish.

The ocean feeding grounds of juvenile Pacific salmon *Oncorhynchus* spp. range over several thousand kilometers in which physical conditions, prey quality and abundance, and predator assemblages vary greatly. Hence, the fate of individual stocks may depend on where they migrate and how much time they spend in different regions. Although it has been reasonably well established that juvenile Pacific salmon undertake a northward migration along the continental shelf (Hartt and Dell 1986; Bi et al. 2007, 2008; Morris et al. 2007; Trudel et al. 2009; Tucker et al. 2009), it has been difficult to assess stock-specific

migration patterns owing to the logistical difficulty of inferring juvenile salmon migration using traditional tagging approaches. Moreover, the extent of the spatial and seasonal variations in the distribution and movement of juvenile salmon from different stocks is poorly known (Welch et al. 2002, 2004; Morris et al. 2007).

Chinook salmon *Oncorhynchus tshawytscha* are widely distributed along the west coast of North America, ranging from central California to northern Alaska (Healey 1991). The ocean migration of Chinook salmon smolts can take place either within

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a few months after emergence from gravel (referred to as sub-yearling or "ocean type") or after completing a full year in freshwater (referred to as yearling or "stream type"). The return of mature Chinook salmon adults to natal spawning grounds (adult run timing) occurs at nearly any time of the year and appears to be closely associated with geographic distribution: spring runs predominate in the north, whereas fall runs are almost exclusively distributed south of 56°N, where they predominate in all runs (Healey 1991). The exceptions are the Fraser River and the Columbia River systems, as well as populations in northern Puget Sound where spring and summer runs are also found. Although not exclusive, smolts of fall-run Chinook salmon typically migrate as subyearlings while spring-run Chinook salmon smolts typically migrate as yearlings (Healey 1991; Teel et al. 2000; Waples et al. 2004). Thus, the geographic distribution of the adult run timing groups largely coincides with the geographic distribution of yearling and subyearling smolt life history forms. Again exceptions are the Fraser and Columbia rivers where both smolt types are found (Healey 1991; Waples et al. 2004); yearling smolts tend to be found in the upper reaches of these large river systems.

The at-sea abundance and distribution of juvenile Chinook salmon has been described previously. Hartt (1980) and Hartt and Dell (1986) report extensive sampling of juvenile salmon and trends in abundance along the coast of North America throughout the North Pacific Ocean from the Columbia River to Bristol Bay, Alaska, over a 15-year period from spring to fall in both inshore and offshore waters. By far the majority of captures (97%) of juvenile Chinook salmon were concentrated in coastal shelf waters and were subsequently identified as stream-type or yearling fish (Healey 1983). Sampling in subsequent years by Miller et al. (1983) and Fisher et al. (1983, 1984) suggest that yearling Chinook salmon in their first ocean-year are more common in the outer coast from coastal Washington and northward while subyearling Chinook salmon were more common in sheltered waters. Thus, yearling Chinook salmon are believed to undertake a rapid and extensive migration along the continental shelf then rear in offshore waters before returning to their natal rivers in the spring and summer of subsequent years to spawn. Subyearling Chinook salmon are believed to establish residence on the continental shelf before returning to their natal rivers in the summer and fall of subsequent years to spawn.

Distributions also appear to vary between smolt types on smaller spatial scales, particularly with respect to bottom depth. Depth is considered a proxy for proximity to shore or the shelf break and potentially indicative of different environmental conditions and species assemblages (e.g., Orsi et al. 2007). Fisher et al. (2007) provided a qualitative description of the depth associations of smolt types in amalgamated catches of Chinook salmon across the North Pacific Ocean. Subyearling Chinook salmon had a shallow, inshore distribution in all regions where they occurred. Median depths were actually consistent between 40 and 60 m and inshore of the median sampling depth. Yearling Chinook salmon were typically caught over deeper bot-

tom depths (~20 m deeper). No consistent associations with water temperature or salinity for either subyearling or yearling salmon were found (Fisher et al. 2007). These observations were not tested statistically, nor were stock-specific effects controlled for. However, these results support previous work that had more constrained regional sampling (Miller et al. 1983; Fisher and Pearcy 1995; Brodeur et al. 2004).

Few studies have examined the stock-specific migration behavior of juvenile Chinook salmon, possibly owing to the difficulty of catching juvenile salmon at sea and determining their origins. These studies generally focused on a relatively small area (<500 km) and may not adequately describe the migration of juvenile Chinook salmon (Teel 2004; Trudel et al. 2004). However, Trudel et al. (2009) reconstructed the initial ocean migration routes of juvenile Chinook salmon originating from Oregon to Southeast Alaska using coded wire tag (CWT) recovery data. This was possible by the recent availability of samples taken in coastal and offshore surveys along the coast of North America in large-scale programs to study juvenile salmonids during their ocean phase (e.g., Brodeur et al. 2004; Trudel et al. 2007, 2009). Over a 12-year period, 1,862 coded-wire-tagged juvenile Chinook salmon were recovered along the coast from Oregon to Alaska from March to November and allocated into seven regional stocks (Southeast Alaska, West Coast Vancouver Island, Strait of Georgia, Puget Sound, Washington, Columbia River, and Oregon). Contrary to the paradigm of migration described above, most juvenile Chinook salmon, except those from the Columbia River, remained within 200–400 km of their natal rivers until their second year at sea, irrespective of their freshwater history and adult run timing. Northward migration of most coastal stocks was initiated during their second or possibly third year at sea, whereas Strait of Georgia and Puget Sound stocks (further referred to as Salish Sea stocks) primarily migrated onto the continental shelf after their first year in the ocean (Trudel et al. 2009). Interestingly, only Columbia River Chinook salmon undertook a rapid northward migration that varied among life histories and stocks. Spring or yearling Chinook salmon were recovered as far north as Prince William Sound, Alaska, during their first summer at sea, whereas very few Columbia River fall or subyearling Chinook salmon were recovered north of Vancouver Island. While the spatial scale of this study is ample and the number of recoveries of this study far surpasses previous work, the analysis is limited to stocks in which fish were tagged and included only a few wild fish.

Genetic mixed-stock analysis with DNA microsatellite variation has been used over the last decade to estimate the origins of ocean-caught Pacific salmon (e.g., Beacham et al. 2002, 2003, 2005, 2006a, 2006b). However, most of these applications have focused on maturing adult fish in relation to fisheries management. Recently, genetic stock identification efforts have also been directed at the study of mixtures of juvenile salmon caught at sea (e.g., Teel et al. 2003; Brodeur et al. 2004; Seeb et al. 2004; Van Doornik et al. 2007) and has successfully reconstructed stock-specific, coast-wide, counter-clockwise

migration for juvenile sockeye salmon *O. nerka* (Tucker et al. 2009). Recent genetic work on juvenile Chinook salmon has also proven successful to contrast the stock composition of salmon caught at sea and infer their migratory behavior (Teel 2004; Trudel et al. 2004). However, these studies focused on relatively few stocks and were limited in geographic scope.

A regional stock structure has been observed in the Pacific Rim analysis of microsatellite variation (Beacham et al. 2006b), such that stocks within particular lakes and river drainages are more similar to each other than to stocks in other lakes or river drainages. There are of course over 1,000 Chinook salmon spawning populations in British Columbia alone (Healey 1991). Not all stocks or river systems are equally sampled and differentiated, but identification is robust when pooled into regional or watershed stocks (Beacham 2006a, 2006b). Based on the recovery of known-origin, coded-wire-tagged fish and simulation studies, regional stock structure allows correct assignment to region even for those portions of the mixed-stock sample that may not be explicitly represented in the baseline (Beacham et al. 2006a; Parken et al. 2008). However, as with any method, further testing with field data is desirable. Analysis of known-origin samples, as opposed to simulations studies, is the most stringent test because sample genotypes are independent of the baseline.

In this study, we contrast the migration trajectories of juvenile Chinook salmon from various production areas using microsatellite DNA markers. The current work thus expands on the CWT results reported by Trudel et al. (2009). As origin of individuals can be estimated for all fish, sample size can be increased to allow for an examination of the consistency in seasonal migration patterns between stocks and life history variants. Furthermore, information can be generated for wild stocks and individuals that are not tagged. For example, results were reported for 7 out of a potential 12 regional stocks in the sampling area (Beacham et al. 2006a, 2006b; Trudel et al. 2009). The results of Trudel et al. (2009) were primarily restricted to fish reared under hatchery conditions, which may not reflect the behavior of wild fish, except for the Columbia River fish, which tend to be primarily of hatchery origin. The current study essentially encompasses the majority of the coastal range of the eastern North Pacific Ocean (Figure 1) where Chinook salmon occur during their first year at sea (excluding northern Alaska and the Bering Sea). As a point of interest, we also present results for Chinook salmon caught in their second year at sea (immatures) while recognizing potential biases in our surface sampling regime (older Chinook salmon are probably under-represented in these samples because of their tendency to be distributed deeper in the water column, Orsi and Jaenicke 1996).

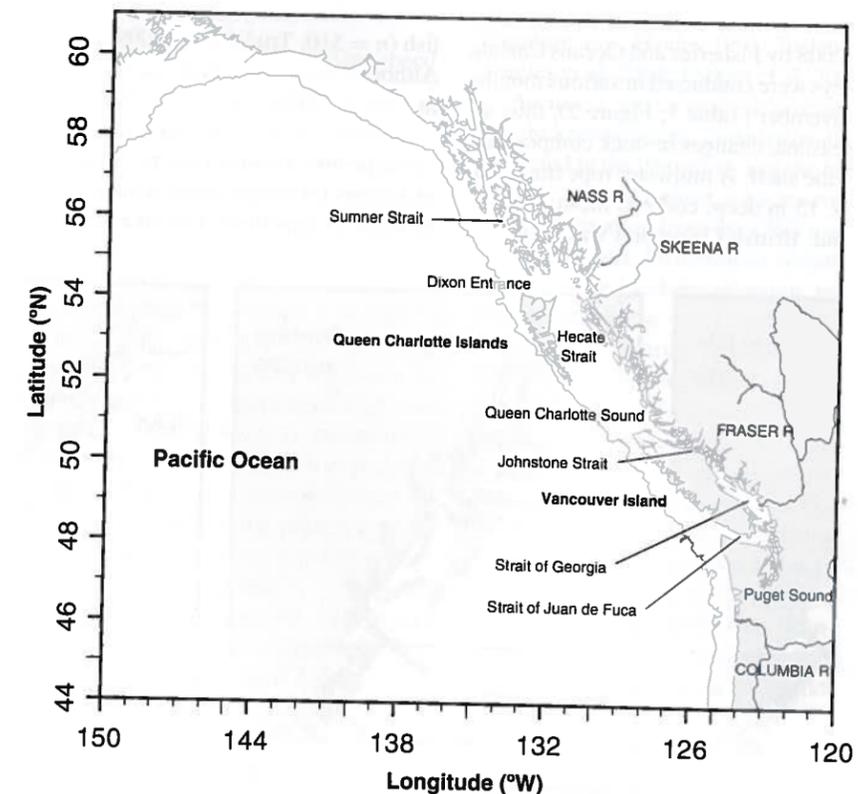


FIGURE 1. Map of the study area in the northeast Pacific Ocean. The Salish Sea includes the waters of the Strait of Georgia and Puget Sound. The solid line beyond the margin of the continent represents the 1,000-m contour. [Figure available online in color.]

