Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current*

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Abstract—Information is summarized on juvenile salmonid distribution, size, condition, growth, stock origin, and species and environmental associations from June and August 2000 GLOBEC cruises with particular emphasis on differences related to the regions north and south of Cape Blanco off Southern Oregon. Juvenile salmon were more abundant during the August cruise as compared to the June cruise and were mainly distributed northward from Cape Blanco. There were distinct differences in distribution patterns between salmon species: chinook salmon were found close inshore in cooler water all along the coast and coho salmon were rarely found south of Cape Blanco. Distance offshore and temperature were the dominant explanatory variables related to coho and chinook salmon distribution. The nekton assemblages differed significantly between cruises. The June cruise was dominated by juvenile rockfishes, rex sole, and sablefish, which were almost completely absent in August. The forage fish community during June comprised Pacific herring and whitebait smelt north of Cape Blanco and surf smelt south of Cape Blanco. The fish community in August was dominated by Pacific sardines and highly migratory pelagic species. Estimated growth rates of juvenile coho salmon were higher in the GLOBEC study area than in areas farther north. An unusually high percentage of coho salmon in the study area were precocious males. Significant differences in growth and condition of juvenile coho salmon indicated different oceanographic environments north and south of Cape Blanco. The condition index was higher in juvenile coho salmon to the north but no significant differences were found for yearling chinook salmon. Genetic mixed stock analysis indicated that during June, most of the chinook salmon in our sample originated from rivers along the central coast of Oregon. In August, chinook salmon sampled south of Cape Blanco were largely from southern Oregon and northern California; whereas most chinook salmon north of Cape Blanco were from the Central Valley in California.

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The need to understand the direct and indirect linkages between oceanographic conditions and salmon survival in the marine environment has increased with the listing of many West Coast salmon stocks as threatened or endangered. Recent studies have shown that long-term changes in climate affect oceanic structure and produce abrupt differences in salmon marine survival and returns (Francis and Hare, 1994; Mantua et al., 1997). A major regime shift in the subarctic and California Current ecosystems during the late 1970s may have been a factor in reducing ocean survival of salmon in the Pacific Northwest and in increasing marine survival in Alaska (Hare et al., 1999). Fluctuations in mortality of salmon in the freshwater and marine environments have been shown to be almost equally significant sources of annual salmonid recruitment variability (Bradford, 1995). Unlike in the freshwater environment, the physical and biological mechanisms and factors in the marine environment that cause mortality of salmon are largely unknown. Predation, inter- and intraspecific competition, food availability, smolt quality and health, and physical ocean conditions likely influence survival of salmon in the marine environment. Thus, increasing our understanding of nearshore ocean environments, their linkages to oceanographic conditions, and the role they play in salmonid survival, could provide management options for increasing adult returns. Characterization of the space-time variability of the environmental conditions that smolts encounter when they enter the nearshore ocean, and the eventual survival of these smolts will allow us to identify which biotic and abiotic ocean conditions are correlated with various ocean survival levels.

Many anadromous salmonid populations along the west coast of the United States have declined over the last few decades (Nehlsen et al., 1991), and most stocks show a regional north-south pattern in degree of extinction risk (Kope and Wainwright, 1998). This pattern suggests that both marine habitat conditions and mesoscale climate patterns affect salmonid population status (e.g. Lawson, 1993). A dramatic example is the population trend of coho salmon (*Oncorhynchus kisutch*) along the Oregon coast. Populations along the coast north of Cape Blanco (43°N) have exhib-

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ited a strong decline in size and survival in the mid-1990s; whereas populations south of Cape Blanco have not shown this trend (Lewis[1]). This finding suggests that these two populations have experienced different ocean conditions.

The quality of the marine habitat (in terms of habitat complexity, prey density, and temperature) undoubtedly influences fish growth and condition. Growth and indices of condition can be used as measures of habitat quality for juvenile salmon and to identify essential links between oceanographic conditions and survival of salmon populations during the critical juvenile life history phase. Measures such as growth (growth rate, size variation, and allometric relationships) (Lorenzen, 1996; McGurk, 1996) and accumulation of energetic reserves used in growth and sustenance during the low-productivity winter periods have been used previously to characterize habitat quality and to describe how it ultimately affects the individual and the population (Perry et al., 1996; Paul and Willette, 1997). Environmental factors are known to affect growth, reproduction, survival, and ultimately population recruitment (Hinch et al., 1995; Marschall and Crowder, 1995; Friedland and Haas, 1996). As such, fish condition, growth rate, and size in the pre-adult stages are parameters that can be used to identify the influence of natural and anthropogenic ocean conditions on marine survival.

Much of our current knowledge of the dominant nekton of the pelagic ecosystem off the coasts of Oregon and Washington is derived from a series of 17 cruises conducted by Oregon State University (OSU) from 1979 to 1985. These collections, consisting of >900 quantitative purse seine sets in the northern California Current, were made to examine geographic distributions and temporal trends of the dominant nekton and how these relate to physical and biotic conditions at the time of capture. The primary purpose of these cruises was to collect data for assessment of the abundance, distribution, growth, migration, and ecology of juvenile salmon in coastal waters. Data on the distribution, migration and growth of juvenile salmon from these cruises have been summarized in Fisher and Pearcy (1988; 1995), Pearcy and Fisher (1988, 1990), and Pearcy (1992). Analysis of the nonsalmonid data includes studies on their abundance and distribution (Brodeur and Pearcy, 1986; Emmett and Brodeur, 2000), feeding habits (Brodeur et al., 1987) and interannual variability in relation to oceanographic conditions (Brodeur and Pearcy, 1992). In addition, the distribution of juvenile salmon (mainly coho and chinook salmon [*O. tshawytscha*]) has been studied more recently as a component of a multiyear Columbia River Plume study (Emmett and Brodeur, 2000; Teel et al., 2003; Brodeur et al., 2003). However, all these cruises extended only as far south as Cape Blanco, with the exception of one cruise (July 1984), which extended as far south as Eureka, California, but included only a few collections south of Cape Blanco (Pearcy and Fisher, 1990). Thus, the region south of Cape Blanco is almost completely unknown in terms of juvenile salmon distribution, pelagic nekton, and biological oceanography in general, despite being an area of very strong upwelling and high productivity. Also, the fine-scale distribution of juvenile salmon in relation to environmental variables has not been studied in any detail.

The California Current is not homogeneous but rather can be divided into distinct subunits or regions, each with its own physical and biological characteristics (U.S. GLOBEC, 1994). A break between the northernmost two regions occurs at Cape Blanco, where the equatorward upwelling jet veers sharply off the shelf and into the California Current (Barth et al., 2000). The upwelling zone north of the cape is narrow, extending out about 30 km, whereas south of Cape Blanco, it can extend up to 100 km offshore. This area also appears to represent a faunal break for some zooplankton communities (McGowan et al., 1999; Peterson and Keister, 2002) and is a break point for alternative salmon migration strategies (Weitkamp et al., 1995; Weitkamp and Neely, 2002).

During the summer of 2000, we conducted broad-scale sampling and fine-scale process studies from central Oregon to northern California to examine the distribution of juvenile salmon and associated species in relation to environmental conditions. This was one component of a multidisciplinary U.S. Global Ocean Ecosystem Dynamics (GLOBEC) Northeast Pacific study examining the northern California Current ranging in scope from the physics up to the top trophic levels (Batchelder et al., 2002). We were interested in examining the distribution of juvenile salmon north and south of Cape Blanco, the origin of these fish, and any regional differences in growth and condition of salmon across the range of sampling. Evidence exists that the physical conditions and the associated biota are different within this geographical scale. Thus, analyses of the relationship between oceanographic conditions and the response of resident biota can provide insights into the linkages associated with physical and biological processes that shape the biological community, and in particular, those associated with salmon recruitment.

Methods

Field surveys

Surveys were conducted over two time periods—early summer (29 May–18 June, 2000) and late summer (28 July–15 August, 2000). Each survey consisted of a mesoscale grid along designated GLOBEC transects that had been monitored for several years and by fine-scale process sampling at stations of interest based on features observed in the physical environment (fronts or eddies) or by acoustic sampling conducted by two accompanying oceanographic vessels (RV *Wecoma* and RV *New Horizon*). Further details on the physical and biological conditions occurring at the time of our sampling have been reported by Batchelder et al. (2002).

For the mesoscale survey, stations were established at 1, 5, 10, 15, 20, 25 and 30 nautical miles from shore on each of five transects. Inclement weather, particularly

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[1] Lewis, M. A. 2002. Stock assessment of anadromous salmonids 2001. Monitoring program report OPSW-ODFW-2002-04, 57 p. Oregon Dept. Fish Wildlife, Portland, OR 97207.

during the first cruise, prevented us from sampling all the stations along each transect. At each station, a Nordic 264 rope trawl built by Nor'Eastern Trawl Systems, Inc. (Bainbridge Island, WA) was towed in surface waters by a chartered fishing vessel (FV *Sea Eagle*) at a speed of 6 km/h. This rope trawl has a maximum mouth opening of approximately 30 m × 18 m. Mesh sizes ranged from 162.6 cm in the throat of the trawl near the jib lines to 8.9 cm in the codend. To maintain catches of small fish and squid, a 6.1-m long, 0.8-cm mesh knotless liner was sewn into the codend. All tows were 30 minutes in duration. All fish and squid caught were counted and measured at sea. After fork length (FL) was measured to the nearest mm, all juvenile salmon were immediately frozen for later determinations of growth, condition, food habits, genetic analysis, and assessment of pathological condition.

The physical and biological environment was monitored and sampled at each station immediately prior to setting the trawl. A CTD (conductivity, temperature, and depth) cast was made with a Sea-Bird SBE 19 Seacat profiler to 100 m at deep stations or within 10 m of the bottom at shallow stations. Chlorophyll and nutrient samples were collected from 3 m depth with a Niskin water sampler. A neuston tow with a 1-m^2 mouth containing 333-μm mesh net was towed for 5 minutes out of the wake of the vessel at each station. General Oceanics flow meters were placed inside the net to measure the amount of water sampled. Additional details on the analysis of these neuston trawls are available in Reese et al.[2]

Condition and growth analysis

Each salmonid was remeasured (FL to the nearest mm) and weighed (to the nearest 0.1 g) in the laboratory. A portion of hepatic and muscle tissue was excised, placed in individual capsules, frozen in liquid nitrogen, and stored at –80°C until analyzed. The bioenergetic health of juvenile salmon was evaluated by assessing changes in water content (as a surrogate measure of fat accumulation) of liver and muscle to estimate dry tissue weight. The water content was determined by drying tissue samples to a constant weight at 105°C. The accumulation of energy reserves during the growth season (energy reserves of salmon in August in relation to salmon collected in June) that would enhance survival of juveniles during the winter when food availability is lower was also measured. The condition of juvenile salmon was assessed by examining weight residuals (by using either the wet weight or dry weight) derived from the allometric relationship between length and weight of individual juvenile salmon after logarithmic transformation (Jakob et al., 1996) of salmon captured in June and August. Wet-weight residuals are representative of the traditional condition index of animals and are a reflection of somatic tissue growth. Dry-weight residuals are responsive to accumulation of fat stores and are a reflection of the bioenergetic health of the individual animal (Sutton et al., 2000; Post and Parkinson, 2001).

