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Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon

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The effect of climate on the post-smolt survival of North American Atlantic salmon is obscure owing to the difficulty in interpreting the only relationships thus far observed between the abundance of these stocks and climate, which focuses on winter conditions. Placing significance on winter post-smolt survival is contrary to conventional thinking that the spring period is more important, because that is when the post-smolts migrate to sea and transition to ocean life takes place. The pre-fishery abundance for North American stocks was compared to thermal conditions in potential post-smolt nursery areas during the period 1982–1999. Pre-fishery abundance was modeled as a reconstruction of one-sea-winter (1SW) and two-sea-winter (2SW) age salmon populations. Cohort abundance was compared to mean temperature and thermal habitat (sea surface area within a given temperature range) in five index areas. Stock size was negatively correlated with mean sea surface temperature during June. Correlations were comparatively stronger between stock abundance and thermal habitat, further asserting that June conditions – the first month at sea for most stocks in the region – may be pivotal to survival. These correlations suggest that post-smolt survival is negatively affected by the early arrival of warm ocean conditions in the nursery area. Hypotheses related to post-smolt migration, predation, and the availability of suitable prey are discussed.

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Introduction

Variability in Atlantic salmon stock size is associated with life-history events that occur during the first year at sea. After growing in freshwater as juveniles, salmon migrate to sea as post-smolts during spring. Their migrations are initiated by physiological changes mediated by environmental cues during freshwater residency (Whalen et al., 1999). The fish are challenged by a wide array of potential sources of mortality at sea; however, most fish are believed to be lost to predation during their first weeks in the ocean (Fisher and Pearcy, 1988; Holtby et al., 1990; Eriksson, 1994; Salminen et al., 1995). The mortality that occurs during this critical period may be controlled intrinsically by the growth rate of the fish and their resulting ability to escape predators; or, mortality rates may be independent of growth and may result from variation in predator abundance and distribution.

An emerging paradigm, which is based on observations of Atlantic salmon in the Northeast Atlantic, suggests that the controlling factor for survival and abundance is growth-mediated mortality. Friedland et al. (1998) observed that patterns of survival of two European salmon stocks, originating in southern Norway and western Scotland, were correlated with the thermal regimes present during the first weeks at sea of post-smolts. During the years when warm thermal regimes invaded the North Sea and southern Norwegian coastal area in a time frame coincident with post-smolt migration, survival was good. Alternatively, when cold conditions persisted during the migration period, survival was poor. Climate mediation of survival was suggested by the environmental correlate; however, the nature of the mechanism was further elucidated with growth data for one stock. Friedland et al. (2000) reported that post-smolt growth followed a pattern similar to the time series

of survival and climate variation. When warm sea surface temperatures (SSTs) were present, survival was higher and post-smolt growth was also correlated. Thus, post-smolt survival of European Atlantic salmon appears to be controlled by the same mechanisms hypothesized for a wide range of marine species: faster growth during a critical period is associated with the ability to escape predation (Anderson, 1988; Pepin, 1991).

The mechanisms controlling survival of North American Atlantic salmon are obscure. Reddin (1988) and Ritter (1989) searched for environmental correlates by relating survival rate to thermal conditions during the post-smolt year. Such variables, as the northern extent of the 4°C isotherm in January and the extent of ocean surface covered by water warmer than 4°C and limited by latitude and longitude cutoffs, also in January, were positively correlated with survival. The working hypothesis offered was that distribution patterns of both post-smolts and predators might be responding to this winter climate signal and resulting in varying survival (Ritter, 1989). Reddin and Friedland (1993) computed a thermal habitat index whereby the habitat sum was weighted by temperature and associated catch rates. They also reported a correlation between winter conditions and stock size of North American stocks. Friedland *et al.* (1993) systematically searched for thermal habitat trends in other seasons that might be related to stock size, but thermal habitat variation in winter provided the strongest correlate to stock size. Though this temperature correlation appeared to be robust to various methods of computation and description, it was also baffling because the notion that the critical period for salmon was in winter was difficult to support with other biological data: Atlantic salmon are quite large by their first winter and have outgrown vulnerability to most predators affecting them earlier in the post-smolt year (Allen *et al.*, 1972).

Post-smolt growth data for North American salmon is equivocal in its support of growth- and size-related control of post-smolt mortality. Studies on hatchery fish show that between-stock survival rates can be related to post-smolt growth (Friedland *et al.*, 1996). However, no evidence has been produced yet that shows that inter-annual variation in survival is related to growth for North American stocks (Friedland, 1998). This may be related to the selection of stocks analyzed thus far; perhaps, the analysis of wild stocks over a wide geographic range will shed further light on this issue.

What is glaringly obvious is the fact that despite the efforts to find them, there are no climate or growth signals associated with the survival of North American salmon during their early marine life. This may be because of the spatial and temporal scales of the data used in prior climate analyses, which were based on ocean data derived from the comprehensive ocean and atmospheric dataset (COADS) and, thus, limited to a spatial resolution of 2° boxes. Additionally, the analyses were intentionally restricted from examin-

ing inshore areas. We report on a comparison of temperature and thermal habitat trends with refined estimates of stock size of North American salmon. The spatial and temporal focus of our comparisons is on inshore areas during spring, thus emphasizing the habitats post-smolts would most likely utilize during their early marine residency. Through these modifications, we hope to address the limitations associated with earlier studies.

Methods

Study area

The study area covers most of the ocean entry and post-smolt nursery habitat of North American Atlantic salmon (Figure 1). Five index areas were established within the region; they were constrained by the availability of temperature data and our assumptions about the extent of post-smolt habitat. Salmon post-smolts are known to orient to the surface (Dutil and Coutu, 1988); thus, sea surface conditions should be indicative of changes within the depth range they utilize. At a minimum, the areas represent the spatial extent of transit habitat during post-smolt migration. For each index area, temperature and thermal habitat indices were computed for the period bracketing the post-smolt migration to sea and early ocean life. The time period when post-smolts enter the marine environment varies among stocks and will be reviewed for a series of index stocks from North America.

Pre-fishery abundance

Trends in abundance were derived from a run-reconstruction model of one-sea-winter (1SW) and two-sea-winter (2SW) age groups. Because the abundance estimates were originally used to generate forecasts for resource managers, the time chosen was immediately prior to the commencement of 1SW fisheries; thus, these abundance values have become known as pre-fishery abundance (PFA) estimates. The reconstruction accounts for all known removals and natural
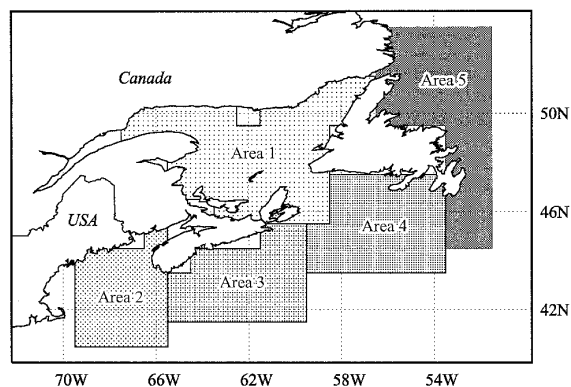

Figure 1. Map of the Northwest Atlantic showing five index areas used to compute thermal habitat indices.

mortality occurring to stocks as prescribed by the ICES North Atlantic Salmon Working Group (ICES, 2002). We proceed by describing the development of PFA estimates and then show their link to the marine environment.