TABLE 1. Number of fishing events in each season and region. Abbreviations are as follows: WCVI = west coast Vancouver Island; CC = the central coast, including central and northern British Columbia; and SEAK = Southeast Alaska.

Region	Jun-Jul	Oct-Nov	Feb-Mar
SEAK	79	433	211
CC	312	409	225
WCVI	298	418	323
Total	689	1,260	759

Our primary objective was to determine whether the results of Trudel et al. (2009) are supported with the addition of stocks and wild fish. As a key component of this objective, we tested whether hatchery-origin fish had different migration patterns than those of wild fish. Our second objective was to quantitatively delineate potential smolt-type differences in migration patterns. To meet these objectives, we tested for differences in the seasonal spatial distributions of stocks and smolt types with respect to latitude, longitude, and depth. In addition, we took advantage of the presence of known-origin, coded-wire-tagged fish in our sample to test the accuracy of genetic stock identification.

METHODS

Sample collection.—Juvenile and immature Chinook salmon were collected from southern British Columbia to Southeast Alaska between 1998 and 2008 by Fisheries and Oceans Canada (DFO). The sampling surveys were conducted in various months from February through November (Table 1; Figure 2), thus allowing reconstruction of seasonal changes in stock composition for different regions along the shelf. A midwater rope trawl (ca. 90 m long × 30 m wide × 15 m deep; cod end mesh, 0.6 cm; Cantrawl Pacific, Richmond, British Columbia) was hauled at

the surface (0–20 m) for 15–30 min at 5 knots primarily with the CCGS *W. E. Ricker*, or a chartered fishing vessel when the *W. E. Ricker* was unavailable (i.e., *FV Ocean Selector*, June 2002; *FV Frosti*, June and October 2005; *FV Viking Storm*, October 2007 and March and June 2008). Sampling was conducted between 0600 and 2000 hours (Pacific Time). Latitude, longitude, and bottom depth were recorded at the beginning and end of the tow. A maximum of 30 Chinook salmon were randomly selected from each net tow. Fork length (FL) and mass were determined onboard the research vessel. A tissue sample was taken from the operculum with a hole punch and preserved in 95% ethanol for genetic stock identification. By convention, all salmon are 1 year older on January 1. However for simplicity of discussion, we defined age categories with respect to time relative to ocean entry in spring. Salmon collected in this study between June and March in their first ocean-year (ocean-age 0: x.0) we refer to as “juveniles” and salmon collected between June and March in their second ocean-year (ocean-age 1: x.1), are referred to as “immatures.” Scales could not be used to age juvenile Chinook salmon, as most of them are descaled during sampling by the trawl net. Instead, ocean-age separation was based on size (FL) at capture (e.g., Healey 1980; Orsi and Jaenicke 1996; Fisher et al. 2007; Peterson et al. 2010). The seasonal size limits for different age-classes of Chinook salmon applied to all fish are presented in Table 2. We evaluated the potential for age misclassification by examining known-age, coded-wire-tagged fish ($n = 510$; Trudel et al. 2009; M. Trudel, unpublished data). Although there was a high degree of variation and some overlap in size for different age-classes of fish, cohorts were readily identifiable with a misclassification error of 7%. Fish were subsequently pooled into ocean-age, temporal, and regional groupings for mixed-stock analysis. To evaluate spatial changes in stock composition for juvenile and immature salmon, we

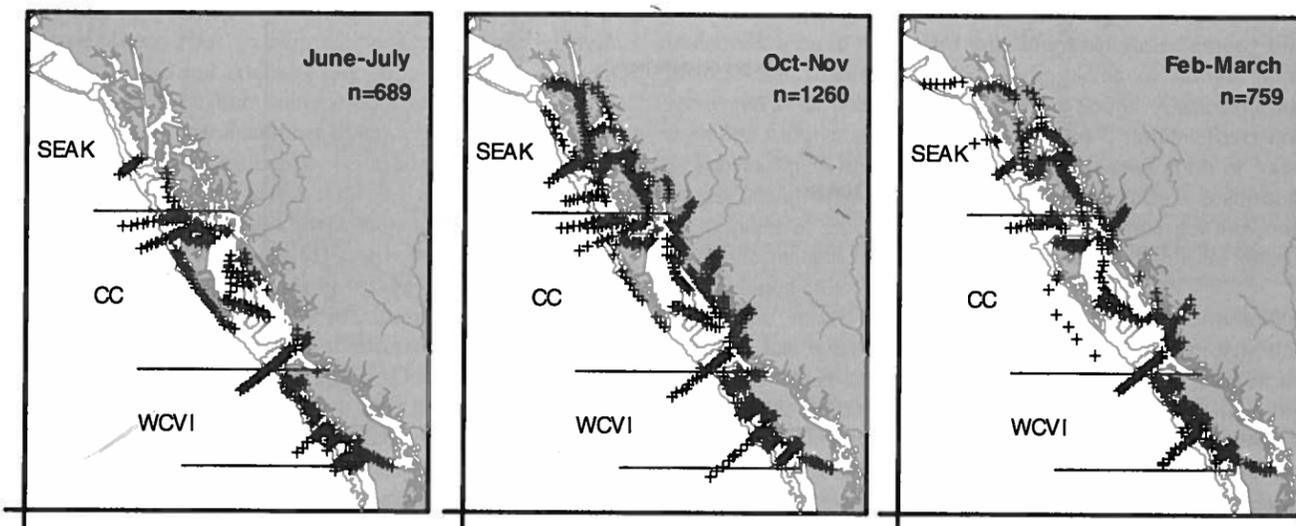


FIGURE 2. Sampling locations (crosses) in the three main catch regions (WCVI = the west coast of Vancouver Island, CC = the central coast [central and northern British Columbia]), and SEAK = Southeast Alaska). [Figure available online in color.]

TABLE 2. Size limits (fork length; mm) used to classify age-classes (juvenile, immature) and smolt classes (subyearling, yearling) of individual Chinook salmon.

Season	Subyearling	Yearling
	Juvenile	
Jun-Jul	<150	150–285
Oct-Nov	<225	225–350
Feb-Mar	<275	275–400
	Immature	
Jun-Jul	285–350	350–450
Oct-Nov	350–425	425–500
Feb-Mar	400–450	450–550

divided sampling locations into three catch regions (Figure 2): west coast of Vancouver Island (WCVI); the central coast (CC: central and northern British Columbia), which also included the west coast of the Queen Charlotte Islands (QCI); and Southeast Alaska (SEAK). Samples were pooled per catch region as above and also by season: June–July, October–November, and February–March. Catch per unit effort (CPUE) for juvenile and immature salmon for each fishing event was calculated separately as per Fisher et al. (2007). Briefly, CPUE was defined as the number of Chinook salmon caught per tow length of 1.5 nautical miles (2.8 km) determined as

$$\text{CPUE} = [(\text{no. Chinook salmon}) / \text{tow duration (h)} / \text{tow speed} \times (\text{nautical miles/h})] \times 1.5 \text{ nautical miles.}$$

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 CPUE values were subsequently pooled for each region and season.

DNA extraction and laboratory analyses.—The DNA was extracted from samples as described by Withler et al. (2000). Briefly, Chinook salmon ($n = 6,266$ juvenile; $n = 659$ immature) were surveyed for 12 microsatellite loci. Further details on the loci surveyed, as well as the laboratory equipment used, were outlined by Beacham et al. (2006a, 2006b). A minimum of seven loci were scored for each fish retained in these analyses. This minimum number of loci was considered sufficient for our analyses, as simulations indicate that the accuracy of the assignments increases rapidly with the number of microsatellites scored up to seven loci (Beacham et al. 2006a).

DNA stock allocation.—Separate analyses of mixed-stock samples of juvenile and immature Chinook salmon were conducted with a modified C-based version (cBAYES; Neaves et al. 2005) of the original Bayesian procedure outlined by Pella and Masuda (2001). A 268-population baseline (Beacham et al. 2006a, 2006b), comprised of approximately 50,000 individuals that ranged from Alaska to California, was used to estimate mixed-stock compositions for each season within each catch region. In the mixed-stock analysis, we assigned fish to 1 of

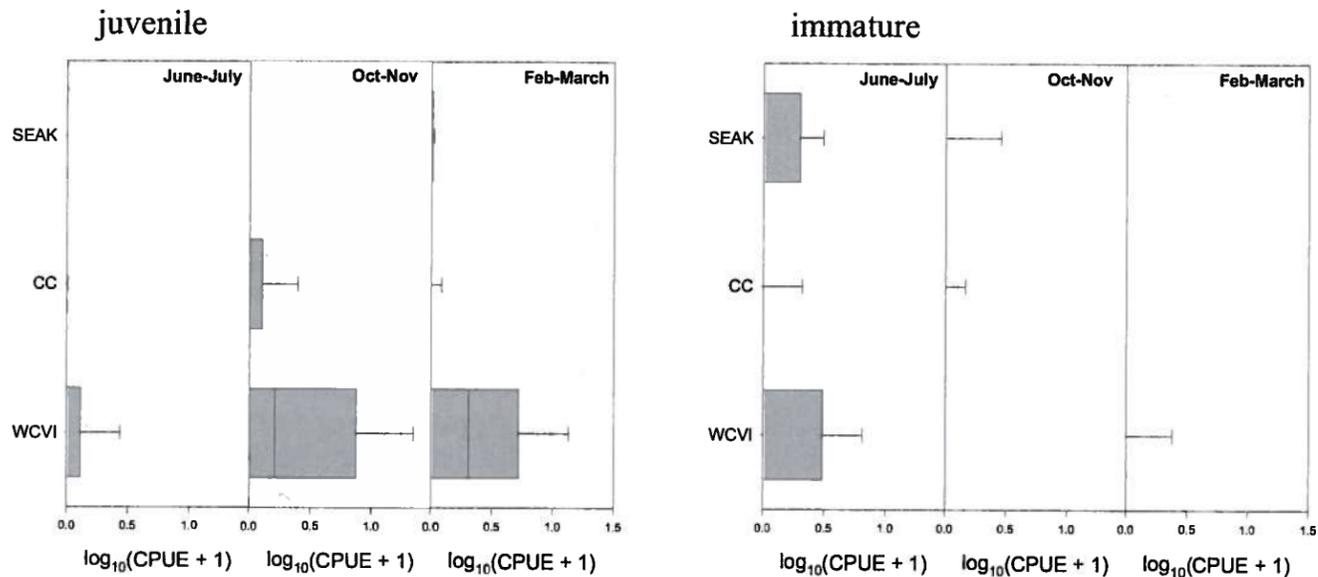
12 regional stocks on the basis of genetic structure (Beacham et al. 2006b). In the analysis, ten 20,000-iteration Markov chain Monte Carlo simulations were run with an uninformative prior with a value of 0.90 for a randomly picked population (Pella and Masuda 2001). Estimated stock compositions were considered to have converged when the shrink factor was less than 1.2 for the 10 chains (Pella and Masuda 2001), and thus the starting values were considered to be irrelevant. The posterior distributions from the last 1,000 iterations for all chains were combined to estimate mean stock composition and variance. In the mixed-stock analysis, cBAYES provides an output of subregional and regional stock of origin for each individual fish along with a probability of assignment. Individual fish were assigned to the stock of origin with the highest probability. For individual allocations, we used a probability of 50% as a lower limit (Beacham et al. 2006a). The probability of correctly identifying Chinook salmon to their appropriate stock is an asymptotic function of the assignment probability with an inflection point around 50%. Therefore, individual salmon that had an assignment probability greater than 50% were considered to be accurately classified to their stock of origin for the purpose of this study. Next we separated subyearling smolts from yearling smolts to evaluate potential differences in migration patterns between smolting classes of both juvenile and immature salmon. We confirmed smolt types (inferred from body size) by stock-specific information on smolt type and adult run timing compiled from the literature (e.g., Healey 1991; Teel et al. 2000; Candy et al. 2002; Waples et al. 2004; Parken et al. 2008).