To contrast growth characteristics during 2000 in different latitudinal ranges of the California Current, we compared ocean growth rates of juvenile coho salmon south and north of Cape Blanco in the GLOBEC study area, and in the area from Newport, Oregon, north to northern Washington. The physical and biological characteristics of these three regions of the coastal ocean differ greatly (U.S. GLOBEC, 1994), and these differences may impact the distribution and abundance of prey of juvenile salmonids and therefore may also affect salmonid growth. Data north of Newport, Oregon, were collected during a separate study of the Columbia River plume and the adjacent coastal ocean (hereafter called the "plume study") using the same trawl and a similar sampling strategy as in the GLOBEC study (see Emmett and Brodeur [2000] and Teel et al. [2003] for details).

Scales were examined from 45 juvenile coho salmon caught during the June and August 2000 GLOBEC cruises and 252 juvenile coho salmon caught during the 2000 plume cruises. The scales were mounted on gummed cards from which acetate impressions were made. Using a video camera attached to a compound microscope and Optimas® imaging software (vers. 5.1, Optimas Inc., Seattle, WA) we measured the distance (scale radius) along the anterior-posterior axis of each scale from the focus (F) to the ocean entry mark (OE) and to the scale margin (Fig. 1). The fork-length of each fish at the time of ocean entry (FL_{OE}) was estimated from the scale radius (SR_{OE}) at ocean entry using the Fraser and Lee back-calculation method (Ricker, 1992):

$$FL_{OE} = \frac{(FL - 36.07)}{SR} \times SR_{OE} + 36.07,$$

where FL = length at capture;
SR = scale radius at capture; and
36.07 = the intercept from a regression of SR on FL for juvenile coho salmon caught in the ocean (Fig. 2A).

In an analogous fashion, fish weight at time of ocean entry (Wt_{OE}) was back-calculated from the estimated fish fork length at ocean entry (FL_{OE}):

$$\ln(Wt_{OE}) = \frac{\left(\ln(Wt)+12.633\right)}{\ln(FL)} \times \ln(FL_{OE}) - 12.633,$$

where Wt = weight at capture; and
–12.633 = the intercept from a linear regression of $\ln(Wt)$ on $\ln(FL)$ for juvenile coho salmon caught in the ocean (Fig. 2B).

The growth rate in FL,

$$(FL - FL_{OE})/\Delta d,$$

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[2] Reese, D. C., T. W. Miller, and R. D. Brodeur. 2003. Community structure of neustonic zooplankton in the northern California Current in relation to oceanographic conditions, 22 p. Unpubl. manuscript. Northwest Fisheries Science Center, NMFS, 2030 S. Marine Science Drive, Newport, OR 97365.

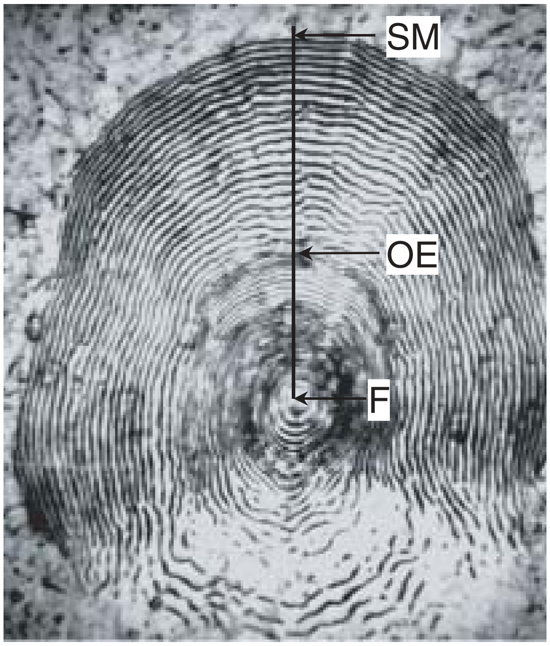

Figure 1

Scale from a 352-mm FL male juvenile coho salmon (*Oncorhynchus kisutch*) caught during the August 2000 GLOBEC cruise showing the axis of measurement (black line), the focus (F), the mark of ocean entry (OE), and the scale margin (SM).

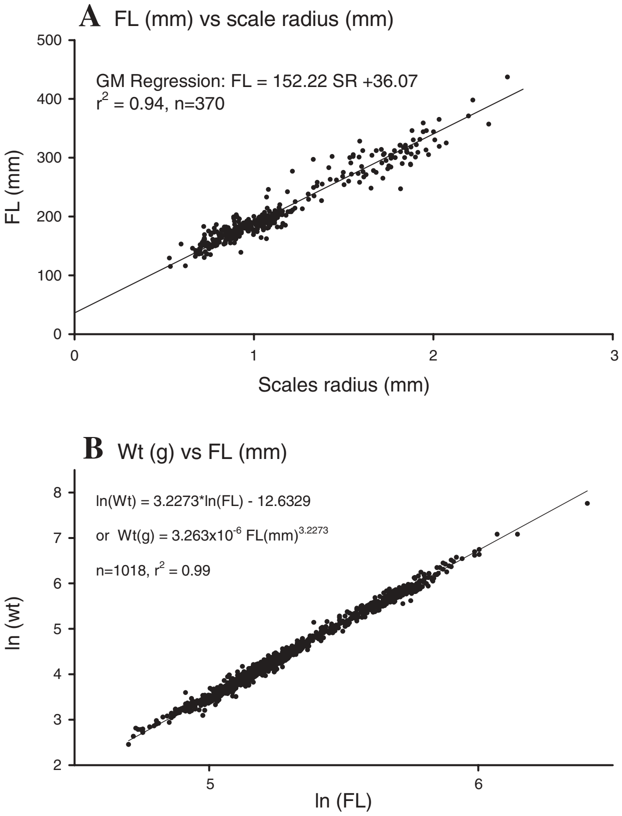

Figure 2

(**A**) Regression of fork length (FL) on scale radius and, (**B**) regression of ln(*Wt*) on ln(*FL*) for juvenile coho salmon (*Oncorhynchus kisutch*) caught during the May 1998–September 2000 Columbia River plume study.

and the instantaneous growth rate in weight:

$$G = \left(\ln(Wt) - \ln(Wt_{OE})\right) / \Delta d,$$

where Δd = estimated days between ocean entry and capture, were estimated for each salmon.

The meaning of the instantaneous growth rate G can be stated as follows: if salmon growth is exponential between ocean entry and capture, then

$$\frac{Wt}{Wt_{OE}} = e^{G \times \Delta d},$$

and at any *instant* the fish's weight increases at the *rate* of G of its body weight per day. G can be multiplied by 100 to give the instantaneous growth rate in terms of percentage of body weight per day.

Although the dates of ocean entry of individual fish were unknown, seaward migration of coho salmon smolts in California, Oregon, and Washington rivers occurs mainly between mid-April and mid-June, and there is no consistent latitudinal trend in timing of the migration (Weitkamp et al., 1995). Peak downstream migration of coho salmon smolts was between mid-May and very early June in the Columbia River estuary, 1978–83 (Dawley et al., 1985), and in the lower Trinity River, California, 1997–2000 (USFWS[3]). In 2000, peak downstream migration of mainly nonhatchery coho salmon smolts at 13 monitoring sites in coastal Oregon rivers north of Cape Blanco occurred from April 2 to May 20; median peak migration occurred 26 April (Solazzi et al.[4]) From the information available on timing of seaward migration of coho salmon smolts, we used an ocean entry date of 15 May when calculating Δd and estimating ocean growth rates of unmarked coho salmon from scales.

In addition to estimating growth rates of juvenile coho salmon from scales, we also estimated instantaneous growth rates in weight between hatchery release and capture in the ocean of 28 coded-wire−tagged (CWT) juvenile coho salmon:

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[3] USFWS (U.S. Fish and Wildlife Service). 2001. Juvenile salmonid monitoring on the mainstem Klamath River at Big Bar and mainstem Trinity River at Willow Creek, 1997−2000, 106 p. Annual report of the Klamath River Fisheries Assessment Program. Arcata Fish and Wildlife Office, Arcata, CA 95521.

[4] Solazzi, M. F., S. L. Johnson, B. Miller, and T. Dalton. 2002. Salmonid life-cycle monitoring project 2001. Monitoring program report OPSW-ODFW-2002-2, 25 p. Oregon Dept. Fish and Wildlife, Portland, OR 97207.

$$G = \left(\ln(Wt) - \ln(Wt_R)\right) / \Delta d,$$

where Wt = weight of the CWT fish at capture;
Wt_R = the average weight of fish in the CWT group at time of release; and
Δd = days between hatchery release and capture in the ocean.

Estimated growth rates of these CWT fish, of known release date and known average release weight were used to validate the growth rates estimated from scale analysis

Our analysis of the growth of chinook salmon based on scale characteristics is not far enough advanced to report in this article. We plan to present these data in a later article.

Contribution of hatchery coho salmon to catches

The total numbers, percentages of marked fish (any external fin clips or internal tags) and grand average weights of hatchery coho salmon smolts released in 2000 are summarized for different release regions in Appendix Table 1. These data were used to compare the estimated average weights of fish at time of ocean entry (from scale analysis) with the average weights of hatchery fish at time of release, and also to estimate the proportions of hatchery coho salmon in our catches. We calculated the expected percentage (*E%*) of marked fish in each catch if 100% of the fish were hatchery fish:

$$E\% = \sum R_i \times A_i,$$

where R_i = the proportional contribution of region *i* to the catch (this paper for the GLOBEC catches, and from Teel et al., 2003 for the plume study catches); and
A_i = the percentage of hatchery fish that were marked in region *i* (from Appendix Table 1).

The percentage of hatchery fish in each catch sample (*H*%) was then estimated as

$$H\% = \frac{O\%}{E\%} \times 100,$$

where *O%* = observed percentage of marked fish.

Genetic analysis

The freshwater origins of juvenile chinook and coho salmon and steelhead (*O. mykiss*) were studied by using standard methods of genetic mixed stock analysis (Milner et al., 1985; Pella and Milner, 1987). According to the methods described by Aebersold et al. (1987), samples of eye, liver, heart, and skeletal muscle were extracted from frozen whole juvenile salmon and analyzed with horizontal starch-gel protein electrophoresis. Data from previous studies characterizing genetic (allozyme) differences among spawning populations in California and the Pacific Northwest were then used as baseline data to estimate the stock compositions of our ocean caught mixed-stock samples. Baselines consisted of 32 gene loci and 116 populations for chinook salmon (Teel et al.[5]), 58 loci and 49 populations for coho salmon (Teel et al., 2003), and 55 loci and 57 populations for steelhead (Busby et al., 1996). Estimates of stock compositions were made by using the maximum likelihood procedures described by Pella and Milner (1987) and the Statistical Package for Analyzing Mixtures (Debevec et al., 2000). Estimates of individual baseline populations were then summed to estimate contributions of regional stock groups. Precision of the stock composition estimates was estimated by bootstrapping the estimates 100 times with resampling of the baseline and mixture genetic data as described in Pella and Milner (1987).

Habitat and assemblage analysis

The raw numbers of fish and squid caught from each trawl were converted to densities based on the volume filtered per trawl to standardize for differences in effort between tows. Density contours of juvenile salmon and other nekton were produced using specialized graphics programs. We then tested whether the habitat associations of the dominant salmonids were significantly different from the total habitat sampled by following the methods outlined in Perry and Smith (1994). This procedure involved comparing the cumulative distributions of salmon catch with observed environmental conditions (temperature, salinity, chlorophyll-*a* at one meter, water depth, and neuston displacement volume). We performed 5000 randomizations of the data and used the Cramér-von Mises test statistic recommended by Syrjala (1996) as being robust to the effects of inordinately large catches.

