Abstract—Data storage tags (DSTs) were applied to Atlantic salmon (*Salmo salar* L.) smolts during their seaward migration in the spring of 2002 at a fish counting fence on Campbellton River, Newfoundland. Our objectives were to discover whether or not salmon smolts could carry DSTs and survive, whether or not useful data on thermal habitat could be obtained and interpreted, and whether or not salmon smolts moved vertically in the water column. Data were downloaded from 15 of the recovered tags and revealed the hourly water temperatures experienced by the fish for periods of 3 to 71 days. The data on the DSTs were analyzed for temperature patterns in relation to migration behavior and diurnal movement of the fish. While in the sea, the DSTs recorded night temperatures of 12.5°C, which were higher than day temperatures of 11.6°C; the record from moored recorders, however, indicated that sea temperatures actually declined at night. It is hypothesized that postsmolts avoid avian predators during daylight hours by positioning themselves deeper in the water column and that they were pursuing prey during the deeper vertical descents or ascents noted during the periods of more rapid changes in temperature.

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Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life

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Our knowledge of the ecology of marine fish, and specifically salmon, at sea has recently been enhanced by information recovered from data storage tags (DSTs) and tracking tags (Sturlaugsson[1]; LaCroix and McCurdy, 1996; Wada and Ueno[2]; Godø and Michalsen, 2000; Reddin et al., 2004). Direct tracking, although valuable, has a number of shortcomings, including the usually short duration of tracking because of the requirement to follow the fish. This short-term tracking often results in interrupted data streams and the added concern that the actual tagging may affect, at least in the short term, the subsequent behavior of the fish (LaCroix and McCurdy, 1996; Walker et al., 2000). Studies of salmon at sea over long periods require new tools and several authors have noted that DSTs are among the least expensive methods of answering some of the questions posed regarding the sea life of salmon. Also, the near extirpation of some stocks, particularly in the Inner Bay of Fundy area of Canada and Maine, U.S.A, requires an explanation of the causative factors (Boehlert, 1997; Anon.[3]; Friedland et al., 2001; Reddin et al., 2004). DSTs should be able to provide better information on the natural behavior of individual fish, their specific habitats, and location over the period of their residence in the sea because of the longer period that information can be collected.

On both sides of the North Atlantic, attention has been recently focused on the downturn in Atlantic salmon stocks and the potential cause or causes (Nickson[4]; Mills[5]; DFO[6];

[1] Sturlaugsson, J. 1995. Migration study on homing of Atlantic salmon (*Salmo salar* L.) in coastal waters W-Iceland—depth movements and sea temperatures recorded at migration routes by data storage tags. ICES C.M. (council meeting) 1995/M: 17, 13 p.

[2] Wada, K. and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. NPAFC (North Pacific Anadromous Fish Commission Doc. 425, 29 p.

[3] Anon. 1998. Report of the Study Group on ocean salmon tagging experiments with data logging tags. ICES C.M. (council meeting) 1998/G: 17, 34 p.

[4] Nickson, Sir D. 1991. Chairman's report, Atlantic Salmon Trust, progress report, December 1991, 1 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire, Scotland PH16 5JQ.

[5] Mills, D. (ed.). 1996. Enhancement of spring salmon. Proceedings of a one-day conference held in the rooms of the Linnean Society of London; 26 January 1996, 135 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire PH16 5JQ Scotland.

[6] DFO (Dept. of Fisheries and Oceans). 1998. Atlantic salmon abundance overview for 1997. DFO CSAS (Canadian Stock Assessment Secretariat), Stock Status Report D0-02(1998), 22 p.

O'Neil et al.[7]; Anon.[8]). Many authors have noted that information on the sea life of Atlantic salmon (*Salmo salar* L.) may aid in our understanding of the recent increased mortalities that occur at sea compared to those experienced in the 1970s (Mills, 1989; Reddin and Friedland, 1993; Dempson et al.[9]; Jacobsen, 2000; Reddin et al., 2000). In the southern end of the range of Atlantic salmon in North America, declines have been so severe that some stocks are now threatened with extinction and others are currently considered to be extirpated (Marshall et al.[10]). The recent listing of seven salmon stocks in the State of Maine under the U.S. Endangered Species Act and in rivers in the upper Bay of Fundy further underscores the urgency to understand more completely the entire salmon's life history, including the period spent in the ocean. Although the cause (or causes) is unknown, the continued declines in abundance appear directly related to increased mortality at sea, perhaps from predation (DFO, 1998; Cairns and Reddin[11]; O'Neil et al.[7]).