Accuracy of genetic allocations.—In our sampling, we caught known-origin, coded-wire-tagged fish. The CWTs were extracted in the laboratory and the binary or numeric codes were visually decoded under a microscope (Trudel et al. 2009). Release information from the CWTs was obtained by querying the Regional Mark Information System (RMIS, www.rmipc.org), including the hatchery of origin, release site, adult run-timing, brood and release years, and release region as defined by the Pacific States Marine Fisheries Commission. To make genetic allocations and CWT data directly comparable, we pooled the hatchery origins of tagged fish into the same 12 regional stocks as above. In this analysis, we included the individual allocations of both juvenile and immature fish. Founding brood stocks for certain hatcheries have been imported from other river systems (e.g., Environment and Natural Resources Institute 2001). Where there were mismatches between CWT origin and estimated genetic origin, we subsequently obtained information on the origin of broodstock either from published material or direct communication with hatchery managers to verify whether there was correspondence with the founding broodstock.

Statistical analysis and mapping.—To describe migration patterns, we proceeded in a multistep manner. First, we considered the seasonal change in mixed-stock compositions of regional stocks for each catch region. Subsequently, we considered individual fish allocations to map and describe potential variation among regional stocks in migration patterns.

In addition we examined differences between yearling and subyearling smolts. For juvenile and immature Chinook salmon, multivariate analysis of variance (MANOVA) was used to investigate the effects of hatchery origin, regional stock, life history, and season on spatial distribution (latitude, longitude, and water depth) (SPSS version 11.5, SPSS, 2002). Survey- and stock-specific distributional maps were generated with an R-based (R version 2.9.2, R Development Core Team 2008) package (PBS mapping 2.55; Schnute et al. 2008).

A: sub-yearling salmon



B: yearling salmon

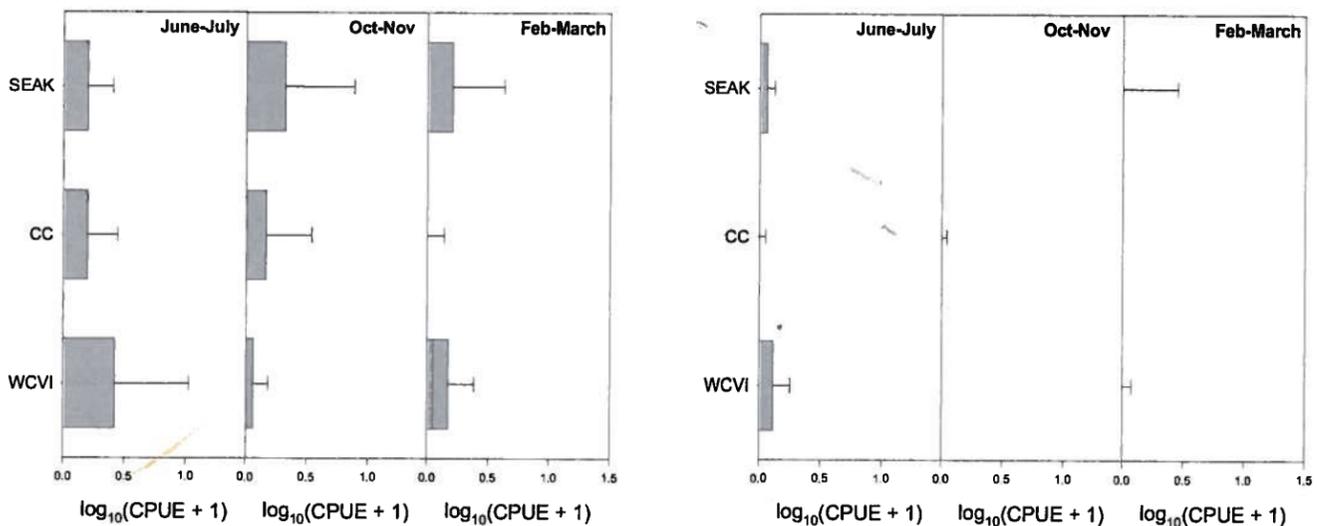


FIGURE 3. Catch per unit effort (CPUE) of (A) subyearling and (B) yearling juvenile and immature Chinook salmon. The dimensions of the boxes represent the 75th percentile, the lines within the boxes the medians, and the error bars the 90th percentile.

RESULTS

Fishing Effort and CPUE

Overall, a total of 2,708 fishing events contributed to the current data set (Table 1; Figure 2). On a seasonal level, effort was highest in fall and lower in summer and winter. In the summer, CPUE of juvenile subyearling salmon was highest in the south (WCVI) and increased threefold in fall and remained high in winter (Figure 3). Further north, CPUE of juvenile subyearling

TABLE 3. Number of individual Chinook salmon successfully allocated to regional populations in each season and region. See Table 1 for abbreviations.

Region	Jun-Jul	Oct-Nov	Feb-Mar
Juvenile			
SEAK	89	868	491
CC	217	484	49
WCVI	657	1,918	1,115
Total	963	3,270	1,655
Immature			
SEAK	76	2	2
CC	100	5	
WCVI	382	9	17
Total	558	16	19

salmon was noted off WCVI in winter representing the appearance of Salish Sea and southern stocks (see below) into the sampling area. In summer, CPUE values in all regions for immature yearling salmon declined to approximately half those of juvenile values from the previous winter. Again, CPUE values declined to near zero in fall and winter.

Accuracy of Genetic Allocations for Tagged Fish

Of 6,266 juvenile and 659 immature Chinook salmon analyzed, 5,888 and 593 were allocated to regional stocks, respectively (Table 3), where 78% of fish had an individual probability of assignment of greater than 95% and 86% of fish had an individual probability of assignment of greater than 90%; the remainder had probabilities that exceeded 60%. Only 378 juveniles and 66 immature salmon were excluded either because not enough loci were scored or the probability of assignment was too low. We identified 339 tagged and an additional 804 marked (adipose clipped) fish in our sample for a total of 1,143 identifiable Chinook salmon of hatchery origin. The percent tagged and marked fish combined (i.e., clearly hatchery-origin fish; Table 4) in each stock ranged from 1% (northern British Columbia mainland [NBC]) to 74% (Columbia River). Of the 339 known-origin, coded-wire-tagged fish, 324 individuals were correctly allocated to regional stock of origin, providing an overall accuracy of 96% for the genetic stock assignments (Table 4). However, classification error rate varied among stocks, ranging from 2% to 3% for Columbia River, WCVI, and transboundary-SEAK to 11% for Puget Sound. Other stocks did not have sufficient sample size to adequately assess

fish in all seasons was very low in CC, and essentially zero in SEAK. The CPUE for immature subyearling salmon in summer was highest off WCVI; moderate CPUE values were observed in SEAK with low levels in CC. The CPUE values declined to near zero values in fall and winter.

As with subyearling Chinook salmon, CPUE for juvenile yearling salmon in summer was highest off WCVI, but CPUE values in CC and SEAK were approximately half that value (Figure 3). The CPUE then increased in northern areas and decreased in southern areas as seasons progressed, which probably represented movement north and or dispersion into off-shelf areas. However, a "second wave" of yearling juvenile Chinook

TABLE 4. Numbers of coded-wire-tagged Chinook salmon caught from 12 regional stocks and subsequent assignment to regional stocks based on DNA. Abbreviations are as follows: CA = California, OR = Oregon, CR = Columbia River, WA = coastal Washington, PS = Puget Sound, FR = Fraser River; SBC = southern British Columbia mainland, ECVI = east coast Vancouver Island, WCVI = west coast Vancouver Island, NBC = northern British Columbia mainland, NS-SK = Nass and Skeena rivers, and TR-SEAK = transboundary and Southeast Alaska.