To explore the relationship between juvenile salmon and other fish species and environmental variables, we used several types of multivariate analyses (McCune and Grace, 2002). Original data from each of the two cruises formed complimentary species and environmental matrices. The June and August cruises were analyzed individually to look at spatial patterns of species composition in relation to environmental gradients (Gauch, 1982). To avoid spurious effects of rare species, we excluded species from the data matrix that had a frequency of occurrence of less than 10% of the possible occurrences for each cruise (McCune and Grace, 2002). To minimize the effect of very large catches, the data were log transformed. Stations with no species present were eliminated from the data set to allow for analysis of sample units in species space. Data transformations and their effects on the summary statistics were examined prior to analysis. Analyses of data were performed by using PC-ORD version 4.28 (McCune and Mefford, 1999).

Agglomerative hierarchical cluster analysis (AHCA) using the Bray-Curtis dissimilarity measure and Wards

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[5] Teel, D. J., P. A. Crane, C. M. Guthrie, III, A. R. Marshall, D. M. Van Doornik, W. D. Templin, N. V. Varnavskaya, and L. W. Seeb. 1999. Comprehensive allozyme database discriminates chinook salmon from around the Pacific Rim. (NPAFC document 440), 25 p. Alaska Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Road, Ancorage, AK 99518.

linkage function was applied to arrange the nekton species assemblages and stations into cluster groups. The cutoff level to form optimal groups within the species and station dendrograms was based on several criteria: 1) biological meaning; 2) significance tests of groups using a multi-response permutation procedure (MRPP); and 3) comparison of cutoff level MRPP results with those groups obtained from one cutoff level below and above the level of interest. A nonparametric procedure, MRPP compares the *a priori* groupings from AHCA and tests the hypothesis of no difference between the groups. For cluster analysis of stations, indicator species analysis (ISA) was used to determine nekton species strongly associated with individual groups. ISA assigns indicator values to each species according to relative abundance and frequency, then tests the significance (Monte-Carlo permutation test) of the highest species-specific indicator value assigned to a particular group.

Nonmetric multidimensional scaling (NMS; Kruskal, 1964) was used to ordinate sample units in species space and to compare station cluster groups to environmental gradients. NMS was chosen for this analysis because it is robust to data that are non-normal and that have high numbers of zeros. Initial runs of NMS from both cruise datasets resulted in three-dimensional solutions. Subsequent reapplication of NMS using a three-dimensional solution (Sorensen distance, 400 maximum iterations, and 40 runs with real data) was applied for the final ordinations. To examine the environmental or station factors associated with each NMS axis that may have affected the distribution of the dominant taxa, we correlated the NMS station and species scores to a suite of environmental variables including water depth, distance offshore, latitude, surface temperature, surface salinity, chlorophyll-*a* concentration, and neuston zooplankton settled volumes. Pearson and Kendall correlations with each ordination axis were used to measure strength and direction of individual species and environmental parameters.

Results

Distribution of juvenile salmon and other species

We collected a total of 18,852 nekton individuals: two cephalopod, one agnathan, two elasmobranch, and 57 fish taxa from 163 surface trawls (see Table 1 for scientific names of all species). With the exception of market squid in June and blue shark in August, most of the nonteleost nekton occurred in only a few collections. Substantially fewer fish were caught in the June cruise than in the August cruise, but the diversity was much higher in the June cruise. The catch in June was dominated by forage fishes such as Pacific herring, surf and whitebait smelt, and juvenile rockfishes, sablefish, and flatfishes. Salmonids, mainly juvenile chinook and coho salmon and steelhead, comprised a relatively minor proportion of the catches (only 114 juvenile salmonids; 1.9 % of the total).

The August cruise was dominated by several large catches of Pacific sardine (Table 1). Jack mackerel was the most common nonsalmonid caught. Many of the juvenile fish taxa caught during the June cruise were absent during the August cruise; those that did occur (sablefish, rex sole) were much lower in abundance. Mesopelagic fishes of the family Bathylagidae and Myctophidae were collected only during the August cruise, mainly because of the inclusion of more offshore stations and occasional collections during nondaylight hours. As in the earlier cruise, salmonids comprised a relatively minor percentage of the catch (3.1%) but were more common and abundant during this survey.

Juvenile chinook salmon were broadly distributed latitudinally during both cruises, but their distribution was mainly restricted to nearshore stations within the 100-m isobath (Fig. 3). Coho salmon juveniles were more common north of Cape Blanco during both cruises and were found generally farther offshore than chinook salmon juveniles (Fig. 3). In contrast, steelhead juveniles were found mainly south of Cape Blanco, especially in June, but their zonal distribution overlapped that of coho salmon juveniles.

Size and condition of juvenile salmon

Fork length of yearling chinook salmon averaged 227 ±42 mm FL in June and 230 ±30 mm FL in August and averaged 135 ±12 mm FL for subyearling chinook salmon in August, whereas juvenile coho salmon averaged 162 ±32 mm FL in June and 286 ±46 mm FL in August (Table 2). No significant differences in fork length of juvenile chinook or coho salmon north or south of Cape Blanco were evident.

Juvenile coho salmon weighed significantly more on a wet-weight basis for a given fork length in the region north of Cape Blanco compared to juveniles captured south of Cape Blanco (Fig. 4). This pattern was also similar and significant when evaluated on a dry-weight basis (bioenergetic growth). Although the stock composition in the two regions could account for some of these differences, the growth responses likely reflect habitat-specific features in the region north of Cape Blanco that benefit coho salmon. No difference in condition of yearling chinook salmon captured north or south of Cape Blanco, on either a wet- or dry-weight basis, was evident (Fig. 4). Information regarding size and condition of subyearling chinook salmon are not presented because few subyearling chinook salmon were caught in June and all but one subyearling chinook salmon in August were caught in the region south of Cape Blanco, OR. Insufficient subyearling chinook salmon were available for an analysis comparable to that done for yearling chinook and coho salmon.

Proportions of wild and hatchery coho salmon

Most of the juvenile coho salmon caught during the plume study north of Newport, Oregon, originated in hatcheries (Table 3). In June and September 2000 we estimated that wild fish comprised only 10% and 25%, respectively, of the catch. Wild fish, however, comprised a proportionally much higher percentage of the catch of coho salmon in the GLOBEC study area in June north of Cape Blanco (67%), and in August south of Cape Blanco (61%), than in the plume study area farther to the north. Most jacks and

Table 1

Phylogenetic listing of nekton catch in numerical composition, frequency of occurrence (F.O.) and size range caught for each cruise. (j) indicates juvenile stage; (a) adult. ML = mantle length, TL = total length, FL = fork length, SL = standard length (in mm).

			June (84 stations)			August (79 stations)		
Class and Family	Common name	Scientific name	Number	F.O.	Size range	Number	F.O.	Size range
Cephalopoda								
Onychoteuthidae	Pacific clubhook squid	*Onychoteuthis borealijaponicus*	19	6	21–80 ML	302	6	21–227 ML
Loliginidae	Market squid	*Loligo opalescens*	301	14	33–122 ML	1	1	35 ML
Agnatha								
Petromyzontidae	Pacific lamprey	*Lampetra tridentata*				1	1	625 TL
Chondrichthyes								
Alopiidae	Thresher shark	*Alopias vulpinus*	1	1	36–576 TL			
Carcharhinidae	Blue shark	*Prionace glauca*				18	10	1300–1660 TL
Osteichthyes								
Xenocongridae	Eel leptocephalus	*Thalassenchelys coheni*	3	1	214–243 TL	2	2	260–305 TL
Clupeidae	Pacific herring	*Clupea pallasi*	1022	9	127–195 FL			
	Pacific sardine	*Sardinops sagax*	7	2	237–260 FL	10,327	15	178–290 FL
Engraulididae	Northern anchovy	*Engraulis mordax*				49	12	148–165 FL
Salmonidae	Chinook salmon (j,a)	*Oncorhynchus tshawytscha*	56	18	121–780 FL	252	26	109–910 FL
	Coho salmon (j,a)	*Oncorhynchus kisutch*	35	15	122–580 FL	111	25	210–736 FL
	Cutthroat trout (j,a)	*Oncorhynchus clarki*	1	1	186 FL	3	3	258–341 FL
	Steelhead trout (j,a)	*Oncorhynchus mykiss*	22	8	176–284 FL	36	13	261–430 FL
Osmeridae	Smelt (j)	Osmeridae	14	4	37–52 SL	74	5	31–50 SL
	Surf smelt	*Hypomesus pretiosus*	846	8	128–184 FL	351	7	140–187 FL
	Whitebait smelt	*Allosmerus elongatus*	946	6	60–114 FL	79	3	76–132 FL
Bathylagidae	Popeye blacksmelt	*Bathylagus ochotensis*				1	1	76 SL
Paralepidae	Slender barracudina	*Lestidium ringens*				3	1	72–76 SL
Myctophidae	Northern lampfish	*Stenobrachius leucopsarus*				96	4	14–70 SL
	Bigfin lanterfish	*Symbolophorus californiensis*				61	4	89–102 SL
	Blue laternfish	*Tarletonbeania crenularis*				10	3	33–87 SL
Gadidae	Gadid (j)	Gadidae	10	3	42–58 SL	13	3	53–57 SL
	Pacific cod (j)	*Gadus macrocephalus*	23	1	38–60 SL			
	Pacific tomcod (j)	*Microgadus proximus*	6	4	35–55 SL	8	2	49–80 SL
Scomberesocidae	Pacific saury	*Cololabis saira*	26	1	182–229 FL	66	6	131–194 FL
Atherinidae	Jacksmelt	*Atherinopsis californiensis*				1	1	302 FL
Trachipteridae	King–of–the–salmon (j)	*Trachipterus altivelis*	2	2	71–270 SL	12	2	40–83 SL
Gasterosteidae	Threespine stickleback	*Gasterosteus aculeatus*	1	1	60 SL			
Scorpaenidae	Pacific ocean perch (j)	*Sebastes alutus*	1	1	33 SL			
	Darkblotched rockfish (j)	*Sebastes crameri*	154	14	29–54 SL	1	1	53 SL
	Yellowtail rockfish (j)	*Sebastes flavidus*	1350	24	20–63 SL	1	1	18 SL
	Shortbelly rockfish (j)	*Sebastes jordani*	1	1	37 SL			
	Black rockfish (j,a)	*Sebastes melanops*	1	1	30 SL	1	1	335 FL
	Bocaccio (j)	*Sebastes paucispinis*	20	5	21–36 SL			
	Canary rockfish (j)	*Sebastes pinniger*	27	5	22–39 SL			
	Bank rockfish (j)	*Sebastes rufus*	8	1	16–28 SL			
	Stripetail rockfish (j)	*Sebastes saxicola*	13	3	32–37 SL			
Hexagrammidae	Lingcod (j)	*Ophiodon elongatus*	20	9	76–81 FL			
Anoplopomatidae	Sablefish (j)	*Anoplopoma fimbria*	182	14	55–136 FL	4	2	173–241 FL

continued

Table 1 (continued)