New techniques have recently been applied to the study of salmon in the sea on both sides of the North American continent for Pacific and Atlantic salmon, and recommendations have been made on their future use (Boehlert, 1997; Anon[3]). Although large scale experiments with complex tags are attractive, the high cost per tag and likelihood of low returns, in part due to reduced commercial fishing for Atlantic salmon, have indicated that a smaller scale experiment with inexpensive simple tags may be the best place to start (Anon.[3]). Reddin et al. (2004) demonstrated that these tags when applied to Atlantic salmon adults could provide insight into some aspects of salmon life history.

Overall, the objectives of the present study were 1) to determine if DSTs could be applied to Atlantic salmon smolts and if data could be successfully recovered, 2) to learn more about the thermal habitat of Atlantic salmon during its early marine life, and 3) to test the hypothesis of the commonly held assumption that salmon are mainly surface or near to surface dwellers. This article describes the results of the migration of Atlantic salmon smolts from Campbellton River, Newfoundland, in relation to sea water temperatures recorded by DSTs in 2002.

Materials and methods

Experimental site

Atlantic salmon smolts, defined by Allan and Ritter (1977) as juvenile salmon that are making the transition from freshwater to the marine environment, were obtained in 2002 for tagging from an enumeration fence on Campbellton River, Newfoundland (Fig. 1) where in past years, high numbers were available in early spring (Downton and Reddin[12]). Also, because Campbellton River has a counting fence that is suitable for obtaining counts of adult salmon as they re-enter freshwater, there was a strong possibility of recapturing a returning tagged salmon so that its tag could be recovered (Fig. 1). Smolt and adult salmon have been counted at Campbellton River annually over the last 11 years (O'Connell et al.[13]). In total, there were about 32,600 salmon smolts counted through the counting fence at Campbellton River in 2002, and of these, 311 (~1% of total smolts) were tagged and released with data storage tags (DSTs). Owing to the size and weight of the tags, only smolts over 20 cm fork length were selected for application of tags. Average length of tagged smolts was 25 cm compared to an average length **of** 18 cm for untagged smolts. Larger smolts were also purposely selected to increase probability of survival.

Tags

The data storage tags (DSTs), sometimes referred to as archival tags, used in this study were iB-4 tags (Maxim/Dallas Semiconductor Corporation, Sunnyvale, CA) and were repackaged for use on fish by Alpha Mach Devices Inc. (Mont St-Hilaire, Québec, Canada). The iB4 tags are small microprocessor-based data loggers embedded in green urethane on which is shown (at bottom right corner of tag) a return address, an identifying number, and the offer of a reward for return of the tag. The iB4 DST records temperature over a range of −5° to 26°C

[7] O'Neil, S., J. Ritter, and K. Robichaud-LeBlanc. 2000. Proceedings of a workshop on research strategies into the causes of declining Atlantic salmon returns to North American rivers. CSAS (Canadian Stock Assessment Secretariat), Proceedings Series 2000/18, 80 p. Department of Fisheries and Oceans, Government of Canada, 200 Kent Street, Stn. 12032, Ottawa, Ontario, Canada K1A 0E6.

[8] Anon. 2003. Report of the Working Group on North Atlantic Salmon. ICES Headquarters, Copenhagen, 31 March–10 April 2003. ICES C.M. (council meeting) 2003/ACFM: 19, 310 p.

[9] Dempson, J. B., D. G. Reddin, M. F. O'Connell, J. Helbig, C. E. Bourgeois, C. C. Mullins, T. R. Porter, G. Lilly, J. E.Carscadden, G. B. Stenson, and D. Kulka. 1998. Spatial and temporal variation in Atlantic salmon abundance in the Newfoundland-Labrador region with emphasis on factors that may have contributed to low returns in 1997. DFO, CSAS, Res. Doc. 98/114, 161 p.

[10] Marshall, T. L., G. J. Chaput, P. G. Amiro, D. K. Cairns, R. A. Jones, S. F. O'Neil, and J. A. Ritter. 1999. Assessments of Atlantic salmon stocks of the Maritimes Region, 1998. DFO, CSAS Res. Doc. 99/25, 80 p.

[11] Cairns, D. K., and D. G. Reddin. 2000. The potential impact of seal and seabird predation on North American Atlantic salmon. DFO, CSAS Res. Doc. 2000/012, 36 p.