DNA allocation	CWT origin												Fin-clipped (%)	
	CA	OR	CR	WA	PS	FR	SBC	ECVI	WCVI	NBC	NS-SK	TR-SEAK		
CA	1													18
OR		4												19
CR			199	1	1									74
WA				2										12
PS					24									56
FR						2								3
SBC							0							3
ECVI								1						11
WCVI									1					3
NBC										1				1
NS-SK											1			4
TR-SEAK												2		35
Total	1	4	205	4	27	2	0	2	54	1	3	36		4

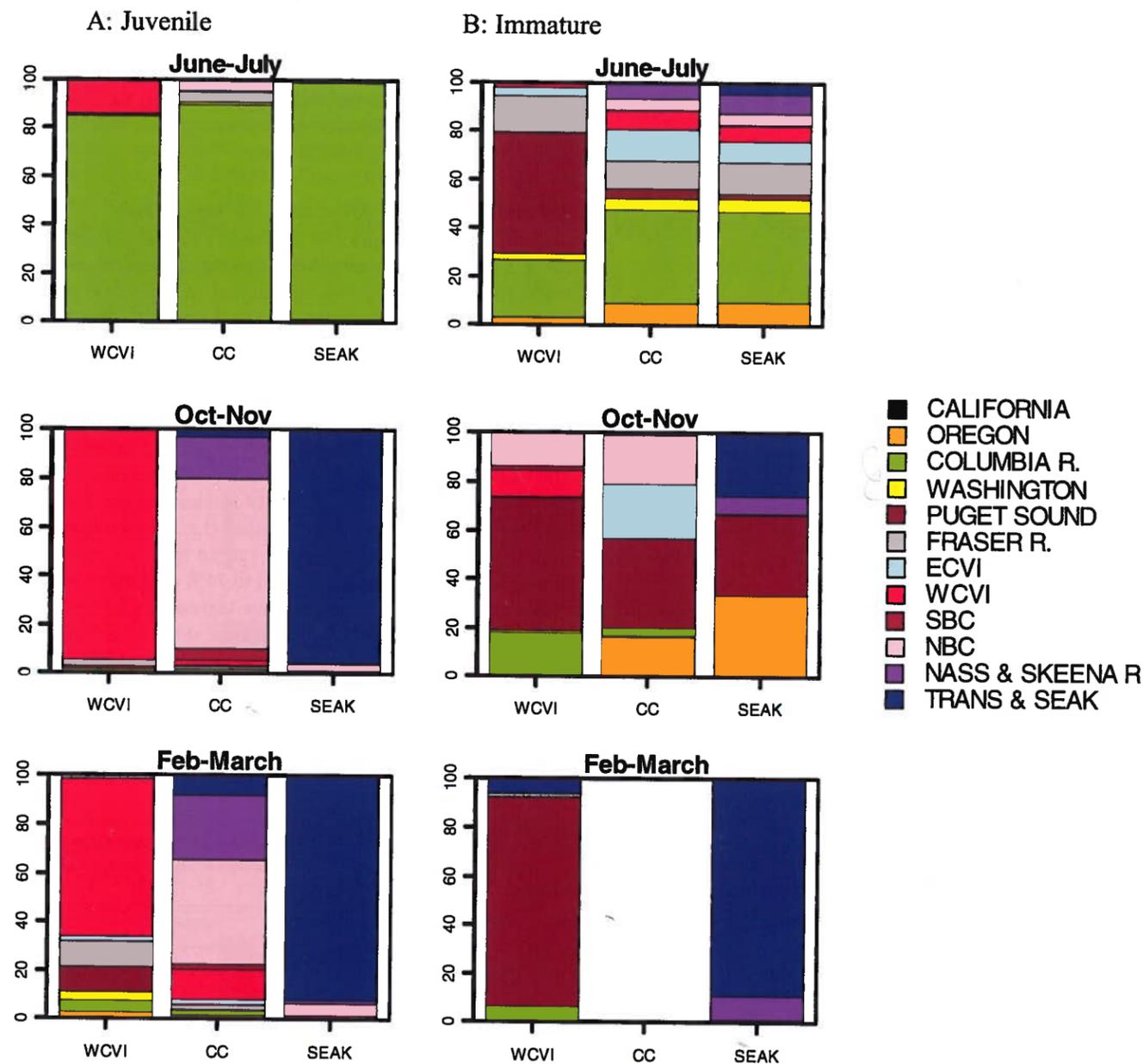


FIGURE 4. Seasonal mixed-stock compositions for juvenile and immature Chinook salmon caught in the three principal sampling regions (see Figure 2); other abbreviations are as follows: SBC = southern British Columbia mainland, NBC = northern British Columbia mainland, and TRANS = transboundary area.

classification error. Of the 15 misallocated fish, four were allocated to stocks geographically adjacent to their known origin.

Regional Mixed-Stock Compositions

Juvenile Chinook salmon.—In summer, Chinook salmon of Columbia River origin dominated catches in all regions, with increasing proportions from WCVI (84%) to CC (89%) and to SEAK (98%) (Figure 4). The west coast Vancouver Island (WCVI) stock formed the majority of the remainder of fish off

WCVI (14%), while Fraser River (4%) and NBC (5%) were the next largest stocks in CC. In fall, local stocks dominated catches in all regions (e.g., 95% WCVI fish in WCVI; 87% NBC and Nass and Skeena rivers fish combined in CC; 96% transboundary and Southeast Alaska fish in SEAK). In all regions, Columbia River fish declined to approximately 1.5% during fall. In winter, WCVI fish continued to dominate catches in WCVI at 65% of the catch. However, there were influxes of Fraser River (10%), Puget Sound (11%), and coastal Washington and Oregon fish

(6% combined). These represent increases from fall when they were all present at less than 1%. Columbia River fish also increased to comprise 5% of the total. In CC, NBC (43%) and Nass and Skeena rivers (27%) fish were caught in the highest proportions. The remainder was primarily Southeast Alaska fish (8%) and WCVI stocks at 12%. Columbia River fish comprised 2% of the total. Transboundary and Southeast Alaska (92%) fish in SEAK continued to dominate catches. The remainder was comprised of predominantly NBC and Nass and Skeena rivers fish.

Immature Chinook salmon.—In summer, Chinook salmon originating from Puget Sound (50%), the Columbia River (23%), and the Fraser River (15%) dominated catches in WCVI (Figure 4). Most stocks were represented in CC and SEAK; however, the majority were Columbia River fish (37%). In fall, the total catch of immature salmon declined by 35-fold (Table 3). However, the proportion of Puget Sound and Columbia River fish were similar to summer in the WCVI region in fall, although the proportion of WCVI and NBC fish increased. Puget Sound fish became a larger portion of the catches in CC (37%) and SEAK (33%) while catches of Columbia River fish declined dramatically (0–4%). In winter, although overall catches were again low in all regions, they were dominated by Puget Sound fish in WCVI (86%) and transboundary and Southeast Alaska (89%) fish in SEAK.

Seasonal Trends in Smolt Type Migration Patterns: Individual Assignments

Of the total number of juvenile Chinook salmon sampled in summer, only 10.7% were determined to be subyearling (predominantly [9.7%] from WCVI). Columbia River yearling fish represented 85% of the total, and ranged as far north as SEAK. In contrast to summer, the majority (62.8%) of the juvenile Chinook salmon caught in the fall were subyearlings (predominantly [55.9%] from WCVI). Transboundary stocks formed the majority of yearling fish during the fall period (24.9%). Again in winter, 62.1% of the catch was composed of subyearling fish, the majority of which were from WCVI (43.8%). Again, the bulk of yearling fish were from transboundary stocks (26.9%). The largest catches of subyearling salmon were in winter for all stocks except NBC and WCVI where catches peaked in fall. The largest stock-specific catches of yearling salmon were in the fall, except for those in the Columbia River (which were caught in summer), and Fraser River and Puget Sound (largest catches were in winter). The latter suggests that these fish are starting to exit the Salish Sea at this time. Therefore, in general, for all stocks in each season, yearling salmon were found more northerly and more westerly than subyearling salmon.

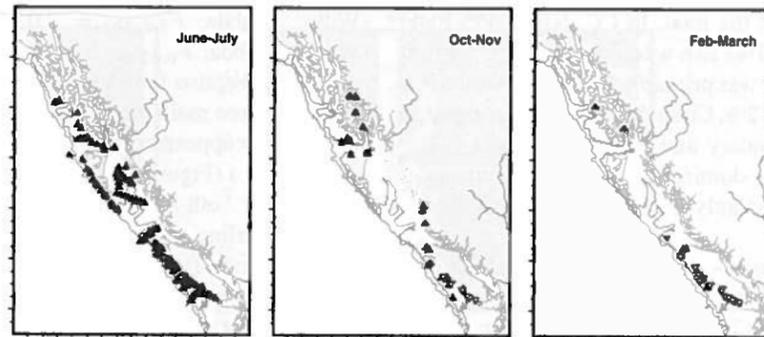
There was no significant difference in the spatial distribution of marked hatchery fish and unmarked fish (assumed to be wild) for both juvenile (MANOVA, Wilks' lambda: $F_{3, 5, 805} = 1.29, P = 0.28$) and immature (MANOVA, Wilks' lambda: $F_{3, 552} = 0.61, P = 0.61$) Chinook salmon. We subsequently removed hatchery origin in MANOVA as a main effect. For ju-

venile salmon, we found a significant effect of stock (Wilks' lambda: $F_{33, 17, 147.5} = 71.31, P < 0.001$), smolt type (Wilks' lambda: $F_{3, 5, 820} = 7.02, P < 0.001$), and season (Wilks' lambda: $F_{6, 11, 640} = 8.73, P < 0.001$) on spatial distributions. We also found significant two-way interactions between all three main effects (P values < 0.001). These reflect both the later appearance of some stocks and subyearlings in our sampling area (Figures 4, 5) as well as the different distribution of stocks for both subyearling and yearling smolts. In general, juvenile yearling salmon from all stocks were sampled earlier (summer versus fall) and found further north, further west, and over deeper water than were subyearling fish (Figure 6a). Juvenile subyearling fish originating from stocks south of the CC sampling area had distributions centered on WCVI and included individuals from southern U.S. stocks (Figure 6a). Stocks to the north had distributions centered on the inside waters of Queen Charlotte Strait or inlets of the central coast of British Columbia (CC) and SEAK. Distributions changed little from fall (when first sampled and identified) to winter. These mean values shifted farther northwest with the seasons (Figure 6a). The exceptions were Puget Sound and Fraser River origin fish, where numbers actually increased off the WCVI from fall to winter, which probably represented recruitment of these fish from the Salish Sea (Figures 5, 6). As well, yearling Chinook salmon had more expansive ranges; for example, individuals from southern stocks were caught throughout the sampling area. Subyearling salmon in the WCVI region were caught in shallower bottom depths than were yearling salmon (Figure 6a). The exception was for fish caught in northern waters (CC and SEAK) where bottom depths were equivalent between smolt types. This is probably due to the overall deeper depths of the shelf in these regions. Median bottom depths for juvenile salmon in all regions were inshore of median depths of sampling (data not shown), which suggests they occupy shallow inshore regions of the coastal shelf. However, sampling depths were deeper for CC and SEAK (median sampling depths were ~178 and 219 m, respectively) than for WCVI (122 m). Depths were shallower in summer than in fall and winter, only increasing for individuals from particular stock groupings as they headed into deeper, northerly waters.

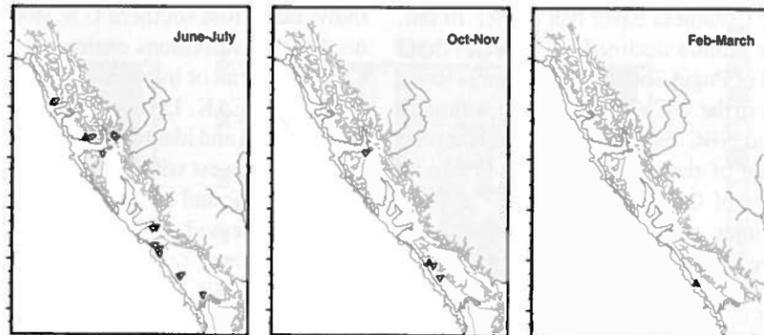
The vast majority (94% of total catch) of immature Chinook salmon were caught in summer (2.7% in fall, 3.3% in winter), 88% of which were identified as subyearling fish. The proportion of yearling salmon increased over summer to 31% in fall and 21% in winter and probably represents movement of yearling fish from U.S. coastal waters and the Salish Sea, respectively, into our sampling area. Across all seasons, both yearling and subyearling immature salmon were predominantly from the Columbia River, Fraser River, and Puget Sound.