			June (84 stations)			August (79 stations)		
Class and Family	Common name	Scientific name	Number	F.O.	Size range	Number	F.O.	Size range
Cottidae	Irish lord (j)	*Hemilepidotus* spp.	2	1	38–40 FL			
	Cabezon (j)	*Scorpeanichthys marmoratus*	12	7	33–38 SL			
	Pacific staghorn sculpin	*Leptocottus armatus*	1	1	180 TL			
Agonidae	Sturgeon poacher (j)	*Podothecus acipenserinus*				1	1	80 TL
Cyclopteridae	Pacific spiny lumpsucker	*Eumicrotremus orbis*				1	1	253 TL
Carangidae	Jack mackerel	*Trachurus symmetricus*	111	3	364–583 FL	839	20	227–589 FL
Bramidae	Pacific pomfret	*Brama japonica*				5	2	387–434 FL
Anarhichadidae	Wolf-eel (j)	*Anarrhichthys ocellatus*	15	13	215–555 TL	8	7	442–582 TL
Ammodytidae	Pacific sandlance	*Ammodytes hexapterus*	4	4	45–82 SL			
Zaprodidae	Prowfish (j)	*Zaprora silenus*	1	1	68 SL			
Scombridae	Chub mackerel	*Scomber japonicus*				74	6	266–421 FL
Centrolophidae	Medusafish	*Icichthys lockingtoni*	3	3	37–50 SL	8	6	87–129 FL
Bothidae	Sanddabs (j)	*Citharichthys* spp.	23	13	35–43 SL	3	2	269–288 TL
	Pacific sanddab (j)	*Citharichthys sordidus*	32	4	32–44 SL			
	Speckled sanddab (j)	*Citharichthys stigmaeus*	60	10	30–43 SL			
Pleuronectidae	Dover sole (j)	*Microstomus pacificus*	2	2	40–50 SL	3	1	27–34 SL
	Sand sole (j)	*Psettichthys melanostictus*	3	3	22–39 SL			
	Slender sole (j)	*Eopsetta exilis*				1	1	66 SL
	Starry flounder	*Platichthys stellatus*				2	1	349–399 TL
	Curlfin sole (j)	*Pleuronichthys decurrens*	5	3	25–31 SL			
	English sole	*Parophrys vetulus*	1	1	303 TL			
	Rex sole (j)	*Errex zachirus*	581	12	34–79 SL	48	11	44–70 SL
Molidae	Ocean sunfish	*Mola mola*				1	1	620 TL
Total			5974			12,878		

about one half of the nonjacks caught north of Cape Blanco in August were hatchery fish.

Two factors, however, may have lead to inaccuracies in estimation of hatchery-wild ratios of coho salmon in the GLOBEC study area. First, because of low sample sizes, the data were pooled from both June and August catches for the genetic stock analysis; therefore we do not know the proportional contributions of the different release areas to the catches in either month alone. Second, all the fish released from Klamath River and Trinity River hatcheries had been clipped on the maxillary. We were unaware that the maxillary clip was being used, did not look for it, and consequently may have classified fish with this mark as unmarked. Therefore, the proportion of hatchery fish in the catch of coho salmon during GLOBEC may have been higher than is shown in Table 3.

Age and growth of juvenile coho salmon

Forty-three percent (24 of 56) of the juvenile coho salmon caught during the August GLOBEC cruise were precocious males ("jacks") according to the testes-weight to body-weight criteria of Pearcy and Fisher (1988). This is a much higher percentage of jacks than found among juvenile fish caught in September 2000 in the plume study off Oregon and Washington, where only 4.5% of fish (6 of 132) were precocious males or females according to the same criteria. Because the jacks were considerably larger than the nonjacks, average growth rates of the two groups were reported separately.

Estimated average growth rates in FL between ocean entry and capture were higher for fish caught in the August 2000 GLOBEC cruises (1.56–2.22 mm/d) than for fish caught in any other cruises (Table 3). The fish caught in August 2000 were also larger when they entered the ocean (average170–178 mm FL) than fish caught in other cruises (average154–160 mm FL). Average growth rate of jacks from north of Cape Blanco (2.22 mm/d), was significantly higher (*t*-test, $P<0.05$) than growth rates of nonjacks (1.56–1.67 mm/d). Growth rates of nonjacks north and south of Cape Blanco were not significantly different (*t*-test, $P<0.05$). The combination of large size at ocean entry

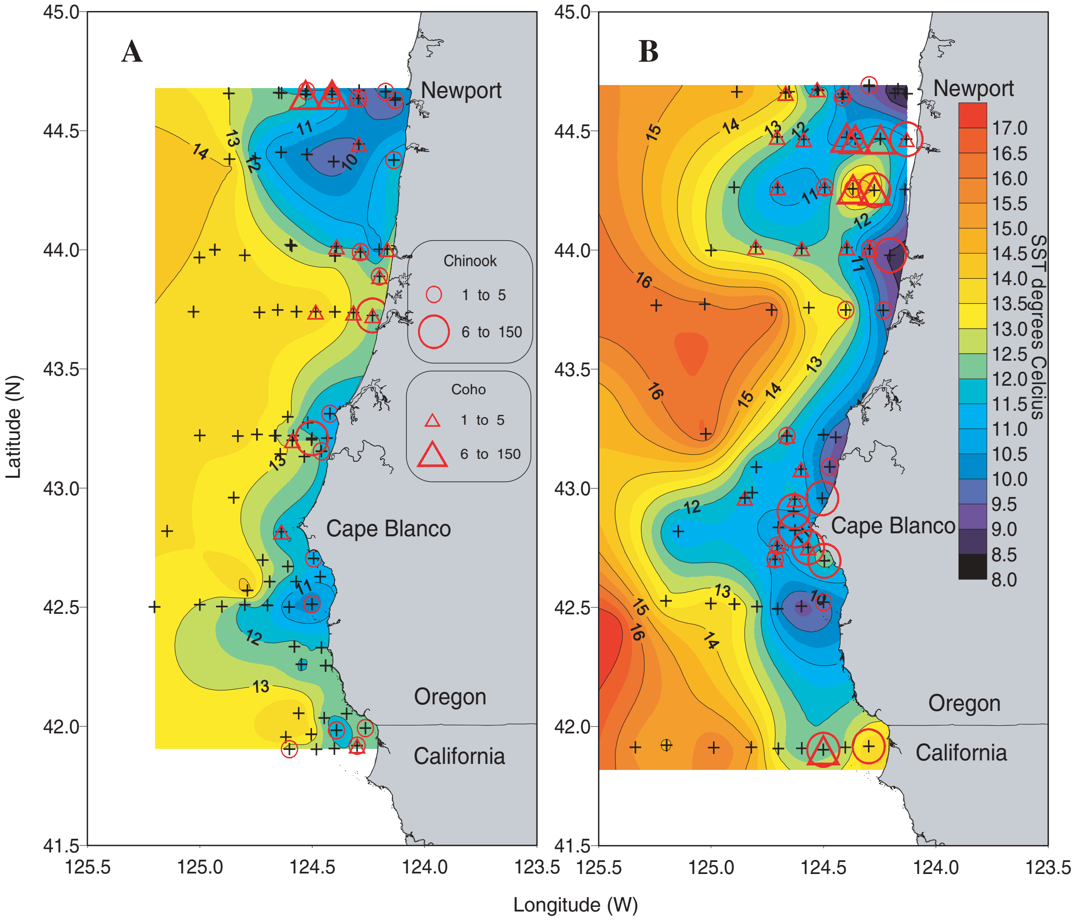

Figure 3

Catch distribution for juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) for the (**A**) June and (**B**) August cruise overlaid on surface temperature contours. Plus signs are stations sampled where no salmon were caught.

and favorable conditions for growth in the ocean probably contributed to the very high percentage of jack coho salmon in August 2000 in the GLOBEC study area.

Estimated average growth rates between ocean entry and capture of juvenile coho salmon were higher in the GLOBEC area than in the plume study area (*t*-tests, $P<0.05$). For fish caught in June, average growth rate was 1.06 mm/d and 0.63 mm/d in the GLOBEC and plume study areas, respectively. For fish caught in August or September, average growth rate was 1.57–2.22 mm/d in the GLOBEC study area and 1.17 mm/d plume in the study area (Table 3). The higher growth rates of coho salmon caught in the GLOBEC study area suggests that in 2000 conditions for growth were better there than those in the plume study area farther north off Oregon and Washington. Average instantaneous growth rates in weight were also higher (*t*-tests, $P<0.05$) for the fish caught in the June and August 2000 GLOBEC cruises (2.0 and 2.1–2.8% body wt/d, respectively) than for the fish caught in the June and September 2000 plume study cruises (1.2 and 1.7 % body wt/d, respectively; Table 4A).

In addition, the average condition index (CI) of juvenile coho salmon in June was significantly higher (*t*-test, $P=0.03$) in the GLOBEC study area (1.12, $n=32$, SD=0.087) than in the plume study area (1.07, $n=245$, SD=0.117). Similarly, the average CI of nonjack juvenile coho salmon was higher (*t*-test, $P=0.002$) in August in the GLOBEC study area (1.24, $n=32$, SD=0.096) than in September in the plume study area (1.18, $n=132$, SD=0.100). Both the high instantaneous growth rates in weight and the high CI of juvenile coho salmon caught in the GLOBEC study area suggest that conditions for growth of coho salmon in this area were very good in 2000. Growth rates estimated from the few CWT fish caught during these cruises (Table 4B) were similar to, and help validate, the growth rates estimated from scales (Table 4A).

Average weights at time of ocean entry back-calculated from scales for coho salmon caught in June in the GLOBEC area and in all months in the plume study area (Table 4A) were slightly higher than the average weights of hatchery coho salmon at time of release (Appendix Table 1). For example, in the plume study area, average back calculated weights at ocean entry ranged from 37.5 g to 42.4 g (Table 4A)—slightly higher than the expected average weights at release of about 32–33 g based on the stock composi-

Table 2

Summary of mean, standard deviation, and range of FL measured in the field, weight measured in the laboratory, and condition index (CI) of subyearling (age 0.0) and yearling (age 1.0) chinook salmon and yearling (age 1.0) coho salmon caught during the June and August cruises north (N) and south (S) of Cape Blanco (latitude 42.837°). Precocious coho salmon are indicated with a "J".

	Field FL (mm)				Laboratory weight (g)			C.I. $(\text{wt}\times 10^5/\text{FL}^3)$	
	n	Mean	SD	Range	Mean	SD	Range	Mean	SD
Chinook (age 0.0)									
June (N)	1	121	—	—	18	—	—	1.04	—
August (N)	1	172	—	—	70	—	—	1.37	—
August (S)	125	134	12	109−175	28	9	12−70	1.10	0.08
Chinook (age 1.0)									
June (N)	27	229	42	144−280	178	91	33−306	1.32	0.10
June (S)	1	174	—	—	67	—	—	1.28	—
August (N)	54	229	26	187−318	164	72	80−468	1.32	0.09
August (S)	35	231	35	190−349	176	94	80−535	1.32	0.07
Coho (age 1.0)									
June (N)	30	161	33	122−276	56	51	19−292	1.13	0.08
June (S)	2	172	0	172−172	49	1	48−49	0.95	0.01
August (N-J)	24	365	31	310−415	690	209	375−1198	1.38	0.12
August (N)	24	285	51	210−385	326	188	97−766	1.26	0.10
August (S)	8	293	33	239−334	308	103	157−433	1.19	0.05

Table 3

Catch, percentage of the catch that was marked, estimated percentage of hatchery origin, size of scale sample, FL at ocean entry (OE) back calculated from scales, FL at capture, and estimated growth rate in FL while in the ocean for juvenile coho salmon caught during the 2000 GLOBEC and Columbia River plume studies. All length data are from the scale sample only. An ocean entry date of 15 May was used when calculating growth rate in FL.