Estimates of total abundance are generated separately for the following geographic regions: Labrador, Newfoundland, Québec, Gulf of St. Lawrence, Scotia-Fundy, and USA. Returns of 1SW and 2SW salmon to each region were estimated by updating methods and variables used by Rago *et al.* (1993a) and reported in ICES (1993) and updated in ICES (2002). The returns for both sea-age groups were estimated using a variety of methods, depending on the data available for individual river systems and/or management areas. These methods included counts at monitoring facilities, population estimates from mark-recapture studies, and the application of angling and commercial catch statistics, angling exploitation rates, and measurements of freshwater habitat. The 2SW component of the multi-sea-winter (MSW) returns was determined using the sea-age composition of one or more indicator stocks. Of the total of 570 rivers, the number of assessed rivers in eastern Canada and the US has ranged from a high of 108 (19%) to a recent low of 72 (13%). Because the number returning to adjacent rivers within a wide area varies in a coherent manner, the use of one or more rivers within a geographic region to describe others should not be problematic.

In the context used in this study, "returns" are the number of salmon that returned to the geographic region, including home-water commercial fisheries, except in the case of Newfoundland and Labrador regions where returns do not include commercial fisheries. This was done to avoid double counting of fish when commercial catches in Newfoundland and Labrador are added to returns of all geographic areas to create the PFA of North American salmon.

The non-maturing component of 1SW fish of the PFA estimator for year i ($NN1_i$), destined to be 2SW returns (excludes 3SW and previous spawners), is constructed by summing 2SW returns in year i+1 ($NR2_{i+1}$), 2SW salmon catches in commercial and aboriginal peoples' food fisheries in Canada ($NC2_{i+1}$), and catches in year i from fisheries on non-maturing 1SW salmon in Canada ($NC1_i$) and Greenland ($NG1_i$). In Labrador, aboriginal peoples' food harvests of small (AH_s, <2.7 kg) and large salmon (AH_l, =2.7 kg) were included in the reported catches for the period 1999–2001. Because harvests occurred in both Lake Melville and coastal areas of northern Labrador, the fraction of these catches that are immature was labeled as af_imm. This was necessary because non-maturing salmon do not occur in Lake Melville where approximately half the catch originated. However, non-maturing salmon may occur in coastal marine areas in the remainder of northern Labrador. Consequently, af_imm for the fraction of aboriginal peoples' harvests that were non-maturing was set at 0.05 to 0.1, which is half of f_imm from commercial fishery samples (range: 0.1–0.2). The equations used to calculate NC1 and NC2 are as follows:

$$NC1_i = f\_imm(H\_s_i + qH\_l_i) + af\_imm(AH\_s_i + qAH\_l_i), \tag{1}$$

and

$$NC2_{i+1} = (1 - q)(H\_l_{i+1} + AH\_l_{i+1}), \tag{2}$$

where H_s_i and H_l_i are the number of "small" (<2.7 kg) and "large" (>2.7 kg) salmon caught in Canada (Salmon Fishing Areas, SFA 1–7, 14b) in year i and q is the fraction of 1SW salmon present in the large-size market category (range: 0.1–0.3).

Similar to 1998–2000, the commercial fishery in Labrador remained closed in 2001. In past reports, salmon returns and spawners for Labrador, which make up one-sixth of the geographical areas contributing to return estimates of maturing 2SW salmon for Canada (NR2), were based on commercial fishery data, but this time series ended in 1998. To estimate PFA, a value for Labrador returns for 2SW for 1998–2001 had to be constructed by developing an appropriate raising factor. This raising factor (RFL2) was derived by dividing PFA without Labrador into PFA with Labrador based on the time series 1971–1997, and was set to the low and high ends of the observed range of values (1.05–1.27). A natural mortality rate (M) of 0.03 per month is assumed to adjust the numbers between the fisheries on 1SW and 2SW salmon (10 months) and between the fishery on 2SW salmon and returns to the rivers (1 month) as subsequently shown:

$$NN1_i = RFL2[((NR2_{i+1}/S1) + NC2_{i+1})/S2] + NC1_i + NG1_i, \tag{3}$$

where $NN1_i$ is PFA of non-maturing 1SW + maturing 2SW salmon in year i, S1 is survival of 1SW salmon between the home-water fishery and return to river [exp (−M1)], S2 is survival of 2SW salmon between Greenland and home-water fisheries [exp (−M10)], and NG_i is the catch of 1SW North American origin salmon at Greenland. A detailed explanation of the model is given in Rago *et al.* (1993b).

Maturing 1SW salmon are, in some areas, a major stock component and measuring their abundance is thought to be important to provide measures of abundance for the entire cohort from a specific smolt class. The calculations are analogous to those for immature 1SW salmon. For the commercial catches in Newfoundland and Labrador, all small salmon are assumed to be 1SW fish, based on catch samples that show its percentage to be in excess of 95%. Large salmon are primarily MSW salmon, but some maturing and non-maturing 1SW may also be present. Estimates of fractions of non-maturing salmon present in the Newfoundland and Labrador catch were based on gonad samples taken from commercial catches. The "large" category in SFA 1–7 and 14B consists of 0.1–0.3 1SW salmon (ICES, 1993; Rago *et al.*, 1993b), while in SFA 8–14A, fish are

mainly maturing (Idler *et al.*, 1981). These values were assumed to apply to the aboriginal food fishery catches in marine coastal areas of northern Labrador.

A raising factor (RFL1) similar to the one for estimating returns of 2SW salmon was developed to include Labrador returns in the maturing component of PFA during the recent closure of the fishery, and estimates for returns to Labrador for 1998–2001 were set accordingly to the low and high ends of the range of observed values during 1971–1999 (1.04–1.59).

The maturing 1SW component for year i ($MN1_i$) is constructed by summing maturing 1SW returns in year i ($MR1_i$) in Canada and the USA and their catches from commercial and food fisheries in Newfoundland and Labrador ($MC1_i$). The same natural mortality rate (M) of 0.03 per month as that for immature fish is assumed to adjust the numbers between the fishery on 1SW salmon and returns to the rivers (1 month):

$$MN1_i = RFL1(MR1_i/S1 + MC1_i), \qquad (4)$$

$$MC1_i = (1 - f\_imm)(H\_s_i + qH\_l_i) + H\_s_i \\ + (1 - af\_imm)(AH\_s_i + qAH\_l_i), \qquad (5)$$

where H_s_i is the number of "small" salmon caught in SFA 8–14a and other symbols are as described before.