[12] Downton, P. R., and D. G. Reddin. 2004. Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2003. DFO, CSAS Res. Doc. 2004/043, 49 p.

[13] O'Connell, M. F., J. B. Dempson, C. C. Mullins, D. G. Reddin, C. E. Bourgeois, T. R. Porter, N. M. Cochrane, and D. Caines. 2003. Status of Atlantic salmon (*Salmo salar* L.) stocks of insular Newfoundland (SFAs 3-14A), 2002. CSAS Res. Doc. 2003/002, 63 p.

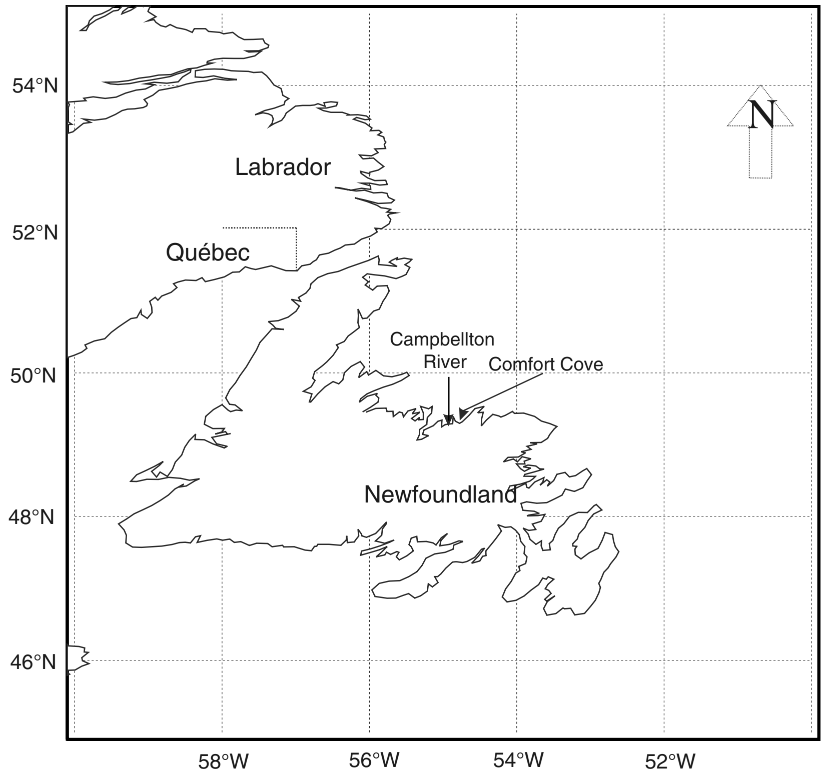

Figure 1

Map of Newfoundland, Labrador, and Québec showing the release location at Campbellton River for Atlantic salmon (*Salmo salar*) smolts with data storage tags attached.

with a precision of ±1°C and an accuracy of 0.15°C. The iB4 data storage tag will store up to 2048 readings but the number of data recorded by each tag depends on the length of time that the tag was at large and the sampling rate of the tag. Our iB4 tags were set to start on the day of tagging and record a temperature every hour—a sampling rate that would allow for 85 days of temperature recordings. Tags were calibrated by the manufacturer and checked for accuracy on return. A tag weighs 5.5 g in air and less than 2.6 g in water, is approximately 24 mm by 17 mm by 8 mm, and has a hole at either end for attachment to a fish. Tag programming, data acquisition, and data downloading were achieved by the user with a connecting clamp interfaced to the serial adapter on any standard IBM compatible computer. No correction for drift in the time function was made because of the short period over which the experiment took place (Walker et al., 2000; Reddin et al., 2004). Tags were attached to salmon smolts by using a double-wire (0.32 mm stainless steel) bridal that was passed through the dorsal musculature and that was anchored to the fish by means of a backing plate on the opposite side of the fish. A reward of $10 Canadian was offered for the return of the tag. The smolts were anaesthetized with clove oil, tagged, and placed in holding tanks in the river and given an approximate 10-hour recovery period before release in the evening on the downstream side of the counting fence. All smolts survived the tagging process. From 311 salmon tagged and released, 15 DSTs were recovered with data intact. All tagged fish were recovered during the year of tagging.