Cruise	Catch (*n*)	Marked	Estimated % hatchery origin	Scale sample (*n*)	Back-calculated FL at OE (mm) mean (SD)	FL at capture (mm) mean (SD)	Growth rate (mm/d) mean (SD)
GLOBEC							
June 2000	32	32%	33%	11	155 (29.0)	177 (42.3)	1.06 (1.01)
Aug 2000							
North of C. Blanco							
Jacks	24	71%	74%	19	170 (22.8)	370 (28.1)	2.22 (0.35)
Nonjacks	24	46%	48%	9	178 (21.6)	309 (46.1)	1.67 (0.51)
South of C. Blanco							
Nonjacks	8	38%	39%	6	178 (13.0)	303 (29.3)	1.56 (0.22)
Plume study							
May 2000	165	68%	76–80%[1]	79	157 (16.5)	166 (17.7)	0.97 (1.15)
Jun 2000	245	76%	90%	97	160 (14.5)	185 (23.4)	0.63 (0.53)
Sep 2000	132	65%	75%	76	154 (19.0)	305 (24.9)	1.17 (0.23)

[1] No genetic stock analysis was available. The higher estimate assumes the same stock composition as in June, the lower estimate assumes that all hatchery fish were from the Columbia River.

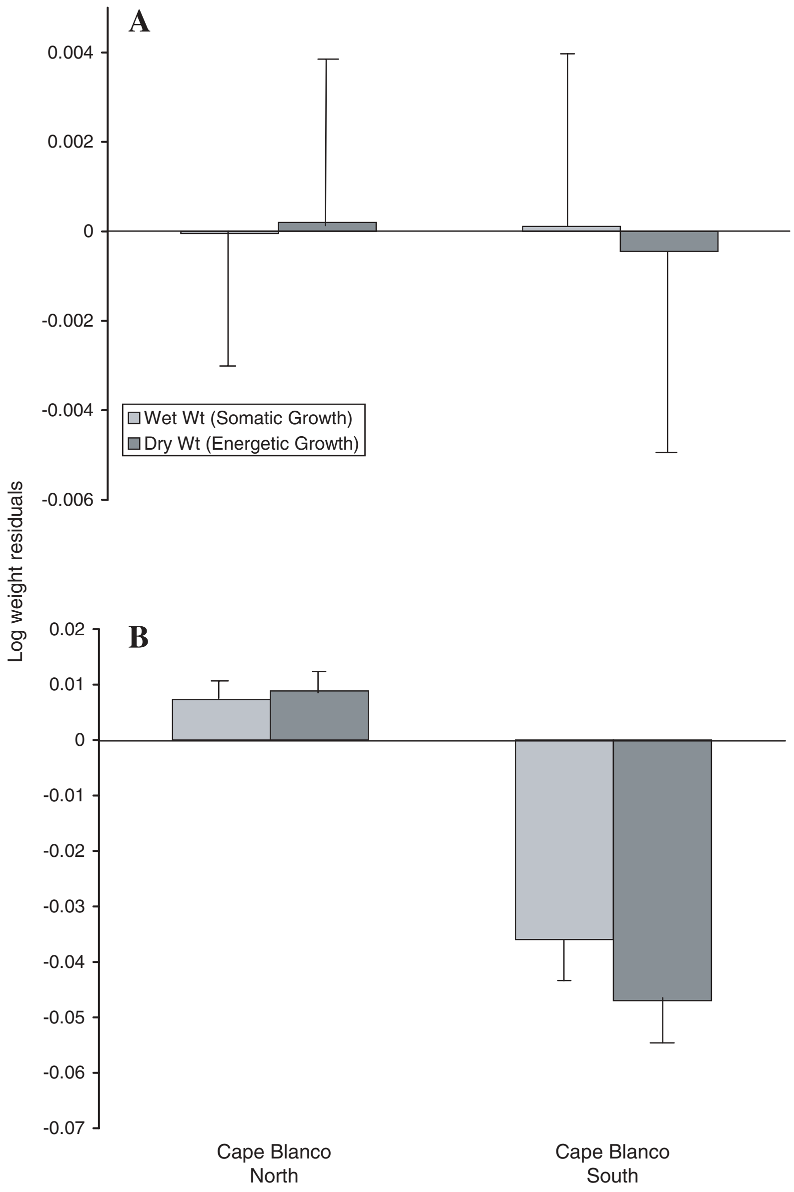

Figure 4

Wet and dry weight residuals (+1 standard error) for (**A**) yearling chinook (*Oncorhynchus tshawytscha*) and (**B**) juvenile coho salmon (*O. kisutch*) collected North and South of Cape Blanco. Weight residuals are derived from the linear relationship between fork length and wet or dry weight (log-transformed data) of juvenile salmon captured in June and August.

tion of these catches (Teel et al., 2003) and the release weights (Appendix Table 1). Similarly, the back-calculated weight at ocean entry in June in the GLOBEC area (45.5 g) was slightly higher than the expected average weight at hatchery release (about 41 g) based on the stock composition (Table 5) and the average release weights. These fairly small differences between back-calculated size at ocean entry and average size at release could be due to growth during downstream migration, selectively higher mortality of small smolts, or a bias in the back-calculation procedure.

However, the average back-calculated weights at time of ocean entry of fish caught in August in the GLOBEC study area (60–69 g) were over two standard deviations above the average weights of hatchery fish released from the Oregon coast or northern California—the main contributors to this catch (Appendix Table 1). These were obviously atypical coho salmon, and the very high proportion of jacks (preco-

Table 4

(**A**) Weights at ocean entry (OE) back-calculated from scales, weights at capture, and estimated instantaneous rates of growth while in the ocean (*G*) for juvenile coho salmon caught during the 2000 GLOBEC and Columbia River plume studies. An ocean entry date of 15 May was used when calculating growth rate. (**B**) Similar data for CWT fish. Growth rates of the CWT coho salmon were estimated for the periods between hatchery release and capture in the ocean.

		Back-calc. Wt. at OE (g)	Weight at capture (g)	*G*
A Cruise	*n*	mean (SD)	mean (SD)	mean (SD)
GLOBEC				
June 2000	11	45.5 (26.8)	78.0 (76.4)	0.020 (0.015)
Aug 2000				
North of C. Blanco				
Jacks	19	68.9 (27.2)	719.7 (200.0)	0.028 (0.005)
Nonjacks	9	59.5 (26.3)	419.2 (177.2)	0.023 (0.006)
South of C. Blanco				
Nonjacks	6	60.3 (12.8)	336.2 (96.2)	0.021 (0.002)
Plume study				
May 2000	79	39.4 (10.8)	47.9 (14.6)	0.020 (0.024)
Jun 2000	97	42.4 (12.5)	71.9 (33.3)	0.012 (0.009)
Sep 2000	75	37.5 (13.7)	347.2 (158.3)	0.017 (0.003)

		Wt. at release (g)	Wt. at capture (g)	*G*
B Cruise	*n*	mean (SD)	mean (SD)	mean (SD)
GLOBEC				
Jun 2000	4	44.4 (1.3)	86.6 (30.9)	0.018 (0.005)
Aug 2000	3	35.6 (9.8)	395.7 (215.0)	0.024 (0.003)
Plume study				
Jun 2000	11	28.3 (4.5)	66.1 (32.3)	0.012 (0.005)
Sep 2000	10	33.4 (10.9)	392.4 (283.3)	0.018 (0.002)

cious, sexually developed males) among the fish was probably a consequence of their very large size at ocean entry and their high rates of growth in the ocean.

Freshwater origins of juvenile salmonids

Allozyme data were collected from samples of 247 chinook salmon, 88 coho salmon, and 58 steelhead. Genetic mixed stock analyses indicated that chinook salmon in June were predominately (54%, SD=0.18) from rivers and hatcheries along the mid Oregon coast, an area immediately north of Cape Blanco (Table 5, Fig. 5). In August, chinook salmon were largely from rivers that enter the sea south of Cape Blanco. Fish from the Sacramento and San Joaquin rivers in northern California were estimated to comprise 90% (SD=0.07) of the chinook salmon sampled in August north of Cape Blanco. The largest concentration of chinook salmon we sampled was south of Cape Blanco in August, and these fish were mostly from rivers in southern Oregon (53%, SD=0.10) and the Sacramento and San Joaquin rivers (20%, SD=0.05). Chinook salmon from the Columbia River Basin were also present, but were estimated to comprise only 18% (SD=0.15) of the June sample and 8% (SD=0.05) of the August sample north of Cape Blanco. Recoveries of hatchery chinook salmon bearing coded-wire tags (CWT) provided direct evidence of stock origins for ten fish, all taken in trawls north of Cape Blanco (Table 5). These data reveal that hatchery fish released from the Umpqua River on the central Oregon coast (n=6), Columbia River Basin (n=3) and Sacramento River (n=1) contributed to our sample of chinook salmon. The proportion of CWT fish from the Umpqua River in our August catch north of Cape Blanco (8%) indicated that the contribution of mid Oregon coastal fish was underestimated in the genetic analysis likely because of the small size of the mixture sample.

Genetic estimates of coho salmon indicated that most fish originated from coastal Oregon rivers north of Cape Blanco (47%, SD=0.10) and from the Columbia River (13%, SD=0.08) (Table 5). However, a substantial proportion (40%, SD=0.09) of coho salmon were from coastal rivers south of Cape Blanco, a region that includes spawning populations in the Rogue and Klamath rivers. Eight coho salmon in our sample contained CWTs and showed that fish from

Table 5

Estimated percentage stock compositions, samples sizes, and recoveries of coded wire tags (CWTs) for chinook and coho salmon and steelhead sampled in trawl surveys along the Oregon and California coasts in 2000. Some of the major baseline stocks are given for coastal stock groups. None of the steelhead sampled contained coded wire tags.

	June (*n*=35) Entire Study Area			August (*n*=157) South of Cape Blanco			August (*n*=55) North of Cape Blanco		
Chinook salmon stock group	Est.	SD	CWT	Est.	SD	CWT	Est.	SD	CWT
Columbia and Snake Rivers	18	0.15	2	3	0.03		8	0.05	1
North Oregon coast (Nehalem, Trask, Alsea, and Siuslaw Rivers)	0	0.00		0	0.00		0	0.00	
Mid Oregon coast (Umpqua, Coquille, Sixes, and Elk Rivers)	54	0.18	3	3	0.03		1	0.02	3
South Oregon coast (Rogue, Chetco, and Winchuck Rivers)	26	0.16		53	0.10		0	0.00	
Klamath and Trinity Rivers	0	0.00		14	0.07		0	0.00	
North California Coast (Mad, Eel, and Mattole Rivers)	2	0.05		7	0.07		1	0.04	
Sacramento and San Joaquin Rivers	0	0.00		20	0.05		90	0.07	1

	June and August (*n*=88) Entire study area		
Coho salmon stock group	Est.	SD	CWT
Columbia River	13	0.08	2
North and Mid Oregon coast (Nehalem, Siletz, Alsea, Umpqua, and Coos Rivers)	47	0.10	5
Rogue and Klamath Rivers	40	0.09	1
North California Coast (Mad, Russian, Little, and Scott Rivers)	0	0.00	

	June and August (*n*=58) Entire study area	
Steelhead trout stock group	Est.	SD
Columbia and Snake Rivers	0	0.00
North and Mid Oregon coast (Nehalem, Siletz, Alsea, Umpqua, Coos, and Coquille Rivers)	1	0.03
South Oregon coast (Elk, Rogue, Chetco, and Winchuck Rivers)	53	0.08
Smith, Klamath, and Trinity Rivers	0	0.00
North California Coast (Mad, Eel, and Ten Mile Rivers)	10	0.05
Sacramento and San Joaquin Rivers	14	0.05
Central and South California Coast (San Lorenzo River and Scott, Pauma, and Gaviota Creeks	3	0.02
Unknown	19	—

hatcheries in the Umpqua River (*n*=5), Rogue River (*n*=1), and Columbia River (*n*=2) were in our study area.