The estimated PFA represents the extant population and does not account for the fraction of the population present in a given fishery area. The model does not take into account non-catch fishing mortality in any fishery, because such estimates are not available on an annual basis and rates are not well described for some fisheries. Commercial catches were not included in the run-reconstruction model for the West Greenland fishery (1993 and 1994), Newfoundland fishery (1992–2001), and Labrador fishery (1998–2001), as these fisheries were closed. As PFA estimates of 2SW salmon require data on returns to rivers, the most recent year for which an estimate is available is 2000.

Probability density function for PFA estimates

With the exception of the Greenland catch ($NG1_i$), none of the input values in the above equations can be estimated precisely. Estimates of total returns ($NR2_{i+1}$, $NR1_i$, and $MR1_i$) are based on a variety of regional extrapolation methodologies and estimates of sea-age composition of the Newfoundland, and Labrador catches (NC1, MC1, and NC2) are based on observed ranges of sea-age compositions within market categories and observed ranges of maturing and non-maturing fractions in the 1SW component of the catch. The implications of the uncertainties in deriving NN1 and MN1 were addressed using Monte Carlo simulation. For each year, the approximate distributions of NN1 and MN1 were estimated by drawing random values for NR1, MR1, NR2, NC1, NC2, and MC1 from their observed range and assuming that they were uniformly distributed and then substituting the new random values

into Equations 3 and 4 to obtain a realization of NN1 and MN1. Their probability density functions were approximated by 2000 independent realizations. Upper and lower bounds on the distributions were represented by the fifth and 95th percentiles.

Thermal habitat indices

Temperature regime of the ocean sea surface was based on data extracted from version 2 of the optimum interpolation (OI) SST analysis (Reynolds *et al.*, 2002). These data are produced weekly on a 1° grid and use *in situ* and satellite SST plus SST simulated by sea-ice cover. Before analysis, satellite data are adjusted for biases using the methods of Reynolds (1988) and Reynolds and Marsico (1993).

Mean monthly temperature was computed for each index area by year from the OI dataset for the period bracketing post-smolt migration for that index area. Mean temperatures by month and year for 1° boxes were computed from weekly temperature fields (four or five estimates). The mean monthly values averaged over the boxes within each index area were correlated with total, 1SW, and 2SW PFA using Pearson's product-moment correlation. Next, monthly average temperatures by box were classified according to 2°C intervals (with midpoints starting at 1.5°C), and areal extent (km^2) of each class was computed by index area, and the year as an index of its availability as "thermal habitat". For practicality, only those temperature intervals that produced time series without missing values were used in the analysis. Again, mean monthly thermal habitat estimates were correlated with total, 1SW, and 2SW PFA using Pearson's product-moment correlation. Significance probabilities were recomputed using the Dunn–Sidak correction for multiple correlations within an index area–abundance grouping (Systat, 2002).

Some key months and years were characterized with SST maps showing the transition of water temperature change over a 1-month period. Particular isotherms are highlighted in these maps.

Results

Time frame of smolt migrations

North American salmon smolts generally migrate to sea in May in the southern part of the range and in June in the northern part. Many rivers have traps designed to intercept migrating smolts, making it possible to characterize the initiation and duration of these migrations (Table 1). In the most northern river system considered (Western Arm Brook, on the west coast of Newfoundland), smolts migrate mostly in June with a peak during the second and third week of the month. Campbellton River, located in the northeast coast of Newfoundland, tends to have an earlier run that peaks in late May. De la Trinité and Saint-Jean rivers show a similar contrast in migration period for rivers from the same province. For rivers further south, peak smolt migrations

Table 1. Duration and timing of peaks in Atlantic salmon smolt migration for representative stocks from Canada and the United States with location, associated index area, and sources.

| Stock | Location | Index area | Smolt run | | Reference |
			Duration	Peak	
Western Arm Brook, NFL, Canada	51°10′N, 57°00′W	1	June 1/July 1	June 7–21	Mullins *et al.*, 2001
Campbellton, NFL, Canada	49°20′N, 55°10′W	5	May 1/June 21	May 15/June 7	Downton *et al.*, 2001
De la Trinité, Québec, Canada	49°25′N, 67°18′W	1	June 1/July 1	June 10/25	Caron *et al.*, 2000
Saint-Jean, Québec, Canada	48°46′N, 64°26′W	1	May 15/June 20	May 20/June 15	Caron and Courtemanche, 2001
Conne, NFL, Canada	48°00′N, 55°20′W	4	May 1/30	May 7/21	Dempson *et al.*, 2001
Northwest Miramichi, NB, Canada	46°56′N, 65°47′W	1	May 1/June 20	May 18/June 1	Chaput *et al.*, 2002
Nashwaak, River (Saint John). NB, Canada	46°07′N, 66°36′W	2	April 20/May 24	May 5/15	Marshall *et al.*, 1999
LaHave River, NS, Canada	44°50′N, 64°70′W	3	May 1/30	May 7/21	Hayes, 1953; Amiro and Jansen, 2000
Narraguagus, USA	44°35′N, 67°40′W	2	May 1/30	May 7/21	Meister, 1969
Connecticut, USA	41°25′N, 72°20′W	2	April 21/May 26	May 1/15	Whalen *et al.*, 1999

range from the second half of May in the Miramichi to the first half of May in the Connecticut River (the southern extent of salmon distribution). Data from four and three stocks were used to estimate the migration time frames for index areas 1 and 2, respectively; only one stock was used for each of the remaining index areas 3–5 (Figure 2).

Pre-fishery abundance

Over the past two decades, there have been significant changes in the total PFA of the salmon stock complex. The abundance of 1SW fish has been estimated as high as 864 000 individuals and has declined to approximately half a million in recent years (Figure 3). The decline in 2SW fish has been more dramatic, going from nearly 575 000 to only

100 000 fish in recent years. The pattern of change is similar in the two age groups ($r = 0.76$, $p < 0.01$). Total abundance of the cohorts, represented by summing PFA of 1SW and 2SW fish, was nearly 1.4 million fish in the 1980s. The size of recent cohorts are only slightly greater than 1SW PFA, reflecting the more dramatic decline in number of 2SW fish.