Data analysis

Temperature data recorded by the recovered DSTs were analyzed and compared to oceanographic and freshwater temperature data collected during the summer of 2002. The freshwater data was recorded by a Hugrun temperature recorder (Hugrun, Sidumuli 13, Reykjavik 108, Iceland) placed in the trap at the Campbellton River counting fence, and the sea temperatures came from Hugrun recorders placed just outside the estuary of Campbellton River at 8 m depth and from another at Comfort Cove at 10 m, both reported by Colbourne[14] (Fig. 1). Periods of daylight and darkness were estimated from the U.S. Navy Observatory[15] online photoperiod calculator. Latitudinal and longitudinal positions

[14] Colbourne, E. 2003. Physical oceanographic conditions on the Newfoundland and Labrador Shelves during 2002. DFO, CSAS Res. Doc. 2003/020, 57 p.

[15] U. S. Naval Observatory, Astronomical Observations Department. 2004. Website: http://aa.usno.navy.mil/data/docs/RS_OneDay.html [accessed on 7 March 2006.]

used to calculate sunrise and sunset for individual fish were based on the latitude and longitude at the mouth of Campbellton River. Although it varies by date, day at the latitude of Campbellton River during summer generally occurs from 0500 hours to 2300 hours and night occurs from 2300 to 0500 hours local time. Each individual temperature record from the tags in Greenwich Mean Time (GMT) was then coded to either day or night. Some salmon smolts in Newfoundland return to their home rivers within a couple of months of migrating to sea as precocious postsmolts and as postsmolts cannot travel extensively from the area of the river mouth, so that the river mouth provides a proxy position to determine day length (Downton and Reddin, 2004). Standard weeks were assigned with the Microsoft Excel function WEEKNUM. The analysis of variance technique used to test for temperature differences between fish was the PROC MIXED procedure in SAS (SAS Institute Inc., Cary, NC) The model treated tag as a random rather than a fixed variable. Day temperatures were compared to those at night and any diurnal vertical movements were considered to be reflected by sudden changes in temperatures. Newfoundland coastal waters always exhibit vertical stratification in late spring and early summer.

Results

Tag and data recovery

In total, temperature records were recovered from 15 of the 18 tagged Atlantic salmon smolts for an overall return rate of 5.8% (Table 1). Of the 18 recovered tags, 13 came from herring nets during the same summer that the fish were released. Average days free for those DSTs recovered in herring bait nets was 14 days and all were recovered within Indian Arm into which Campbellton River flows. In addition, two were recovered at the counting fence, one was recovered during a swimming survey of the lower portion of the river, one was angled, and another was found by a swimmer a full year after the fish was tagged and released. The great number of tags recovered in herring gear was due to tags becoming entangled in the nets. The longest period of recorded water temperatures while fish were free swimming was 71 days and the shortest was 3 days (Table 1). All tags were recovered during the first summer after their release, except the one found by the swimmer.

Water temperature profiles

Temperatures were recorded every 60 minutes for all recovered tags. The overall sampling frequency or the number of data points collected per tag ranged from a low of 32 for DST257 to a high of 1681 for DST45 and the second longest was for DST267 with 1373 (Table 1). The most complete records were recorded by DSTs 45 and 267 because the fish to which they were attached spent the least amount of time in freshwater and returned to freshwater after spending a minimum of eight weeks at sea. Both of these fish returned at 0+ sea age, a trait which is observed in about 15% of the salmon returning to Campbellton River in recent years (Downton et al., 2004). The water temperature profiles from the DSTs revealed a complex pattern of daily variations (Figs. 2–4). A number of points of interest can be made from the individual DST records. The temperature records from the DSTs when compared to local freshwater and marine temperatures allowed the time of day to be ascribed for most fish when the transition from the river to sea occurred (Fig. 3). The records indicated that 8 out of 13 fish made the transition from freshwater to the sea during daylight, whereas both fish recovered at the counting fence after spending time at sea re-entered freshwater during the night. Because they had the longest period of free swimming activity recorded on the DSTs, tags 45 and 267 were selected for further analysis including comparison for freshwater and sea temperatures (Fig. 3). Within the daily variations, temperature profiles from individual DSTs showed several prominent features:

1 a period of freshwater residence during which time the freshwater and DST temperatures corresponded closely, followed by entry into the sea at which time the temperatures recorded by the DSTs diverged from the recorded freshwater temperatures (Fig. 4, A and B);

2 a period of low variability in temperature fluctuations at the beginning of the marine record (with a coefficient of variation of less than or equal to 10%), continuing for at least a couple of weeks (Fig. 4C);

3 after the period of low variability, a series of rapid daily changes in temperature from either warm to cool or, for a few limited cases, from cool to warm (with coefficients of variation of greater than 30%) (Fig. 4, D and E) and during this period, DST temperatures sometimes varied by as much as 13°C over a couple of hours;

4 a distinct trend to increasing temperatures as the summer progressed which was due to gradual heating of the surface layer and deepening of the thermocline (Fig. 3); and

5 a series of steady temperatures near the end of the ocean period before entry into freshwater (with coefficients of variation of less then 12%) (Fig. 4F).