Genetic analysis of steelhead samples showed that a large proportion were from the Rogue River and nearby coastal streams (53%, SD=0.08). Steelhead from the Sacramento and San Joaquin rivers (14%, SD=0.05) and northern California coastal rivers (10%, SD=0.05) were also present. Estimates for steelhead originating from rivers north of Cape Blanco and from south of the San Francisco Bay were near zero. Approximately 19% of the steelhead mixture was not allocated to any source population, suggesting that our baseline data for the species is incomplete. No steelhead in our collections contained CWTs.

Species associations of juvenile salmonids and other species

From cluster analysis of species based on station assemblages (Fig. 6), MRPP of both sample periods showed strong within-group agreement ($P<0.0001$) at the first level (two groups); all subsequent groups had sequentially higher levels of within-group agreement. As a result, the cutoff level was determined by balancing a lower percent information remaining (<30%) in the model while retaining biologically meaningful groups. For June this cutoff resided at the second level (three groups) and for August, at the third level (four groups). For the June cruise, all salmonids includ-

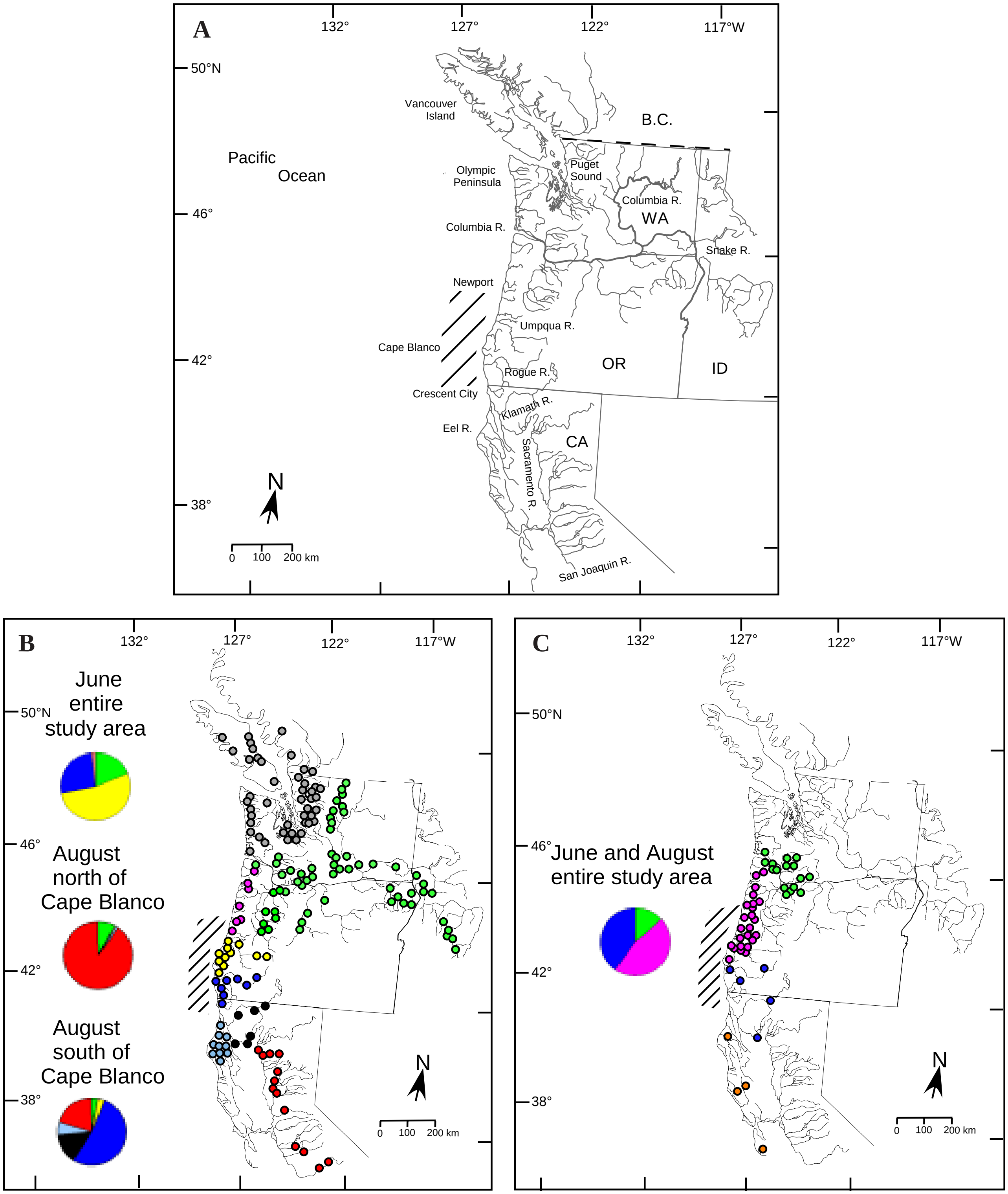

Figure 5

(**A**) Map of study area and location of GLOBEC sampling (hatching). (**B**) Stock compositions of chinook salmon (*Oncorhynchus tshawytscha*). Stock groups are North of Columbia River (grey), Columbia River Basin (green), north Oregon coast (pink), mid Oregon coast (yellow), south Oregon coast (dark blue), Klamath River Basin (black), north California coast (light blue), and Central Valley (red). (**C**) Stock compositions of coho salmon (*O. kisutch*). Stock groups are Columbia River (green), mid and north Oregon coast (pink), Rogue and Klamath rivers (blue), and north California coast (orange).

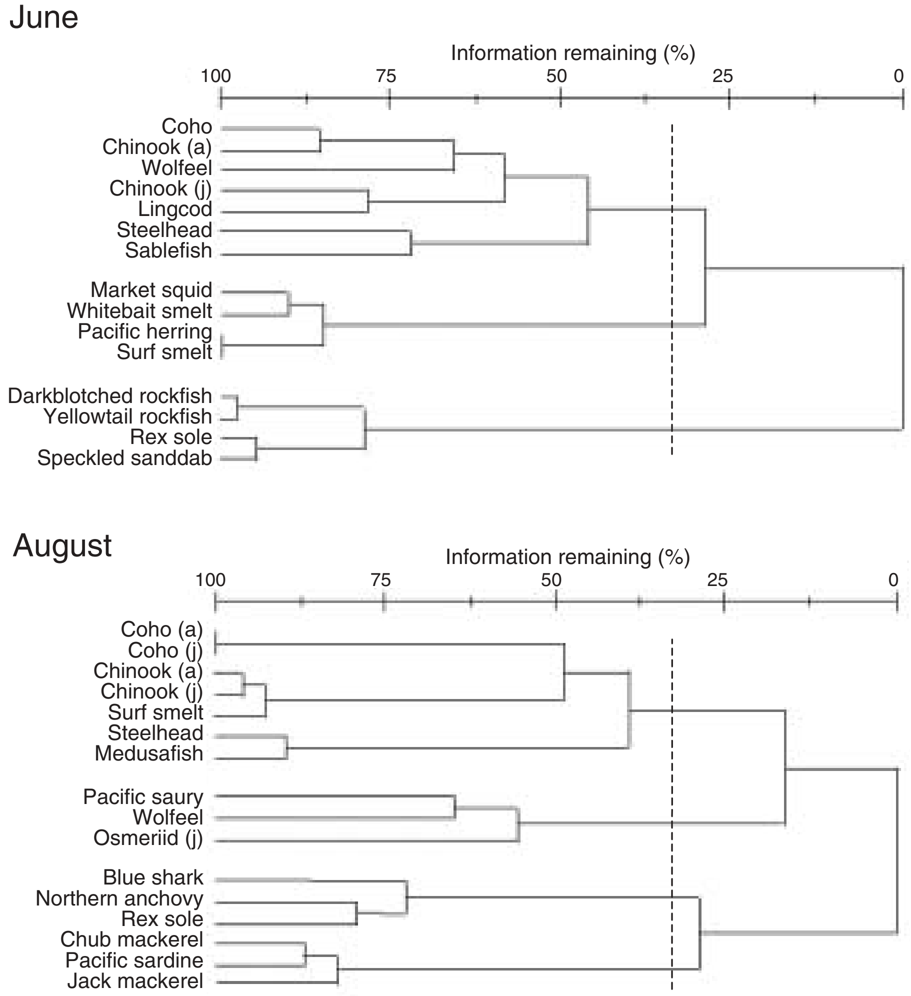

Figure 6

Cluster species groupings by cruise. The dashed lines indicate the cutoff levels for each cluster group. See Table 1 for scientific names.

ing steelhead were classified within the same grouping that included several pelagic juvenile taxa, including wolf-eel, lingcod, and sablefish (Fig. 6). Two other clusters that were not associated with juvenile salmon included a southern inshore group consisting of market squid, Pacific herring, and two species of smelt and an offshore northern group consisting primarily of juvenile rockfish and rex sole. For the August cruise, all salmonid juveniles and adults again clustered together in one large group with surf smelt and medusafish (Fig. 6). The remaining three groups were much smaller and consisted primarily of offshore pelagic species.

Cluster analysis of stations based on species assemblages, and subsequent examination of the cutoff level using MRPP, resulted in three groupings from both sample periods (Fig. 7). MRPP revealed strong within-group agreement for all levels ($P<0.0001$); however, delineation at three groups was based on maintaining lower percent information remaining (<30%) and still having a meaningful level of resolution. There was some measure of geographic separation among the three groups (Fig. 7). In June, group A was predominantly inshore and mostly in the southern half of the sampling area, group B was found mainly in the middle shelf region and was more northern, and group C was found predominantly offshore. In August, group A consisted of only three stations, all south of Cape Blanco, whereas groups B and C both spanned the entire shelf and offshore region and had no particular north-south affinity (Fig. 7). ISA of the groups from both sampling periods showed that only groups A and C had indicator species (Tables 6 and 7), whereas the intermediate groups had none.