Thermal conditions in the nursery area

The pattern of vernal warming differed among the five index areas (Figure 4). Some areas experienced much cooler winter conditions with widespread ice in the surface waters. Average April temperatures were just above 0°C in areas 1 (Gulf
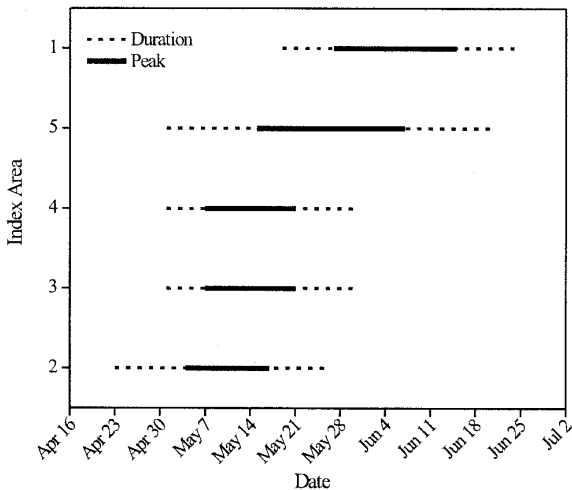
Figure 2. Duration and variation in peak abundance of smolt runs by index area.
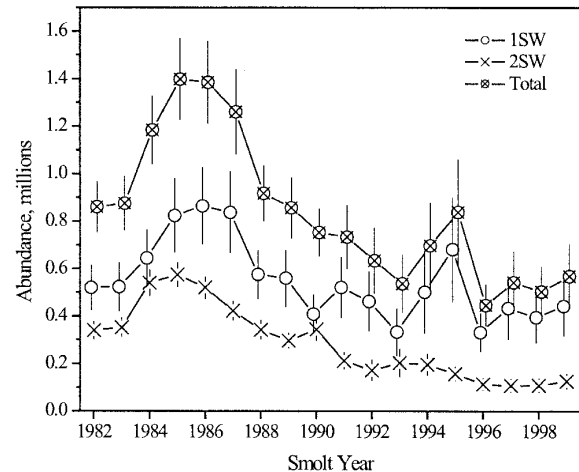
Figure 3. PFA of North American Atlantic salmon by age (1SW, 2SW, and total) and by smolt-migration year (error bars indicate 90% confidence interval).
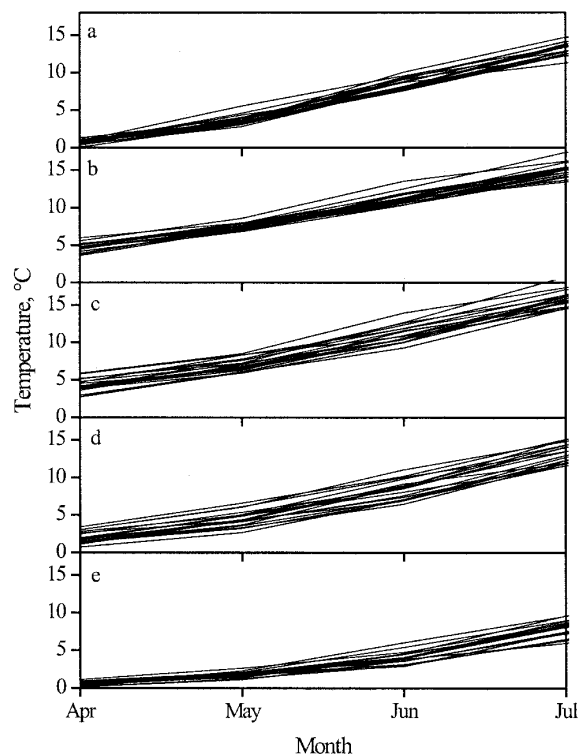
Figure 4. Mean monthly SSTs for index areas 1–5 (a–e) by year, 1982–1999.

Table 2. Descriptive statistics for thermal habitat area by month within index areas 1–5: mid-point of thermal habitat range, areal extent, and standard deviation.

Area	Month	Mid-point (°C)	Extent (km²)	s.d.
1	May	1.5	79 664	34 579
	May	3.5	153 171	43 395
	May	5.5	96 129	26 272
	June	3.5	26 285	16 479
	June	5.5	54 861	16 731
	June	7.5	83 967	18 562
	June	9.5	98 088	26 283
	June	11.5	95 308	35 021
	July	9.5	31 166	20 589
	July	11.5	78 699	31 585
	July	13.5	121 909	20 302
	July	15.5	84 154	29 704
2	April	3.5	56 508	16 122
	April	5.5	57 243	16 202
	April	7.5	23 001	9580
	May	5.5	46 857	11 025
	May	7.5	58	12 142
	May	9.5	36 318	13 595
	June	9.5	58 903	11 636
	June	11.5	52 202	16 012
	June	13.5	34 314	9219
3	April	1.5	43 674	7672
	April	3.5	41 355	9862
	April	5.5	34 732	5110
	April	7.5	22 508	6696
	May	3.5	39 983	10 251
	May	5.5	43 655	12 998
	May	7.5	39 465	6989
	May	9.5	28 600	5230
	June	9.5	50 865	12 162
	June	11.5	44 570	9478
	June	13.5	33 544	9890
4	April	1.5	120 797	30 492
	May	3.5	96 798	40 251
	May	5.5	69 508	26 126
	June	7.5	79 159	18 397
	June	9.5	73 860	22 719
5	May	1.5	168 890	24 127
	May	3.5	46 491	18 838
	June	1.5	77 696	35 633
	June	3.5	94 896	20 863
	June	5.5	53 829	18 358
	June	7.5	35 154	15 971
	July	5.5	66 014	21 398
	July	7.5	70 810	18 227
	July	9.5	48 117	12 216
	July	11.5	35 606	13 554

of St. Lawrence) and 5 (Newfoundland shelf), whereas areas 2–4 (associated with the Gulf of Maine and Scotian Shelf) were in the range of 3–5°C during April. All the areas reached at least 10°C by July in all the years with the exception of area 5 (5–9°C). The range of mean SST varied by season and area: all areas showed the greatest variation during June, and areas 3 and 4 showed the greatest variation overall.

Trends in thermal habitat area estimates reflected those observed in mean SST. Between areas 1 and 5, temperature ranges could be characterized each month (Table 2). Thermal habitat estimates for area 1 (the largest area with approximately 325 000 km²) ranged from approximately 26 000 to 153 000 km² for a given temperature range in each month (1.5 to 15.5°C). The standard deviation tended to be 30% of the mean thermal habitat area, which applied to other areas as well. Area 2 (approximately 150 000 km²) was characterized by thermal habitat ranges from 3.5 to 13.5°C. Areas 3 and 4 were of similar size to that of area 2, totaling approximately 170 000 and 190 000 km², respectively. Area 4 could be characterized by five monthly thermal habitat ranges for the 3-month period, which was conspicuously less than the other areas. The greater inter-annual variations in temperature for this area produced more incomplete time series (Figure 4d). Area 5 (235 000 km² and furthest north) contained the coldest thermal habitat, of the five areas, reflecting the strong influence by the cold Labrador Current.