As with juveniles, we found a significant effect of stock (Wilks' lambda: $F_{30, 1, 656.13} = 8.85, P < 0.001$), smolt type (Wilks' lambda: $F_{3, 564} = 10.19, P < 0.001$), and season (Wilks' lambda: $F_{6, 1, 128} = 6.02, P < 0.001$) on the spatial distributions of immature Chinook salmon. We also found significant interactions between stock and smolt type (Wilks'

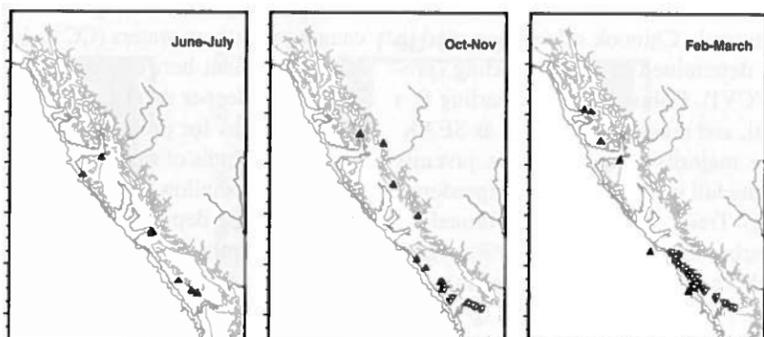
A: Columbia River system
Juvenile



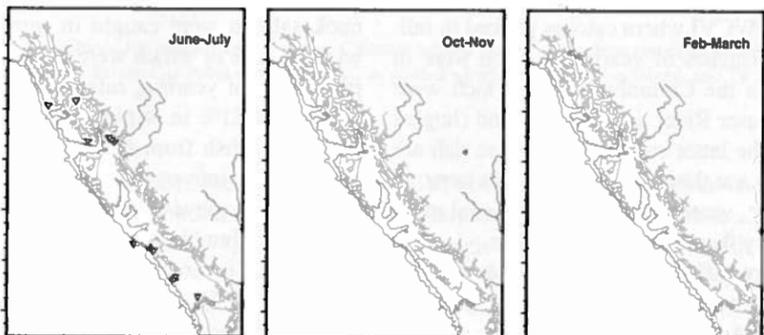
Immature



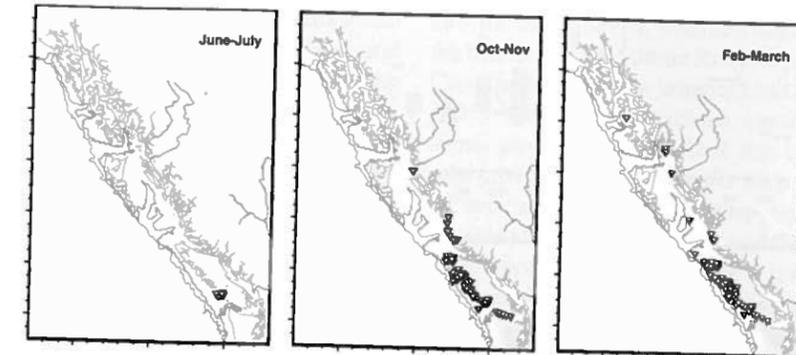
B: Fraser River
Juvenile



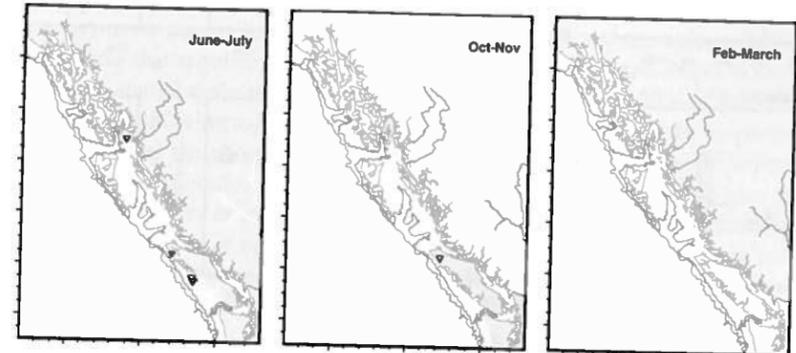
Immature



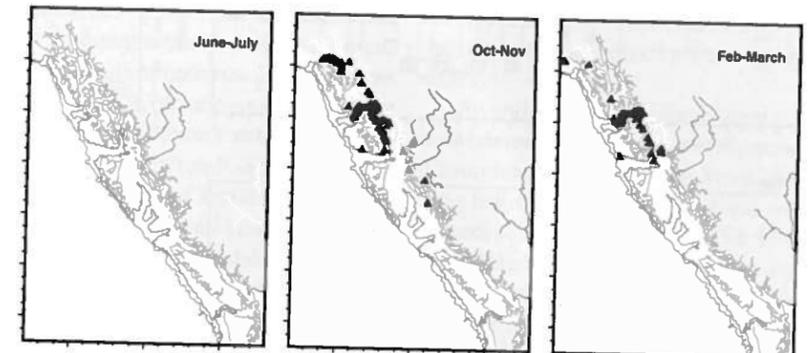
C: WCVI
Juvenile



Immature



D: Trans-boundary and SEAK
Juvenile



Immature

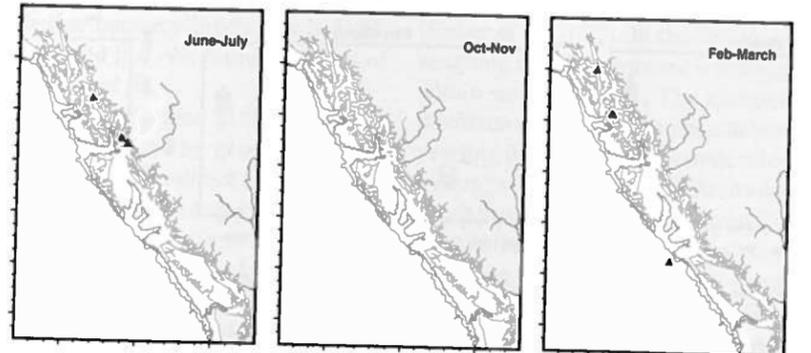


FIGURE 5. Representative stock-specific coastal distributions of individual sub-yearling (inverted gray triangles) and yearling (black triangles) Chinook salmon within the study area: (A) Columbia River system, (B) Fraser River, (C) west coast Vancouver Island (WCVI), and (D) transboundary and Southeast Alaskan rivers (SEAK). The lines represent the 200-m and 1,000-m contours. [Figure available online in color.]

FIGURE 5. Continued.

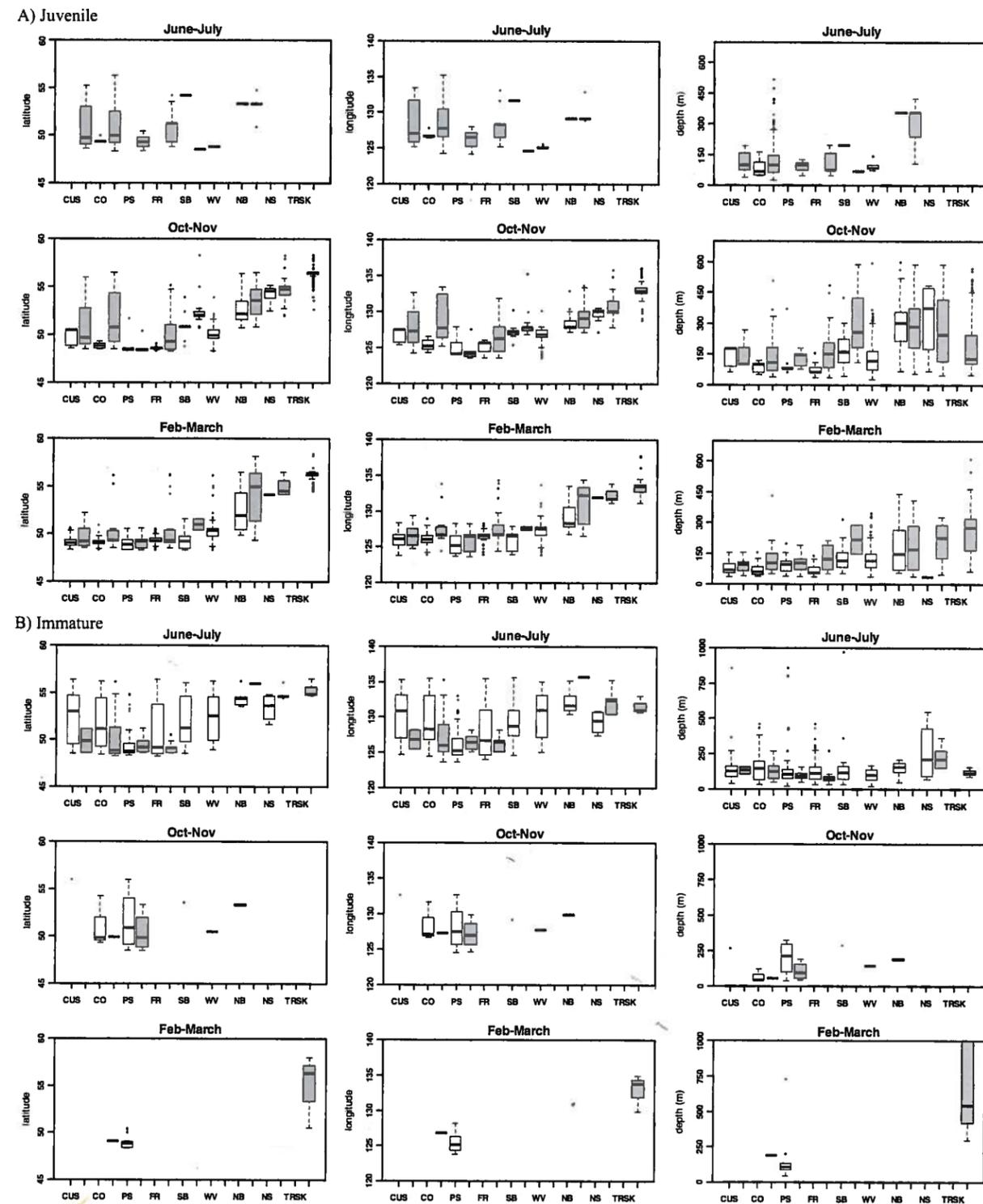


FIGURE 6. Box plots of latitude, longitude, and bottom depths (m) for individual (A) juvenile and (B) immature subyearling (white bars) and yearling Chinook salmon smolts (gray bars) for each regional stock (some pooled for ease of presentation). Abbreviations are as follows: CUS = coastal U.S. stocks, including those from California, Oregon, and Washington; CO = Columbia River; PS = Puget Sound; FR = Fraser River; SB = southern British Columbia mainland and east coast Vancouver Island; WV = west coast Vancouver Island; NBC = northern British Columbia mainland; NS = Nass and Skeena rivers; TRSK = transboundary and Southeast Alaska. The dimensions of the boxes represent the 25th and 75th percentiles, the lines within the boxes the medians, and the error bars the 10th and 90th percentiles.

lambda: $F_{15, 1,538} = 9.81, P < 0.001$) and between stock and season (Wilks' lambda: $F_{39, 1,650} = 2.74, P < 0.001$). However, the patterns were opposite. Subyearling fish in each stock had more expansive geographic ranges extending northwest and bottom depths were equivalent (Figure 6b). We suspect, for the most part, that these were probably overwintering fish that were beginning to move while there was recruitment of yearling fish from the Salish Sea and areas to the south.