Ordination analyses and environmental correlates

NMS ordination of the June sampling period (Fig. 8A) revealed most of the variance in the data: axes 1 and

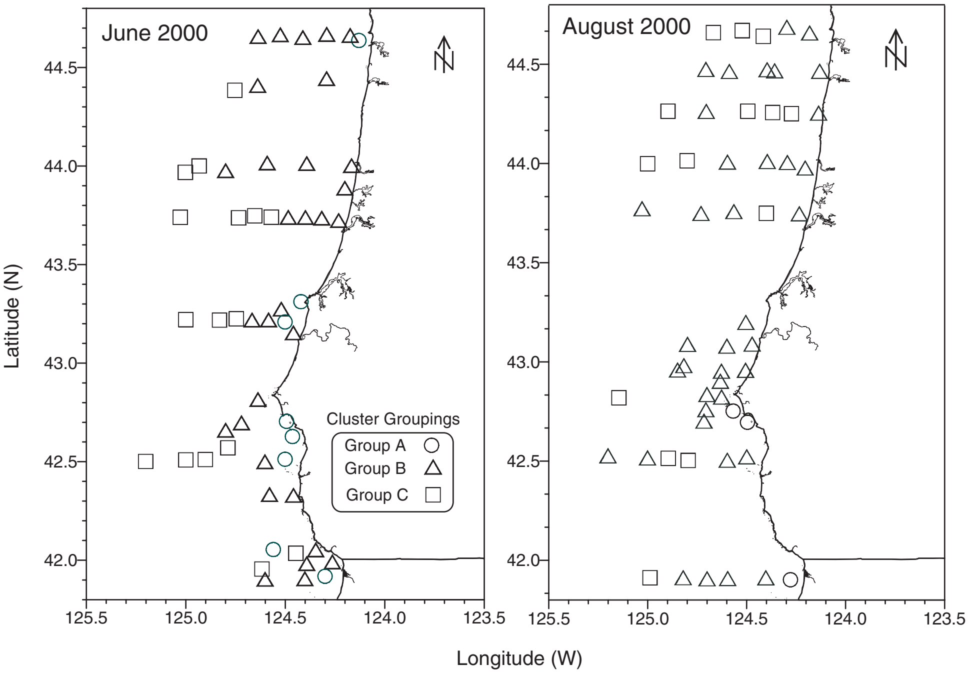

Figure 7

Map showing locations of cluster station groupings by cruise.

Table 6

Indicator species analysis showing indicator values for dominant pelagic nekton captured in pelagic trawls during June 2000 and mean, standard deviations (SD), and *P*-values for each cluster grouping. Cluster Group B did not have any species that were determined to be indicators of that group.

			Indicator value IV from randomized groups		
Group	Species	Observed indicator value (IV)	Mean	SD	*P*-value
A	chinook (age 0.0)	61.0	15.7	6.54	<0.001
A	lingcod	26.1	12.6	5.67	0.024
A	Pacific herring	71.7	12.8	5.88	<0.001
A	surf smelt	86.5	11.8	5.59	<0.001
A	whitebait smelt	31.5	10.4	5.55	0.007
A	market squid	50.8	15.0	6.20	<0.001
C	darkblotched rockfish	66.8	15.8	6.31	<0.001
C	rex sole	46.0	15.0	6.24	0.002
C	sablefish	31.1	16.2	6.32	0.035
C	speckled sanddab	52.5	13.4	5.94	0.001
C	yellowtail rockfish	98.8	19.0	6.30	<0.001

3 represented 31% and 23%, respectively (stress=16.3). Temperature, depth and salinity best explained the ordination of stations, representing a cross shelf gradient from nearshore high levels of salinity to increasing temperature and depth offshore. Ordination of August stations (Fig. 8B) represented 42% of the variance in the data, and 23% of the variance was loaded on axis 2 and 19% on axis 3 (stress=19.4). As with June, salinity increased toward the coast and temperature and depth increased off the shelf. The groups derived from the cluster analysis tended to group together in multivariate space, with the exception of group B in the June cruise (triangles in Fig. 8A).

Table 7

Indicator Species Analysis showing indicator values for dominant pelagic nekton captured in pelagic trawls during August 2000 and mean, standard deviations (SD), and *P*-values for each cluster grouping. Cluster Group B did not have any species that were determined to be indicators of that group.

			Indicator value IV from randomized groups		
Group	Species	Observed indicator value (IV)	Mean	SD	*P*-value
A	chinook (age 1.0)	76.5	21.3	11.18	0.004
A	chinook (age 0.0)	80.4	22.1	11.62	0.003
A	surf smelt	97.9	12.4	8.21	<0.001
C	chub mackerel	33.3	12.8	8.88	0.021
C	jack mackerel	73.7	23.0	11.86	0.006

Table 8

Results of statistical tests for habitat associations between juvenile salmon and environmental or station variables from each cruise in 2000. Fish marked by zeros indicate subyearlings and those marked with one indicate yearlings. Shown are the *P*-levels for 5000 randomizations of the cumulative frequency of the habitat variable and the proportion of the standardized salmon catch associated with each habitat observation. Results are based on the Cramér von-Mises test statistic determined from binned data for depth and neuston biomass. Significance values <0.05 are shown in boldface.

Cruise	Taxon and age	Surface temp.	Surface salinity	1-m chlorophyll	Bottom depth	Neuston biomass
Jun	chinook (age 1.0)	0.30	0.60	0.13	0.18	0.13
	coho (age 1.0)	0.33	0.48	0.21	0.17	0.31
Aug	chinook (age 0.0)	0.36	0.25	0.13	0.35	0.42
	chinook (age 1.0)	**0.04**	**<0.01**	**<0.01**	**0.02**	0.29
	coho (age 1.0)	0.68	**0.04**	0.07	**0.02**	0.45

There were few instances where the habitat associations of juvenile salmon were significantly different from the distribution of environmental variables sampled (Table 8). None of the variables were significant for yearling chinook and coho salmon in the June sampling (no subyearling salmon were caught during that cruise). In August, all the variables except neuston biomass were significant for yearling chinook salmon. These fish were collected at cooler temperatures, higher salinities, higher chlorophyll-*a* concentrations, and at shallower depths than have been typically recorded (Fig. 9). Coho salmon juveniles were found in higher salinities and shallower depths than at the sampled habitat (Fig. 9). These results correlated with the capture of juvenile chinook salmon and to a lesser with extent coho salmon at nearshore stations in the upwelling zone.

Discussion

Understanding the mechanisms underlying the dynamics of multispecies communities is one of the biggest challenges in ecology. Most communities contain many interacting species, each of which is likely to be affected by multiple biotic and abiotic factors. In order to effectively characterize a system, we need to differentiate variability resulting from both temporal and spatial factors. Our observations took place during two time periods of about 20 days each and thus were not synoptic "snapshots" of the system. Indeed, during our June sampling, conditions changed markedly from the beginning to the end of the cruise because of the arrival of an anomalous major southwest storm (Batchelder et al., 2002), which likely completely altered the hydrography and biology of the system. Thus, short-term temporal variability may obscure patterns observed over the spatial scale of our sampling.

The pelagic nekton community sampled during these cruises was not that different from what had previously been shown for purse seine and trawling collections off the coast of Oregon and Washington (Brodeur and Pearcy, 1986; Emmett and Brodeur, 2000; Brodeur et al., 2003). The early summer nekton community was dominated by coastal forage fishes such as smelts and Pacific herring, but also comprised juveniles of many rockfish, sculpin, and flatfish species. These winter-spring spawning species eventually settle out to demersal habitats sometime in summer (Shenker, 1988; Doyle, 1992), which may in part explain the paucity of these taxa in the August cruise. In contrast, the August nekton community consisted of large, highly migratory species such as Pacific sardines, jack mackerel, and chub mackerel. Pacific sardine, which was almost completely absent from the system in the 1980s, has undergone a substantial resurgence and is now one of the most abundant species off the coast in summer (Brodeur et al., 2000; Emmett and Brodeur, 2000; McFarlane and Beamish, 2001). It should be noted, however, that some of the differences between cruises could be accounted for by the inclusion of substantially more offshore stations during the second cruise. Our results from the community analyses suggest that juvenile salmon tend to co-occur with each other and with a variety of other pelagic nekton, including adult salmon, and that this spatial overlap varies temporally. Brodeur et al. (2003), in analyzing community structure based on previous pelagic sampling data off Oregon and Washington, arrived at similar results. In both studies, the geographic boundaries of the pelagic assemblages often overlap and are not as distinct as demersal assemblages. However, the pelagic environment is much more spatially and temporally heterogeneous than the demersal environment, and many of the species examined in our study are highly mobile and are likely to respond quickly to changing conditions. Research is presently underway to examine the trophic interactions among salmonids and with other sympatric nekton species in order to determine what ecological relationships (e.g. predation, competition), if any, are occurring in this system.

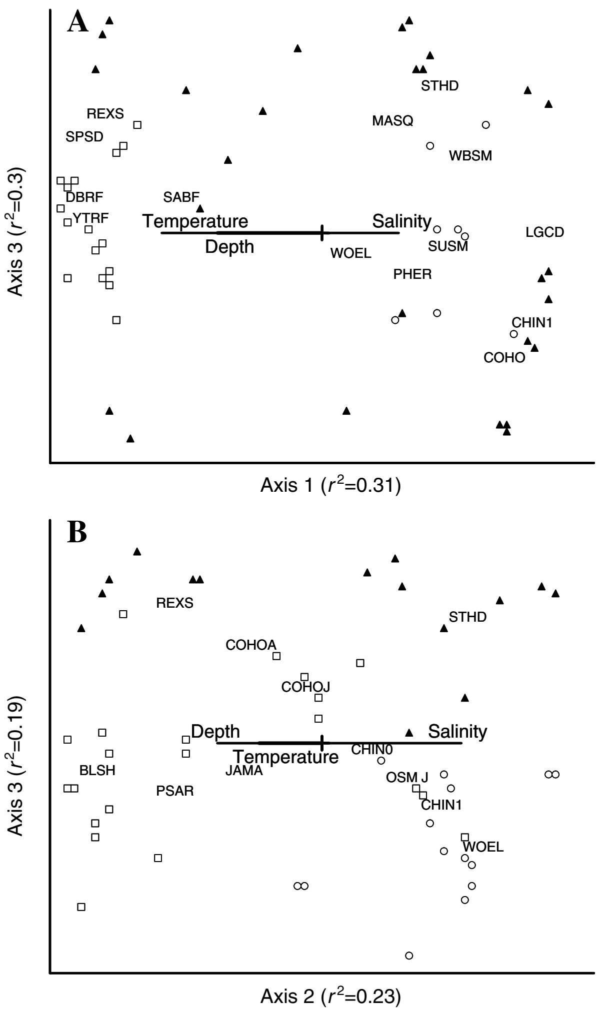

Figure 8

Nonmetric multidimensional scaling (NMS) ordination plot of stations and nekton species with environmental parameters from June (**A**) and August (**B**) 2000 GLOBEC cruises. Station symbols denote: onshore (○), mid-shelf (▲), and slope (☐) groupings; Species abbreviations denote the following taxa: CHIN 0 (chinook, age 0), CHIN 1 (chinook, age ≥1.1), STHD (steelhead trout), SUSM (surf smelt), PSAU (Pacific saury), WOEL (wolf-eel juvenile), OSM J (osmerid juvenile), REXS (rex sole, larval), MEDF (medusafish), PSAR (Pacific sardine), JAMA (jack mackerel), CHMA (chub mackerel), NANC (northern anchovy), BLSH (blue shark).