Relationship of PFA with thermal conditions

The correlative comparison of mean SST and PFA (Table 3) yielded only a significant correlation ($p < 0.05$) for 2SW fish in June in area 1. The sign was negative, indicating that high abundance was associated with cooler conditions over the time series. However, after the Dunn–Sidak correction for multiple correlations, this correlation proved not to be significant.

Table 3. Pearson's product-moment correlation between SST and PFA by index area and month (p_{DS}, Dunn–Sidak adjusted probability; *p < 0.05).

Area	Month	1SW			2SW			Total		
		r	p	p_{DS}	r	p	p_{DS}	r	p	p_{DS}
1	May	0.10	0.69	0.97	−0.14	0.58	0.93	−0.02	0.95	1.00
	June	−0.31	0.21	0.51	−0.53	0.02*	0.07	−0.45	0.06	0.18
	July	0.24	0.34	0.71	0.04	0.89	1.00	0.15	0.55	0.91
2	April	0.06	0.80	0.99	0.05	0.86	1.00	0.06	0.82	0.99
	May	0.02	0.94	1.00	−0.07	0.79	0.99	−0.03	0.92	1.00
	June	−0.30	0.22	0.52	−0.35	0.16	0.41	−0.35	0.16	0.41
3	April	−0.37	0.13	0.34	−0.27	0.27	0.62	−0.35	0.16	0.40
	May	−0.24	0.33	0.70	−0.20	0.44	0.82	−0.23	0.35	0.72
	June	−0.28	0.26	0.59	−0.30	0.23	0.53	−0.31	0.21	0.50
4	April	−0.31	0.22	0.52	−0.24	0.35	0.72	−0.29	0.24	0.56
	May	−0.21	0.41	0.79	−0.13	0.60	0.94	−0.18	0.47	0.85
	June	−0.25	0.31	0.68	−0.25	0.32	0.68	−0.27	0.28	0.63
5	May	−0.02	0.94	1.00	−0.02	0.94	1.00	−0.02	0.94	1.00
	June	−0.05	0.85	1.00	−0.20	0.42	0.81	−0.13	0.61	0.94
	July	0.09	0.73	0.98	0.04	0.86	1.00	0.07	0.78	0.99

The correlative comparisons of thermal habitat and PFA (Table 4) yielded some highly significant positive correlations for both 1SW and 2SW fish and the 7.5°C thermal habitat area in area 1 in June that are consistent with the weak relationship identified in the mean SST data. The correlations for 2SW and the total were also significant after the Dunn–Sidak correction. Significant correlations were also found for 1SW (April 7.5°C and June 9.5°C in area 2; June 11.5°C in area 3) and 2SW (June 11.5°C in areas 2 and 3), but none of these were significant after correction. None of the correlations for areas 4 and 5 were significant.

The spatial and temporal properties of the correlations in area 1 during June were examined through the analysis of the SST data at its original 1° latitude and longitude resolution, and through the use of the weekly temperature and thermal habitat fields. The correlation coefficients between the abundance time series and mean June SST for each 1° box within area 1 were contoured to reveal spatial trends (Figure 5). Spatially disaggregating the data reduced the correlation for 1SW fish suggesting this correlation is dependent on spatial combination of the data (Figure 5a). In contrast, the correlation between 2SW abundance and SST remained strong, and the highest values were centered in the western portion of the Gulf of St. Lawrence, coincidentally located close to the major salmon rivers of New Brunswick (Figure 5b). The correlation for total PFA largely show the same pattern as for 2SW fish, but the inclusion of 1SW fish reduces the significance (Figure 5c). Spatial disaggregation of thermal habitat data would not be meaningful.

Correlation coefficients between PFA and weekly mean SST for area 1 were highest during latter half of June (week beginning on June 8 through week beginning on June 22; Figure 6a), whereas the 7.5°C thermal habitat area provided the strongest correlations during the week beginning on

June 22 (Figure 6b). Thus, both weekly SST and thermal habitat data suggest that the critical period for salmon survival in area 1 is during the latter half of June, coinciding with the end of the peak smolt run in the area (Figure 2).

SST distributions during June suggest widely varying conditions between years producing large and small smolt recruitments. During 1986, a year associated with high abundance estimates, the Gulf of St. Lawrence and associated coastal waters remained within the 8–10°C temperature range for the entire month (Figure 7a–d). In contrast, during 1998, a year that produced fewer recruits, the Gulf of St. Lawrence had SSTs in excess of 10°C, and water of >12°C was present by the end of the migration period (Figure 7e–h). These distributions are consistent with correlations between mean SST and abundance, and thermal habitat and abundance.

Discussion

The results provide a first indication that climate variation during spring may play a pivotal role in the patterning of post-smolt survival, and thus stock abundance, for North American salmon stocks. The examination of post-smolt ecology for these stocks is clouded by the problem of interpreting their habitat use in the absence of detailed migration information that shows their exact locations at sea after they exit their home rivers. Recent intensive studies have shown that European post-smolts migrate to the Norwegian Sea (Holm *et al.*, 2000) by utilizing favorable currents (Jonsson *et al.*, 1993). North American post-smolts face unfavorable currents to reach their eventual overwintering areas to the north of Newfoundland and in the Labrador Sea since they travel against the prevailing Labrador Current circulation (Reddin and Short, 1991). For many of the most productive stocks comprising the North

Table 4. Pearson's product-moment correlation between thermal habitat area and PFA by month and index temperature range (p_{DS}, Dunn–Sidak adjusted probability; *p < 0.05; **p < 0.01).