DISCUSSION

Understanding the spatial distribution and movements of juvenile salmon in the ocean is an important first step in discerning how ocean and climate variability influence salmon survival. That is, we need to know where salmon occur throughout their life cycle and understand how they move among habitats before we can begin to explore mechanisms that regulate their growth and survival and define the relevant spatial scale at which these mechanisms operate (Trudel et al. 2009). Owing to limitations of traditional tagging techniques as well as the geographic scope of sampling, delineating stock-specific migration patterns has remained elusive until recently (e.g., Tucker et al. 2009). The importance of generating such information is underlined by stock-specific differences in marine survival that may reflect underlying differences in marine migration pathways (e.g., Welch and Parsons 1993; Welch et al. 2000).

Our primary objective was to determine whether the results of Trudel et al. (2009), obtained using CWT recoveries from hatchery fish, are supported by recoveries of wild fish and additional stocks. As well, we sought to quantitatively delineate potential smolt-type differences in migration patterns. In the present study, we characterized stock- and life history-specific juvenile and immature migration patterns of Chinook salmon through the application of genetic stock identification (GSI) techniques. The results here support the main findings of Trudel et al. (2009). However, given increased sample sizes for all stocks and additional stocks, we can extend those results; coastal residency of local stocks in their first year at sea with differences between smolt classes for southern stocks (not restricted to Columbia River fish) as yearling Chinook salmon moved quickly into waters north of WCVI, including SEAK. As a key component of this objective, we tested whether hatchery-origin fish had different migration patterns from wild fish. We found no effect of hatchery origin on the distribution of fish.

Interpretations of the analyses performed in this study are contingent on accurate stock assignment by genetic analysis. The analysis of 339 tagged fish provided a direct means of validating genetic stock assignments. By far the majority of tagged-fish captures were from the Columbia River ($n = 205$) system; however, we had samples from all regional stocks. Ninety-six percent of the tagged Chinook salmon were correctly assigned to the region of origin in mixed-stock analysis. However, classification error rate varied among stocks and ranged from 2% to 11%, probably owing to gaps in the baseline. The GSI was also

highly accurate to the specific populations (data not shown). For example, many hatcheries in SEAK, including the release agencies for our samples, obtained their original broodstock from the transboundary Stikine River, in particular from the Andrews Creek population (Environment and Natural Resources Institute 2001). These were in fact the specific population level assignments given to tagged SEAK fish by the GSI. Thus, these results provide strong support for the proper allocation of Chinook salmon caught at sea for the purposes of this analysis. Given the importance of GSI for various applied purposes, a more detailed exploration and analysis of the accuracy of individual population specific assignments, baseline selection (Seeb et al. 2007), and a number of specific issues related to the number and which alleles are retained are the subject of future work.

The proportion of clearly marked hatchery-origin fish was highly variable among regions: 74% and 56% of fish identified as Columbia River and Puget Sound origin, respectively, were marked and less than 20% of fish were marked in the remaining regions. This underlies the importance of the current genetic results, which expands our understanding of stock-specific migration by increasing sample size and the number of regional stocks. Our finding of no difference in migration patterns between hatchery and wild fish is consistent with other studies of Chinook salmon (Healey and Groot 1987; Weitkamp 2010). Most Chinook salmon hatchery stocks were founded from local wild stocks (Myers et al. 1998), which suggests that either selective forces associated with hatchery rearing (e.g., Quinn 2005; Araki et al. 2008; Bailey et al. 2010) do not effect migration patterns, or hatchery and wild individuals now potentially belong to homogenized populations (e.g., Williamson and May 2005).

Juvenile Chinook salmon were primarily caught on the shelf and inlets of the west coast of Vancouver Island, northern British Columbia, and in Sumner Strait (Southeast Alaska). Subyearling fish in their first year at sea were essentially restricted to waters south of northern WCVI. In contrast, yearling fish were distributed across the entire sampling area during their first year at sea with the highest CPUE occurring off WCVI, and then shifting to the north as seasons progressed. For the most part, juvenile salmon were found within the 200-m contour, which supports previous observations of both mean and median depths (Fisher et al. 2007). In the central and northern portion of our sampling area, this contour is in close proximity to the mainland within inner channels. The exception to this juvenile salmon distribution was the summer catches of fast-migrating southern yearling fish in northern waters, which transited through deeper waters (>200 m) of Hecate Strait and waters off the west coast of Haida Gwaii (formerly the Queen Charlotte Islands). Moreover, subyearling fish were found in closer proximity to shore over shallower bottom depths than were yearling fish, which also supports previous observations (Fisher et al. 2007). It would appear that Chinook salmon demonstrate consistent depth distributions that only vary between stocks depending on when and where they are found on the coast.

In summer, Chinook salmon originating from the Columbia River dominated the catches in all regions (~90%), and the majority of these were yearling spring Chinook salmon; some subyearling Chinook salmon from upper Columbia River summer-fall runs were found off WCVI in significant proportions (~20%; Table A.1 in the appendix), though none were identified north of Vancouver Island. As with coho salmon *O. kisutch* (Morris et al. 2007) and sockeye salmon (Tucker et al. 2009), the northward ocean migration speed of yearling spring Chinook salmon, particularly Columbia River fish, is highly variable, with both fast and slow migrants (J. P. Fisher, personal communication). This may be linked to timing of smolt out-migration as well as behavior. Across all regions, proportions of Columbia River Chinook salmon subsequently declined to less than 2% in fall and winter; the majority of these fish were sub-yearling smolts. This demonstrates both the northward passage (in some cases very rapid for those caught in SEAK) of yearling Columbia River Chinook salmon and the emergence and subsequent residence of other coastal stocks. For example, WCVI fish were dominant off the west coast of Vancouver Island in fall and winter with proportions exceeding 65% while stocks from northern British Columbia were dominant in the central region of our study area, and transboundary and Southeast Alaska fish were dominant in SEAK waters in fall and winter. However, not all fish from these stocks are resident as small proportions of fish originating in more southern production areas were caught farther north and fish from southern British Columbia were absent after their first fall. An even smaller number of fish are caught south of their rivers of origin. Given the high degree of accuracy of DNA allocations we do not believe these are misallocations. Indeed, Trudel et al. (2009) noted some southern migration and residency of juveniles from Puget Sound stocks and an influx of juvenile Fraser River and Puget Sound stocks to the west coast of Vancouver Island over the winter months.

One of the limitations of the current study was low sampling effort in waters south of Vancouver Island and north of Southeast Alaska. However, previous work has evaluated seasonal mixed-stock compositions of juvenile Chinook salmon off northern Oregon and Washington (Teel 2004), although these were not classified as subyearling or yearling. In May, most fish captured near the mouth of the Columbia River were spring-run Chinook salmon from upstream stocks. In June, nearly all interior spring-run individuals were sampled farther north off the Washington coast. Spring-run fish from the interior Columbia River basin were the most abundant group off northern Oregon and Washington throughout the early summer (58%) and were nearly absent in September (Teel 2004). This northward displacement is coincident with the high catches of yearling Chinook salmon (predominantly Snake River spring-summer fish and upper Columbia River spring fish; Table A.1) from the WCVI to SEAK in June–July noted here. For the most part, these fish were absent from our sampling area by October. In contrast to interior spring-run juveniles, Columbia River basin fall-run Chinook salmon were present off northern Oregon and

coastal Washington throughout the summer sampling period (Teel 2004), and predominated in September (45% and 89%, respectively). We found small proportions of juvenile fall-run Columbia River fish off WCVI in the summer (18% of total Columbia River fish), but these populations dominated catches of Columbia River fish off WCVI in the fall (75%) and winter (61%). The current work appears to be a coherent extension of Teel's (2004) results.

While the patterns for subyearling and yearling Chinook salmon from the Columbia River system are striking, there are also differences between smolt variants of other southern stocks, particularly southern U.S. stocks (California, Oregon, and Washington); yearling fish tended to initiate northward migration earlier and faster after entering the ocean, which paralleled the within-system trend noted for Columbia River fish. The numbers and CPUE of yearling Chinook salmon dropped dramatically between winter (February–March) and summer (June–July) of their first and second years at sea. This was particularly apparent in the central coast of British Columbia, where very few juvenile salmon were caught during the winter. In contrast, subyearling fish were still found in high abundances across coastal waters during the summer of their second year at sea. Thus, yearling fish appear to leave the sampling regions earlier than subyearling fish. Northward or off-shelf migration of most subyearling stocks was initiated during their second year at sea. However, they could also move to deeper waters while remaining on the shelf (Orsi and Jaenicke 1996) and therefore may have been missed by surface trawls. The exception was Puget Sound fish as we continued to catch these fish during the winter of their second year at sea, which suggested they had just recently left the inner waters of the Strait of Georgia and Puget Sound; catches of second-year Puget Sound fish had declined from the previous fall. East-coast Vancouver Island fish also appear to establish residency off WCVI during their second year at sea as opposed to moving north into Queen Charlotte Sound.

Yearling Fraser River fish were caught in small numbers off WCVI and in areas north in summer and fall of their first year. Movement out of the Strait of Georgia could be via the Strait of Juan de Fuca or north via Johnstone Strait (Figure 1). Similar to Puget Sound fish, no juvenile subyearling Fraser River Chinook salmon were caught outside the Strait of Georgia in summer and, in fact, were caught only in outside waters in substantial numbers in fall and winter of their first year, and not in regions north of WCVI until the second summer at sea. Unlike yearling salmon, it seems likely that movement out of the Strait of Georgia was solely through the Strait of Juan de Fuca. Within the Fraser River system, subyearling Chinook salmon originate from both the lower Fraser River and the South Thompson River and there appear to be some differences in migration between them. South Thompson River fish formed the majority of juvenile Fraser River fish in fall (61%) and winter (74%), while lower Fraser River fish constituted 6–7% (Table A.1). However, the total proportion of immature lower Fraser River fish increased in summer to 50% (confined solely to WCVI) suggesting that a

large portion of these fish are leaving the Strait of Georgia later than many South Thompson River subyearlings. While South Thompson River fish still constituted 46% of all immature Fraser River fish, almost equal numbers were distributed in the three sampling areas. As adults, lower Fraser River subyearling salmon are commonly caught off WCVI while are rarely caught in central British Columbia, northern British Columbia, and Alaska fisheries (Pacific Salmon Commission 2008). As adults, South Thompson River subyearling salmon display the opposite pattern as they are routinely caught in Alaskan, northern, and central British Columbia fisheries. Interestingly, it was only the South Thompson River subyearlings that were caught in waters north of WCVI during the second summer at sea, suggesting a link between early marine migration patterns and subadult–adult distribution patterns.