From the results of our sampling, we concluded that juvenile salmonids, with the possible exception of steelhead, occupy the cool, high salinity, inshore upwelling regions off the southern Oregon coast. However, particularly for the June cruise, many of the coho and chinook salmon juveniles collected may have recently entered the ocean with little time to disperse offshore, so that the capture location may not reflect true habitat preferences. Moreover, the vertical dimensions of our trawl also precluded us from sampling the nearshore, subtidal regions where some subyearling chinook may reside shortly after entering the ocean.

Salmon and steelhead differed considerably in stock composition. The pattern for coho salmon was similar to that of chinook salmon in that fish from sources both north and south of Cape Blanco contributed to our catches. However, steelhead from rivers north of Cape Blanco were absent, presumably having migrated offshore and north shortly after entering the sea, as shown by Pearcy et al. (1990). Although our stock composition estimates for steelhead should be viewed with caution because of an incomplete genetic baseline and a relatively small number of samples, our findings support Pearcy et al.'s suggestion that steelhead from rivers south of Cape Blanco have a unique marine distribution and reside throughout the summer in the upwelling zone off northern California and southern Oregon.

Our study revealed seasonal shifts in the abundance and stock composition of juvenile salmonids. Although salmonids comprised small portions of the vertebrate catches of both the June and August cruises, juvenile chinook salmon, coho salmon, and steelhead were much more abundant later in the summer, likely indicating that fish moving into our study area are from shoreline or riverine habitats. The greater abundance of chinook salmon in late summer can be explained in part by the northern migration of fish that originated in rivers south of our study area. Chinook salmon from the Sacramento and San Joaquin rivers in California's Central Valley comprised substantial proportions in the August catches both south (20%) and north (90%) of Cape Blanco. In contrast, the few chinook salmon caught in June were mostly (54%) from streams that enter the sea immediately north of Cape Blanco such as the Umpqua, Coquille, Sixes, and Elk rivers. Chinook salmon

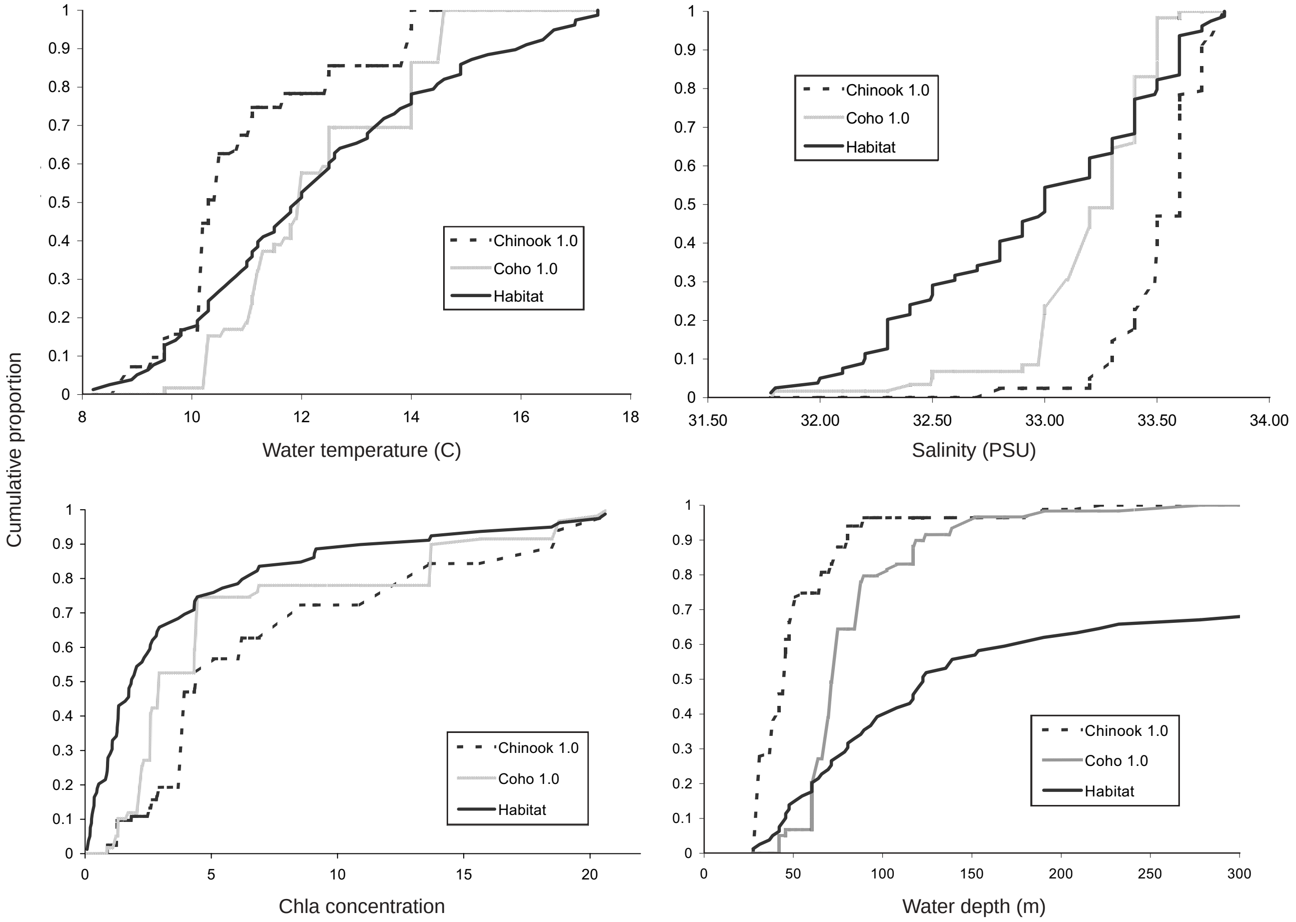

Figure 9

Cumulative distribution curves for salmon and environmental or station variables. Only the August variables that showed at least one significant difference are included. See Table 8 for results of the statistical tests.

from these rivers are known to primarily migrate north of our study area along the coast (Nicholas and Hankin, 1988). By August, fish from these stocks were nearly absent from our samples. Oregon rivers south of Cape Blanco, an area that includes the Rogue, Chetco, and Winchuck rivers, produce chinook salmon with a more southerly pattern of ocean migration (Nicholas and Hankin, 1988; Myers et al., 1998). Chinook salmon from these rivers were found throughout the summer and contributed 53% to our largest catches of chinook salmon along transects south of Cape Blanco in August.

Results from our 2000 GLOBEC cruises identified Cape Blanco as an important breakpoint in salmonid life-history variation. Stock distributions of both juvenile salmon and steelhead indicated that different migration patterns of fish originating from southern and northern rivers are evident during their early marine phase. Our August survey also revealed sharp contrasts in life-history type and freshwater origin between the juvenile chinook salmon population in the marine area north of Cape Blanco and that to the south. Chinook salmon captured north of Cape Blanco were nearly all yearlings and largely from the Sacramento River drainage. Subyearlings predominated in our catches south of Cape Blanco and included a much larger proportion of fish from coastal streams in southern Oregon and northern California.

Comparisons of our results with similar studies conducted further north show differences in salmonid migrations on a somewhat broader geographic scale. In several years of sampling during the summers of 1981 through 1985 off the central Oregon to northern Washington coast, most juvenile chinook salmon bearing CWTs were from Columbia River hatcheries (Pearcy and Fisher, 1990; Fisher and Pearcy, 1995). Only one tagged chinook salmon from a river south of Cape Blanco (Klamath River) was captured. Pearcy and Fisher also found that juvenile coho salmon were largely from the Columbia River and that smaller contributions were from coastal rivers north of Cape Blanco. Their findings have been corroborated by more recent surveys in the same region (Emmett and Brodeur, 2000) using genetic data (Teel et al., 2003). Samples from subsequent cruises will be used to examine the persistence of such fine- and broad-scale geographic structure in the juvenile migrations of salmonid stocks.

A major source of error in our estimates of growth rates of juvenile coho salmon back-calculated from scales was uncertainty of when individual fish entered the ocean. We used a single date of ocean entry for all fish (15 May), but individual fish, of course, entered the ocean at different times over the course of a month or more. Consequently, coefficients of variation were relatively large (84–119% and 75–120% of mean growth rate in FL and weight, respectively) for fish caught in May and June, when errors in estimated growth periods likely were large in relation to the actual growth periods. Conversely, coefficients of variation were relatively small (14–30% and 10–26% of growth rate in FL and weight, respectively) for fish caught in August or September, when errors in estimated growth periods likely were small in relation to the actual growth periods. (Note the decrease in standard deviation of mean growth rates with month of capture in Tables 3 and 4A). Growth rates of CWT coho salmon between hatchery release and capture in the ocean (Table 4B) were very similar to the growth rates of unmarked salmon estimated from scales for the same months and areas. In addition, the growth rates of the former group (CWT coho salmon) helped to validate the growth rates of the latter group (Table 4A).

Significant differences in growth and condition of juvenile coho salmon indicate that different oceanographic environments exist north and south of Cape Blanco. The length of the fish indicated that substantial growth occurred in juvenile coho salmon during the study period. Assessment of other growth features (condition) revealed that juvenile coho salmon grew better north of Cape Blanco. Because we included measurement of condition in both the June and August period in the evaluation, changes in stock composition, described earlier, may be partly responsible for this observation. Although genetic stock composition was different between months, month of sampling was not a significant factor, suggesting that stock composition is not likely a significant factor affecting the difference in condition (a performance metric) of juvenile salmon north and south of Cape Blanco.

Several lines of evidence further support the hypothesis that areas north of Cape Blanco benefit juvenile yearling chinook and coho salmon. There were greater numbers of juvenile yearling chinook and coho salmon to the north of Cape Blanco. Although our overall sampling effort was greater north of Cape Blanco, in the mesoscale portion of our survey designed to assess general distribution patterns, more yearling chinook and coho salmon were captured north of Cape Blanco. Secondly, when we evaluated the growth rate of juvenile coho salmon in the GLOBEC region compared to juveniles captured off northern Oregon and Washington, juveniles from the GLOBEC region grew much better. The similar tracking of resource (distribution and abundance) and performance (measured in terms of either somatic and energetic growth or growth rate) metrics for juvenile yearling chinook salmon and coho salmon north of Cape Blanco suggests that habitat quality in this region was better. The results of this study help define the biogeographical zones for salmon growth and establish regional-based management strategies for depleted salmon stocks.

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Appendix Table 1

Summary of releases of coho salmon smolts in 2000 by region. This summary of releases of all hatchery coho salmon smolts by region was calculated from data in the Pacific States Marine Fisheries Commission Regional Mark Information System (http://www.rmis.org/ [accessed 5 April 2003]) and in USFWS 2001 (see Footnote 2 in the general text).

	No. of release groups	Total fish released	Release weight (g)	
			Marked	mean (SD)
All British Columbia	250	13,612,715	71.4%	19.6 (5.7)
Washington: St. Juan de Fuca, Puget Sound, Skagit River, Nooksack River, etc.	83	15,316,299	86.4%	29.1 (19.7)
Washington:				
North of Columbia River to Cape Flattery	63	7,630,257	76.7%	31.6 (5.3)
Columbia River	140	29,879,137	89.0%	32.0 (6.4)
Oregon Coast north of Cape Blanco	14	809,962	95.6%	41.6 (7.4)
Southern Oregon and Northern California: Rogue, Klamath, and Trinity Rivers	5	745,060	99.8%[1]	42.1 (4.4)

[1] 100% of the fish released from Klamath and Trinity Rivers were clipped on the maxillary.