Mid-point			1SW			2SW			Total		
Area	Month	Temperature (°C)	r	p	p_{DS}	r	p	p_{DS}	r	p	p_{DS}
1	May	1.5	−0.22	0.37	1.00	0.00	0.99	1.00	−0.12	0.63	1.00
	May	3.5	−0.01	0.97	1.00	0.04	0.88	1.00	0.01	0.96	1.00
	May	5.5	−0.30	0.23	0.96	−0.38	0.12	0.79	−0.36	0.14	0.84
	June	3.5	0.09	0.72	1.00	0.17	0.50	1.00	0.14	0.59	1.00
	June	5.5	−0.14	0.57	1.00	0.08	0.76	1.00	−0.04	0.88	1.00
	June	7.5	0.61	0.01**	0.08	0.71	0.00**	0.01**	0.70	0.00**	0.01*
	June	9.5	0.21	0.39	1.00	0.05	0.85	1.00	0.14	0.57	1.00
	June	11.5	−0.45	0.06	0.55	−0.10	0.70	1.00	−0.30	0.23	0.96
	July	9.5	0.22	0.38	1.00	0.34	0.17	0.89	0.30	0.23	0.96
	July	11.5	−0.23	0.36	1.00	−0.17	0.50	1.00	−0.21	0.39	1.00
	July	13.5	0.05	0.84	1.00	0.21	0.40	1.00	0.14	0.59	1.00
	July	15.5	0.43	0.07	0.59	0.29	0.24	0.97	0.39	0.11	0.76
2	April	3.5	−0.25	0.31	0.97	−0.19	0.46	1.00	−0.23	0.35	0.98
	April	5.5	−0.11	0.67	1.00	−0.10	0.69	1.00	−0.11	0.66	1.00
	April	7.5	0.51	0.03*	0.24	0.47	0.05	0.37	0.52	0.03*	0.22
	May	5.5	0.05	0.84	1.00	0.00	0.99	1.00	0.03	0.91	1.00
	May	7.5	−0.12	0.64	1.00	−0.06	0.80	1.00	−0.10	0.70	1.00
	May	9.5	0.04	0.89	1.00	0.01	0.98	1.00	0.02	0.93	1.00
	June	9.5	0.61	0.01**	0.07	0.44	0.07	0.48	0.56	0.02*	0.14
	June	11.5	−0.37	0.13	0.71	−0.47	0.05*	0.37	−0.45	0.06	0.45
	June	13.5	−0.25	0.32	0.97	−0.37	0.13	0.72	−0.33	0.18	0.84
3	April	1.5	0.22	0.39	1.00	0.16	0.52	1.00	0.20	0.42	1.00
	April	3.5	−0.41	0.09	0.66	−0.16	0.52	1.00	−0.31	0.21	0.93
	April	5.5	−0.17	0.50	1.00	−0.11	0.67	1.00	−0.15	0.55	1.00
	April	7.5	0.11	0.65	1.00	0.22	0.38	1.00	0.18	0.49	1.00
	May	3.5	0.18	0.48	1.00	−0.05	0.85	1.00	0.07	0.77	1.00
	May	5.5	−0.21	0.41	1.00	−0.13	0.61	1.00	−0.18	0.48	1.00
	May	7.5	−0.14	0.58	1.00	−0.06	0.81	1.00	−0.11	0.67	1.00
	May	9.5	−0.09	0.71	1.00	0.01	0.97	1.00	−0.05	0.86	1.00
	June	9.5	0.30	0.23	0.94	0.23	0.37	0.99	0.28	0.26	0.96
	June	11.5	−0.52	0.03*	0.27	−0.52	0.03*	0.27	−0.55	0.02*	0.18
	June	13.5	−0.22	0.39	1.00	−0.15	0.54	1.00	−0.20	0.43	1.00
4	April	1.5	0.05	0.86	1.00	−0.10	0.68	1.00	−0.03	0.91	1.00
	May	3.5	0.09	0.72	1.00	−0.03	0.89	1.00	0.03	0.90	1.00
	May	5.5	0.01	0.98	1.00	0.07	0.79	1.00	0.04	0.88	1.00
	June	7.5	0.42	0.08	0.34	0.26	0.30	0.83	0.37	0.14	0.51
	June	9.5	0.02	0.94	1.00	−0.18	0.47	0.96	−0.08	0.74	1.00
5	May	1.5	−0.18	0.47	0.99	−0.08	0.74	1.00	−0.14	0.57	1.00
	May	3.5	0.22	0.38	0.98	0.02	0.95	1.00	0.13	0.61	1.00
	June	1.5	−0.19	0.45	0.99	0.10	0.70	1.00	−0.06	0.83	1.00
	June	3.5	0.16	0.52	1.00	−0.11	0.65	1.00	0.03	0.90	1.00
	June	5.5	0.10	0.69	1.00	−0.15	0.56	1.00	−0.02	0.94	1.00
	June	7.5	−0.02	0.93	1.00	−0.18	0.48	1.00	−0.10	0.68	1.00
	July	5.5	−0.10	0.70	0.99	0.03	0.89	1.00	−0.04	0.89	1.00
	July	7.5	−0.19	0.46	0.92	−0.29	0.24	0.67	−0.25	0.31	0.78
	July	9.5	0.14	0.59	0.97	0.05	0.84	1.00	0.10	0.69	0.99
	July	11.5	0.43	0.08	0.27	0.27	0.29	0.74	0.37	0.13	0.42

American stock complex, viz. the Miramichi River and other rivers emptying into the Gulf of St. Lawrence, the first weeks at sea are most likely spent in coastal habitats. There are indications that these inshore habitats may serve not only as migration transit areas, but also as nurseries during the post-smolt growth season (spring and summer), at least in some years (Friedland et al., 1999).

The correlation between stock abundance and climate during June, the time frame associated with the first weeks at sea for many stocks, and in the Gulf of St. Lawrence, the area producing a high proportion of the annual smolt cohort, is encouraging. The negative correlation with surface temperature, the positive correlation with the extent of the 7.5°C, and the association of poor recruitment with the presence of warm water suggest that survival is favored when Gulf waters are warmed up slowly and stay below 10°C over large areas during the first weeks at sea.
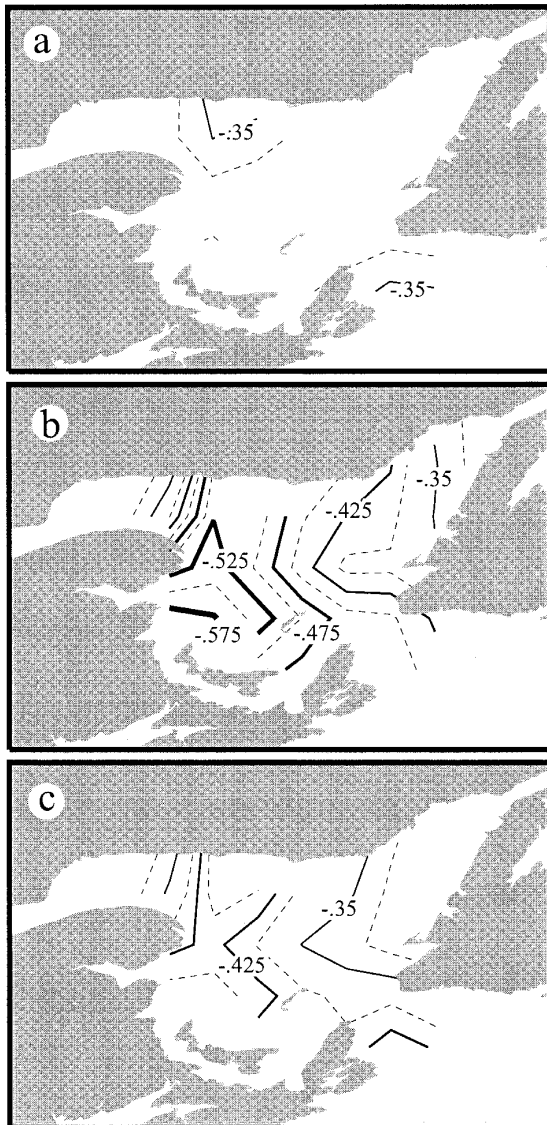
Figure 5. Contour plots of correlation coefficients between (a) 1SW, (b) 2SW, and (c) total PFA and SST for each 1° of latitude and longitude box in index area 1 during June.
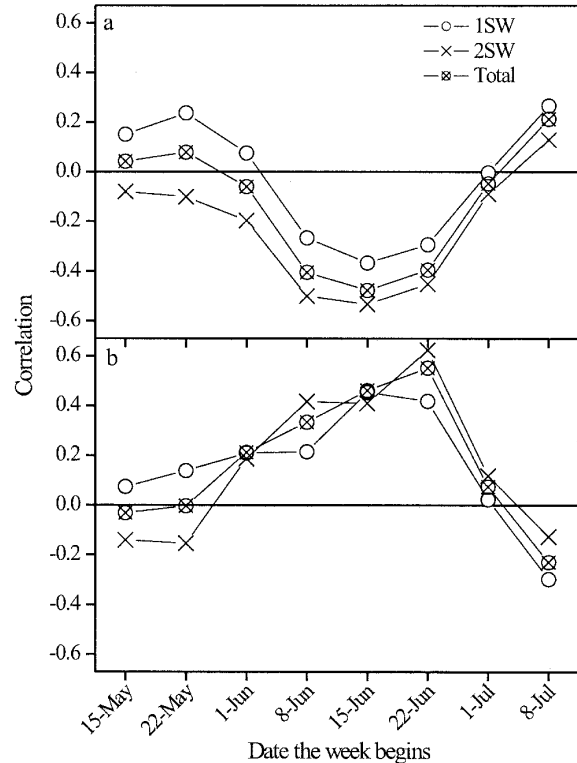