All northern stocks, for which the vast majority tend to be yearling smolts (despite some variability in adult run timing), were caught in high numbers during the fall reflecting later smolting times (Healey 1991) and later dispersal from the near shore environment onto the continental shelf. Catches tended to be concentrated in inner waters of northern British Columbia and SEAK (Figures 5, 6). This observation agrees with previous work and suggests that Southeast Alaska and northern British Columbia yearling Chinook salmon may remain resident within local, inside straits of Alaska for an extended period before migrating offshore (Jaenicke and Celewycz 1994; Orsi and Jaenicke 1996; Orsi et al. 2000; Trudel et al. 2009). However, catches of all northern stocks were greatly reduced by winter and were found farther north in the inside waters of Southeast Alaska. Small numbers of northern stocks were caught in their second summer and fall at sea but virtually none were caught at older ages. Thus, they are somewhat reflective of the yearling behavior defined previously for southern stocks. However, it was not possible to determine when these fish migrated out of Southeast Alaska, as no samples north of Southeast Alaska were analyzed.

The resident migration pattern of subyearling Chinook salmon is in stark contrast to both yearling Chinook salmon and other species for which stock-specific migration has been outlined. While stocks of yearling Chinook salmon, coho salmon (Morris et al. 2007), and sockeye salmon (Tucker et al. 2009) all display both fast and slow migrants, they have generally dispersed off the coastal shelf at some point between fall and winter. The incentive for such different strategies remains unclear. How these fish potentially differ in other respects (e.g., diet, food consumption rates) could be determined by future research. Temporal differences in diet, growth, energy reserves, and abundances of juvenile salmon have recently been outlined (e.g., Brodeur et al. 2007; Fisher et al. 2007; Trudel et al. 2007; Cross et al. 2009). These suggest potential links between large scale changes in ocean conditions and large variation in ocean survival and returns of salmon to natal rivers to spawn. Nevertheless, it remains unclear whether these links would manifest themselves as direct effects on migration behavior per se or how

migration would be influenced by interannual differences in the ocean environment. The results outlined here and in Trudel et al. (2009) do, however, underline the importance of considering relevant spatial scales for assessing the effects of ocean conditions on Pacific salmon as these vary with stock and life history. Effects of ocean conditions on subyearling Chinook salmon are expected to be manifested at a local scale for most coastal stocks (i.e., within 200–400 km of the natal river), compared with the scale of the northern California Current (i.e., Oregon to the west coast of Vancouver Island) for Columbia River and other southern subyearling fish. Even broader and more complex spatial and temporal scales must be considered for Columbia River yearling Chinook salmon as ocean conditions vary among both regions and months and stocks display differential migration speeds.

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Appendix: Detailed Data

TABLE A.1. Numbers of individual juvenile and immature subyearling and yearling Chinook salmon allocated to 12 regional and respective subregional populations (according to Beacham et al. 2006a, 2006b classifications) caught in three principal catch regions (WCVI = west coast Vancouver Island, CC = central and northern British Columbia coast, and SEAK = Southeast Alaska), in three seasons between 1998 and 2008. Smolt classifications were based on length (mm).

Age-class	Regional population	Subregional population	Smolt class	June–Jul			Oct–Nov			Feb–Mar			
				WCVI	CC	SEAK	WCVI	CC	SEAK	WCVI	CC	SEAK	
Juvenile	California	Central Valley, fall	subyearling									1	
			yearling	1								1	
			subyearling				2						5
		Columbia River	Lower Columbia River	yearling									1
				subyearling									1
				yearling	3								
	Snake River, fall	Snake River, spring	subyearling	11	20	1		2				1	
			yearling	1								3	
			subyearling	20	2		2		1	1		4	
	Snake River, spring–summer	Upper Columbia River, spring	subyearling	4								2	
			yearling	273	88	41		3	3	5			
			yearling	125	54	29		3		1			
Upper Columbia River, summer–fall	Upper Columbia River, summer–fall	subyearling	2				7				20		
		yearling	73	10	2		12	2	2	2	6	1	

(Continued on next page)

TABLE A.1. Continued.

Age-class	Regional population	Subregional population	Smolt class	June-Jul			Oct-Nov			Feb-Mar		
				WCVI	CC	SEAK	WCVI	CC	SEAK	WCVI	CC	SEAK
East Coast Vancouver Island Fraser River		Upper Willamette River	subyearling							14		
		ECVI	yearling	38	19	14	1	1	1	2		1
			subyearling		1		1	1		21	1	
		Lower Fraser River, fall	subyearling				4			1		
		Lower Fraser River, spring	yearling	2	4			1	1			1
		Lower Fraser River, summer	subyearling							1		
		Lower Thompson River	yearling	1	1			1		2		
		Mid-Upper Fraser River	yearling	1	3			3		7	1	2
		North Thompson River	subyearling							1		
		South Thompson River	subyearling					6		6		
Nass and Skeena Rivers		Upper Fraser River	yearling					30		79		
		Nass River	yearling		1			3		6		
			subyearling					5		4		
			yearling					39	5	3	2	
		Skeena River, Bulkley	yearling					1		8		
		Lower Skeena River	subyearling					18			4	
			yearling					3	1	1	1	
		Mid Skeena River	subyearling					1				
		Upper Skeena River	yearling					16				
		Northern British Columbia	Northern British Columbia mainland	subyearling		1			159	1	6	9
	Queen Charlotte Islands	yearling		10	1		178	19	9	5	19	
		yearling					3		7			
Oregon		Northern and central Oregon	subyearling							18		
			yearling	1		1	2			1		
		Southern Oregon	subyearling							5		
Puget Sound		Puget Sound	subyearling				8	1		62		
			yearling	3			8			55		
Transboundary and Southeast Alaska rivers		Alaska	yearling						13		4	
		Stikine River	yearling						622		423	
		Taku River	yearling						69		7	
		Unuk River	yearling					13	125	4	18	
Southern British Columbia		Southern British Columbia mainland	subyearling				1	3				
			yearling	1			18	1	1	1		
		Coastal Washington	subyearling				4			39		
Washington		Coastal Washington	yearling		2				1	2		
			yearling	1						1		
West coast Vancouver Island		WCVI	subyearling	93			1816	11		723	6	4

TABLE A.1. Continued.

Age-class	Regional population	Subregional population	Smolt class	June-Jul			Oct-Nov			Feb-Mar		
				WCVI	CC	SEAK	WCVI	CC	SEAK	WCVI	CC	SEAK
Immature	California	Central Valley, fall	subyearling	1								
		Central Valley, spring	subyearling	1								
	Columbia River	Lower Columbia River	subyearling									
			yearling					1				
		Mid Columbia River, spring	yearling	8				1				1
		Snake River, fall	yearling	18								
		Snake River, fall	subyearling	4	9	6						
			yearling		1							
		Snake River, spring-summer	yearling	1		4						
		Upper Columbia River, spring	yearling								1	
		Upper Columbia River, summer-fall	subyearling	45	13	12						
		Upper Willamette River	subyearling	8	13	7				1	1	
East coast Vancouver Island	Fraser River	ECVI	yearling		3							
			subyearling	13	12	8				1		
	Fraser River	Lower Fraser River, fall	subyearling	28								
			yearling	11								
		Lower Thompson River	subyearling		1							
		Mid upper Fraser River	subyearling								1	
		South Thompson River	subyearling	16	10	10						
		Upper Fraser River	yearling	1								
		Nass and Skeena Rivers	subyearling		1							
			yearling		2							
		Skeena River, Bulkley	yearling								1	
		Lower Skeena River	subyearling		2	1						
Northern British Columbia	Oregon	Northern British Columbia mainland	subyearling							2	1	
			yearling						2			
		Northern and central Oregon	subyearling							5	1	
		Southern Oregon	subyearling							7	7	
			yearling							1		
			yearling							1		
Puget Sound		Puget Sound	subyearling							8		
			yearling							1		
			subyearling	192	4	2				2	1	1
Transboundary and Southeast Alaska rivers		Puget Sound	yearling	8	1					3	1	
		Alaska	yearling									
		Alsek River	yearling									
		Taku River	yearling								1	
Washington	West coast Vancouver Island	Unuk River	yearling								1	
		Coastal Washington	subyearling	9	5	5						
		WCVI	subyearling	9	8	6				1		