Figure 6. Correlation coefficients between 1SW, 2SW, and total PFA, and (a) weekly SST and (b) weekly 7.5°C thermal habitat index for area 1 (date represent the beginning of the week).

The strengths and weaknesses (Gargett *et al.*, 2001) of correlations are well known. Therefore, we are compelled to use caution in interpreting our results. Nevertheless, we see the new information as an opportunity to develop mechanistic hypotheses on what might be happening to salmon in the sea. Many ongoing research programs, like surveys for post-smolts, could use this information to guide future activities. We also see the potential for several research approaches that are currently undeveloped and will explore four areas of hypothesis development in greater detail: how ocean conditions may affect growth of post-smolts, whether variations in climate have altered predation pressure, or alternatively prey abundance, and how migration may be affected by variations in climate.

Temperature conditions may affect post-smolts directly through the physiological effects of temperature on growth or indirectly through the development of annual bloom conditions and the resulting secondary production in the form of forage species. Because salmonid growth increases linearly with water temperature, given an adequate food supply (Brett, 1979), we are faced with the dilemma of making sense of the outcome that warmer conditions are associated with poorer survival. Perhaps, growth is faster in cold conditions because the fish can use a smaller food ration more efficiently with lower metabolism. High temperature may increase metabolic demand beyond food resources available to the fish and inhibit growth. Indeed, fish on low food rations have a lower thermal preferendum than fish on high rations (Despatie *et al.*, 2001), suggesting that growth will be optimized at a lower temperature when food is limiting. Temperature, among a wide array of factors, affects the timing and development of spring blooms. In the Gulf of St. Lawrence, temperature has been identified as an important factor controlling the succession of phytoplankton communities (Levasseur *et al.*, 1984; Therriault *et al.*, 1990), but spring blooms in the Gulf typically do not develop until late June or early July, and may be controlled
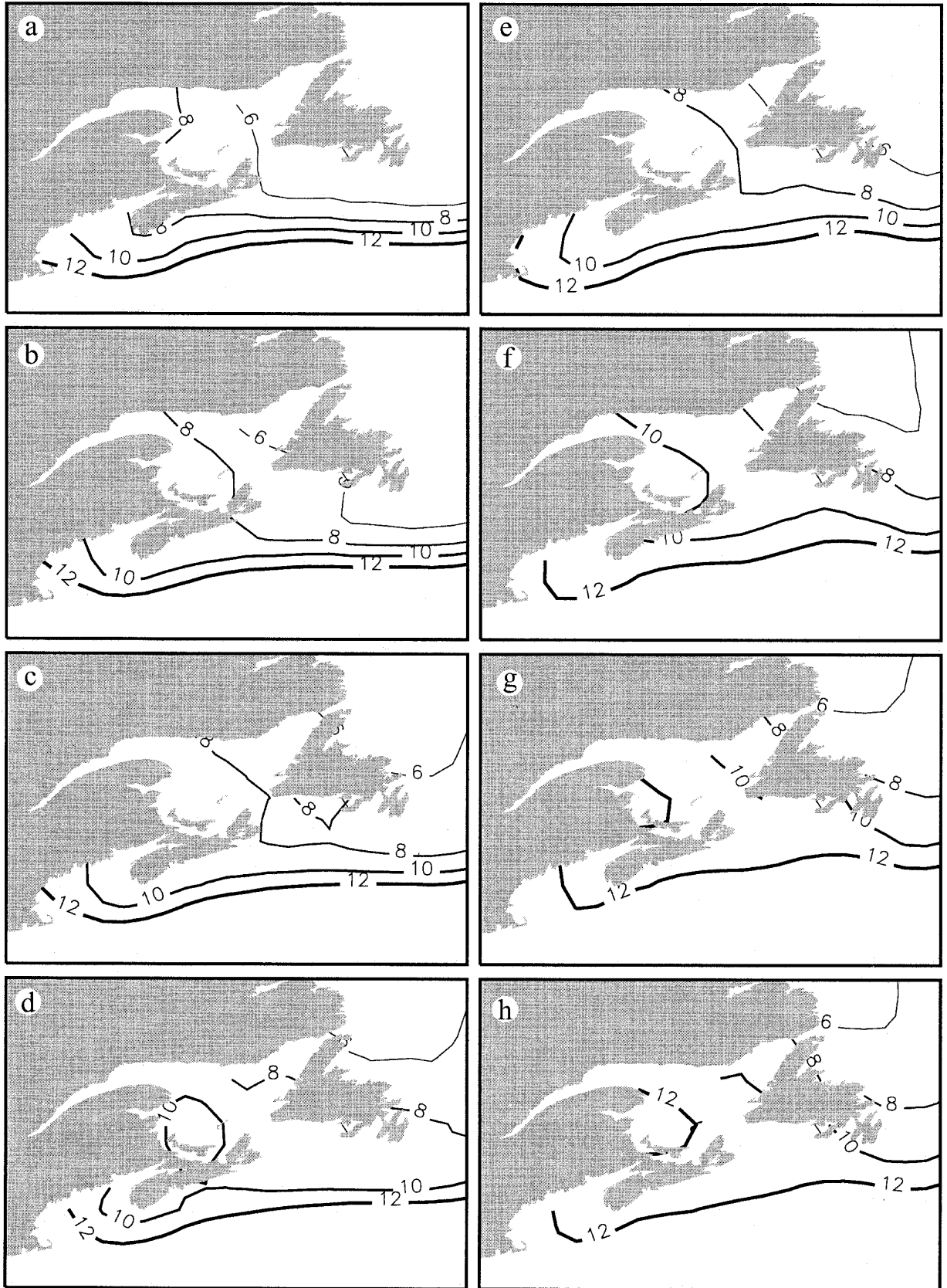
Figure 7. Distributions of weekly SST during June for 1986 (a–d) and 1998 (e–h) ordered by the first to last week of the month.

to a greater degree by other factors, such as freshwater runoff or advective losses of phytoplankton from the relatively thin surface mixed layer (Fuentes-Yaco *et al.*, 1997; Zakardjian *et al.*, 2000; Plourde *et al.*, 2001). The late development of the bloom begs the question as to whether primary production in the same season is important to salmon, because post-smolts would have been feeding for many weeks before the bloom enters the food chain. As elsewhere, the development of the spring bloom varies by size fraction, which in turn may affect availability to different grazers and ultimately the food resources of post-smolts (Tamigneaux *et al.*, 1999).

The onset of bloom conditions in adjacent coastal waters is earlier (often as early as April/May) than in the Gulf and, thus, may contribute more directly to post-smolt growth. However, Head (2000) suggests that bloom initiation on the Scotian Shelf is not dependent on temperature, and, besides, our results indicate that it is the climate variation in June that co-varies with salmon abundance. In addition, ocean color data indicate that the phytoplankton production on the Scotian Shelf has markedly increased from the 1970s to the 1990s, while salmon survival has decreased (Zwanenburg *et al.*, 2002). Overall, there is little coherence in any argument suggesting that warmer spring conditions have enhanced post-smolt growth through changes in primary production.

The amount of foraging habitat for post-smolts in the surface mixed layer may be related to the dynamics of the cold intermediate layer (CIL), a persistent mass of cold ($<0°$C) water lying immediately below the surface mixed layer and characteristic of the Gulf and some adjacent waters. The thickness of the CIL is influenced by the severity of winter conditions, which affects the thickness of the surface mixed layer, which varies accordingly. CIL thickness is strongly negatively correlated with distribution, condition, and growth of demersal species, such as Atlantic cod (Castonguay *et al.*, 1999; Dutil *et al.*, 1999). It would be interesting to attempt to relate salmon mortality with CIL conditions in the various parts of its range.

Inordinate predation pressure on early life-history stages of ground fish caused by the release of fishing pressure on pelagic species (Atlantic mackerel *Scomber scombrus* and Atlantic herring *Clupea harengus*) is an emerging theme, as the scientists try to interpret ground-fish recruitment patterns (Swain and Sinclair, 2000). The abundance of small pelagics since the mid-1980s could also have adversely affected post-smolt survival through predation after their first entry to the marine environment. The association of more rapid warming and poor survival of post-smolts may be interpreted as an indication that some predators invade post-smolt nurseries behind specific isotherms (Hinch *et al.*, 1995). Alternatively, post-smolts may shift their seaward distribution, owing to warmer conditions, and move to areas where predators are more common. Migratory pelagic predators like mackerel are often associated with thermal transition zones (Garrison *et al.*, 2000). However, this linkage appears to be rather

plastic and is not associated with a specific barrier as suggested by the June $7.5°$C thermal habitat area responsible for the correlations observed in this study (D'Amours and Castonguay, 1992). Cod distribution in the Gulf of St. Lawrence changes seasonally, and is associated with movements into cold water ($<4°$C) in summer, spatially removed from post-smolt distributions (Castonguay *et al.*, 1999; Swain, 1999). Predation by gannets is patterned in fixed fields reflecting their home range relative to the rookeries, thus a change in prey distribution caused by temperature conditions may affect the predation for a given set of rookeries (Montevecchi *et al.*, 2002). However, even the most liberal application of gannet predation rates does not explain the mortality of post-smolts during the first summer. Seals breed in much of the post-smolt nursery areas and have increased in number in recent years, a trend consistent with the decline in salmon stocks (Stenson *et al.*, 2002). However, warmer conditions should create less spatial overlap with post-smolts during the summer months. A review to find the "perfect" predator, i.e. one with an impact on post-smolts in the nursery areas that varies in concert with the June climate signal, is frustrating. This frustration may be interpreted as supporting the idea that predation pressure is near saturation, and that factors related to predation avoidance are more important.

Post-smolts undergo an important ontogenetic change in feeding that may be key to their survival during the first year at sea. On first entering the marine environment, they feed mainly on terrestrial insects and marine invertebrates and then make a transition to piscivory, usually concentrating on the 0-group of winter-spawned species. For example, Salminen *et al.* (2001) reported that post-smolts in the Baltic first feed on young of the year herring. Feeding data available for North American nurseries indicate that herring do not necessarily serve this function. Dutil and Coutu (1988) found that the dominant food item in the diet of Gulf of St. Lawrence post-smolts was sand lance (*Ammodytes americanus*) larvae, one of the dominant ichthyoplankton species over large areas in the Gulf and neighboring waters (Locke and Courtenay, 1995; Lazzari, 2001). Wright and Bailey (1996) suggested that coupling between hatching and the onset of spring secondary production is important for the growth and survivorship of sand lance (*Ammodytes marinus*) from the Shetland Islands area. Changes in availability of this species have been implicated as critical to the success of seabirds (Rindorf *et al.*, 2000). Similarly, capelin larvae are also abundant in most Gulf areas and may provide another food resource for post-smolts as they switch to a piscivorous life style. Does June climate variation correlate with the availability of a preferred ichthyoplankton prey? Because most of these species are only assessed intermittently, further work is required before conclusions can be drawn.

Post-smolts represent a relatively minor component of the food web and, therefore, may be affected by

fluctuations in predator and prey levels as much as they are controlled by individual demands of swimming and migration. They may have strong migrational behaviors that select for temperature ranges and thus influence swimming expenditure to avoid undesirable thermal conditions. The association of warm conditions in June with poor survival may reflect increased swimming demanded of these cohorts as they seek optimal temperatures. Patterns of survival for salmon stocks throughout the North Atlantic illustrate that stocks with shorter migrations to the feeding grounds have higher survival rates (Bley and Moring, 1988; Friedland, 1994). The relationship between migration and survival may be an important scalar on the stock level as well.

Acknowledgements

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