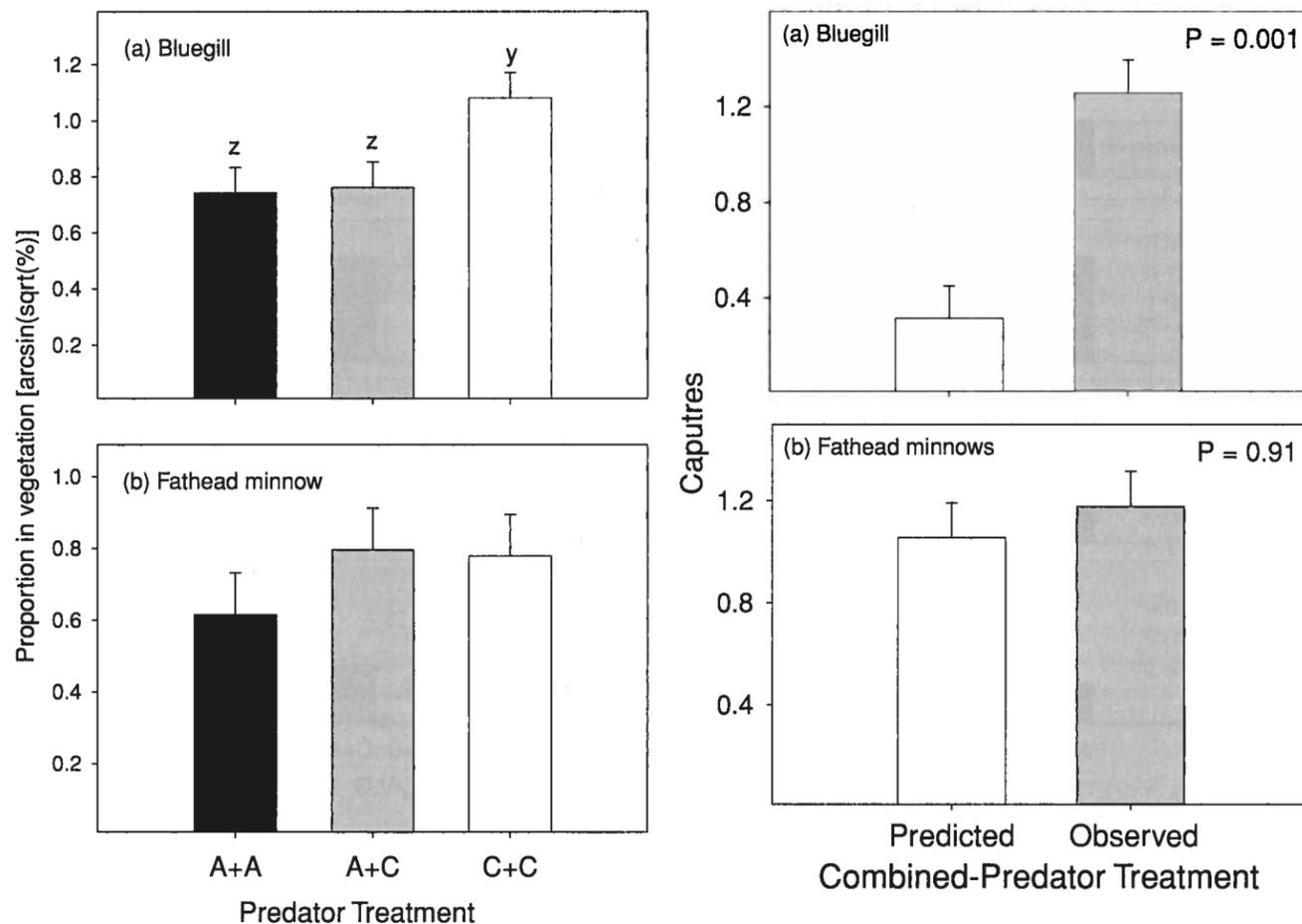


FIGURE 3. Proportions of (a) bluegills and (b) fathead minnow found in vegetation across predator treatments. Values were arcsine-square-root transformed to satisfy the homogeneity-of-variance assumption for normality. Different letters indicate significant treatment effects at the 0.05 level.

combining foraging modes does not improve capture success. Vulnerability of fathead minnow was higher than for bluegills for both of the individual predators (ambush only, cruising only), so no increase in captures occurred with combined predators. In addition to the limited antipredator defense and fusiform shape of fathead minnow, their high vulnerability may have been enhanced because the source population was naïve to predators. Determining how the level of predator experience influences the response of prey to multiple predators is an important next step to understanding multiple predator effects. The strong antipredator defense of bluegills limited the number of captures by either ambush or cruising predators when only one predator species was present in the food web. Predicting outcomes of multiple predator interactions will require incorporating understanding of prey characteristics.

In addition to a maneuvering antipredator defense, bluegills changed their habitat use and amount of activity depending on which predator type was present in the food web. When the

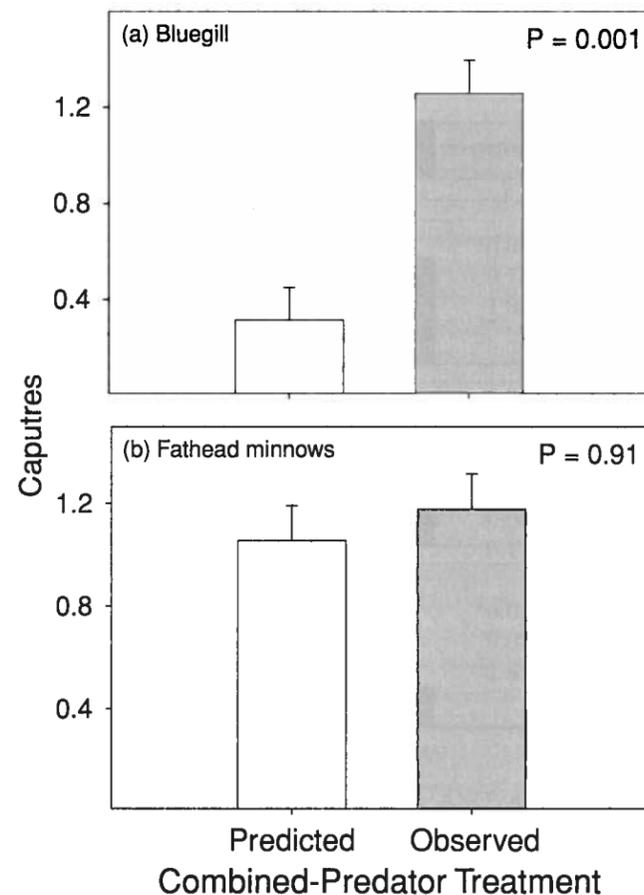


FIGURE 4. Predicted and observed captures of (a) bluegills and (b) fathead minnow in the combined predator treatment. Captures were \log_e transformed to satisfy the homogeneity-of-variance assumption for normality. The P -values are from the least-squares multiple comparison test.

cruising predator was present in either the individual or the combined predator food web, bluegills were found most often in the structured habitat. Bluegills were also less active in the presence of the cruising predator. Responses to predators can contribute to the nature of the combined-predator effect on prey (Soluk 1993; Crowder et al. 1997). Both location and activity patterns suggest the antipredator response of bluegills was to avoid the cruising predator in the open water and rely on their maneuvering defense around structured habitat. The response to the cruising predator increased their encounter rate with the ambush predator. In contrast to bluegills, fathead minnow did not alter their habitat use with changes in predator species. Fathead minnow were least active in the presence of the ambush predator and most active with combined predators. Antipredator behaviors of prey, including habitat use and activity level, can alter multiple predator effects and probably influence food web dynamics.

Overall, the ambush predator had the majority of captures in the combined-predator food web that led to a risk-enhanced

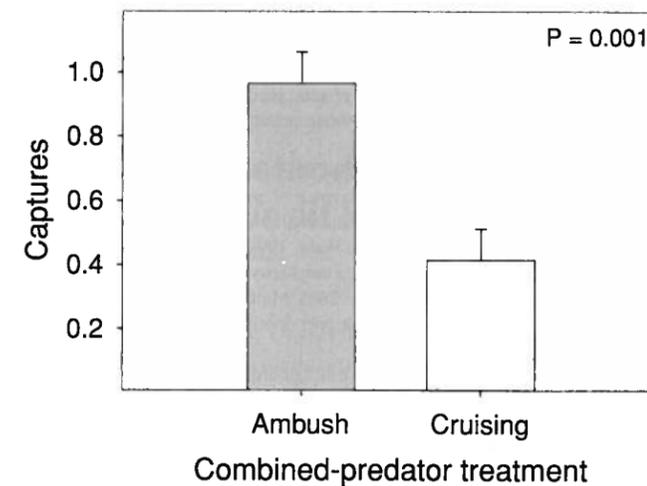


FIGURE 5. Total captures of bluegill and fathead minnow in the combined-predator treatment. Captures were \log_e transformed to satisfy the homogeneity-of-variance assumption for normality.

effect for bluegills. In the combined-predator food web, the cruising predator increased the encounter frequency for the ambush predator that, in turn, increased their number of captures. Encounter rate of prey is a mechanism that has been found to facilitate captures for predators (Eklov and VanKooten 2001). The complementary foraging strategies of the predators created conflicting demands on the bluegill prey. A positive interaction between predators did not occur with fathead minnow because capture success of fathead minnow was high for both individual and combined predators. The neutral effect of fathead minnow needs to be confirmed at larger spatial and temporal scales where additional complexity may affect capture success of predators.

A positive synergistic interaction between ambush and cruising predators, in addition to a risk-enhanced effect on bluegills, is consistent with the patterns of predator growth and combined-predator effects on prey found in ponds (Carey and Wahl 2010). Positive effects on predators were observed in this mesocosm experiment and the Carey and Wahl pond study; however, the predator species benefiting from the combined-predator treatment differed between spatial scales. In the pond study, combined predators in the food web increased growth rates of the cruising predator (Carey and Wahl 2010). In contrast, the ambush predator benefited from combining predators by capturing more prey in the mesocosms. Determining why different predator species benefit from combining foraging strategies will further generalize multiple predator interactions. A number of environmental variables differed between the mesocosms and ponds that could alter outcomes. For instance, water clarity was lower in the ponds than in the clear water mesocosms. Turbidity may affect these two species differently (Carter et al. 2010) and may alter the interaction between these visual feeders (Vanlandeghem et al. 2011). Alternatively, turbidity may influence prey behavior such as habitat use or reaction distance to predators

(Miner and Stein 1996). Furthermore, there is a need to take into account life history changes, seasonal and daily activity patterns, and size structured interactions to more closely mimic natural systems. Caution is necessary when extrapolating from small-scale experiments to natural systems, as may be desired in efforts to inform management. Nevertheless, the presence of multiple predator interactions highlights the importance of simultaneously managing the multiple sympatric fisheries that occur in most systems. Considering the interaction of multiple sport fishes may guide agencies in fulfilling their mission of providing quality angling opportunities and restoring native populations.

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ARTICLE

Is Cating's Method of Transverse Groove Counts to Annuli Applicable for all Stocks of American Shad?

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Abstract

A scale aging method was reported by Cating in 1953 for American shad *Alosa sapidissima* in the Hudson River and subsequently validated by recapturing fish marked and released in the Connecticut River. However, American shad spawn in all major rivers from Canada to Florida and their scales record growth events occurring in three distinct biogeographic provinces. Thus, a single scale aging method may not be applicable across the latitudinal range of this species. To address this concern, scales from American shad from one southern river (the St. Johns), three Middle Atlantic rivers (the Delaware, Hudson, and Connecticut), and one northern river (the Merrimack) were examined. Scales were cleaned, impressed in acetate, and analyzed by the same reader using a digital imaging system. The transverse grooves, the key morphological character used in Cating's method, were counted to the distal edge of the freshwater zone and the first three annuli. In most instances, these groove frequencies were statistically different from Cating's data for the Hudson River. Moreover, our data showed enough overlap in groove frequencies that they cannot be relied on as diagnostic characters for the freshwater zone and first three annuli in fish with difficult-to-interpret scales. Scale size explained more of the variance in groove frequencies than fish age did. Regardless of the specific process creating transverse grooves, we provide evidence that Cating's method should not be used to age American shad.

The American shad *Alosa sapidissima* is an anadromous species ranging from Florida to Canada (Munroe 2002). American shad are found in most of the larger rivers along the eastern coast of North America. After hatching, juvenile shad spend several months in freshwater before heading downstream to the sea,

eventually forming large migratory aggregations from multiple river systems (Talbot and Sykes 1958; Dadswell et al. 1987). American shad spend 3–6 years at sea, migrating to the Bay of Fundy at some point before maturing and returning to their natal rivers to spawn. The range and movements of shad across large

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