Between the periods of low temperature variability at the beginning and end of the various series, there was a period of rapid changes in temperature when the fish were assumed to have dived deeper in the water column, followed by ascents to near surface. The frequency of these rapid changes in temperature provides some information on the number of dives per day which numbered between 1 and 3 and may be a proxy for the length of time spent feeding and chasing after prey or fleeing from predators.

Table 1

Release and recovery details for eighteen iB-4 data storage tags (DSTs) applied to Atlantic salmon (Salmo salar) smolts at Campbellton River, Newfoundland, 2002. N/A= data were not available.

DST number	Number of records	Date and time tag was turned on	Date and time when tag was recovered	Fork length (cm)	Return date	Days free	Comments
22	327	5/17/02 8:20	5/17/02 8:20	22.0	spring, 2002	15	Caught in herring bait net in Indian Arm
							Tag found 25 m below counting fence site
43	N/A	5/19/02 7:59	5/19/02 9:28	24.0	24 May 2002	—	No fish was attached to tag
45	1681	5/19/02 8:06	5/19/02 9:36	28.0	28 Jul 2002	71	Caught at the upstream counting fence
55	N/A	5/19/02 8:30	5/19/02 10:19	27.0	03 Jul 2003	—	Found in estuary by swimmer
74	N/A	5/21/02 8:46	5/21/02 10:23	23.0	spring, 2002	—	Caught in herring bait net in Indian Arm
84	180	5/23/02 10:40	5/23/02 15:32	26.0	spring, 2002	8	Caught in herring bait net in Indian Arm
97	305	5/24/02 8:16	5/24/02 10:30	24.0	spring, 2002	14	Caught in herring bait net in Indian Arm
98	588	5/24/02 8:21	5/24/02 10:30	27.5	spring, 2002	26	Caught in herring bait net in Indian Arm
103	302	5/24/02 8:36	5/24/02 10:30	26.0	spring, 2002	14	Caught in herring bait net in Indian Arm
107	634	5/24/02 9:09	5/24/02 10:30	26.0	spring, 2002	28	Caught in herring bait net in Indian Arm
129	562	5/26/02 8:21	5/26/02 11:00	25.0	spring, 2002	25	Caught in herring bait net in Indian Arm
195	213	5/30/02 9:08	5/30/02 10:48	26.0	spring, 2002	10	Caught in herring bait net in Indian Arm
238	133	6/1/02 8:12	6/1/02 10:14	25.0	spring, 2002	7	Caught in herring bait net in Indian Arm
245	129	6/2/02 7:35	6/2/02 9:04	25.0	spring, 2002	6	Caught in herring bait net in Indian Arm
247	401	6/2/02 7:39	6/2/02 9:12	24.0	19 Jun 2002	17	Angled upstream
257	32	6/2/02 8:07	6/2/02 9:56	25.0	spring, 2002	3	Caught in herring bait net in Indian Arm
267	1373	6/2/02 8:29	6/2/02 10:49	34.0	30 Jul 2002	59	Recovered by upstream counting fence
293	240	6/4/02 6:59	6/4/02 9:50	26.0	spring, 2002	11	Caught in herring bait net in Indian Arm

Thermal ecology

A comparison of temperatures for night and day for the two tag recoveries with detailed data indicated differences between daily night and day temperatures for weeks 24 to 29 (11 June–22 July) (Fig. 5). The tagged salmon appeared to be at lower temperatures during the day than at night. Although there were only slight differences between day and night for the cumulative temperatures in some weeks (i.e., week 24 [11–17 June]), for others the differences were quite large (i.e., week 27). These differences were reflected in the overall mean of 12.5°C at night compared to the overall mean of 11.6°C during the day—values which are significantly different from each other ($t = -6.32$, $P < 0.0001$) and which possibly reflect temperatures at different depths. Although there was some variation among fish, this pattern was gener-

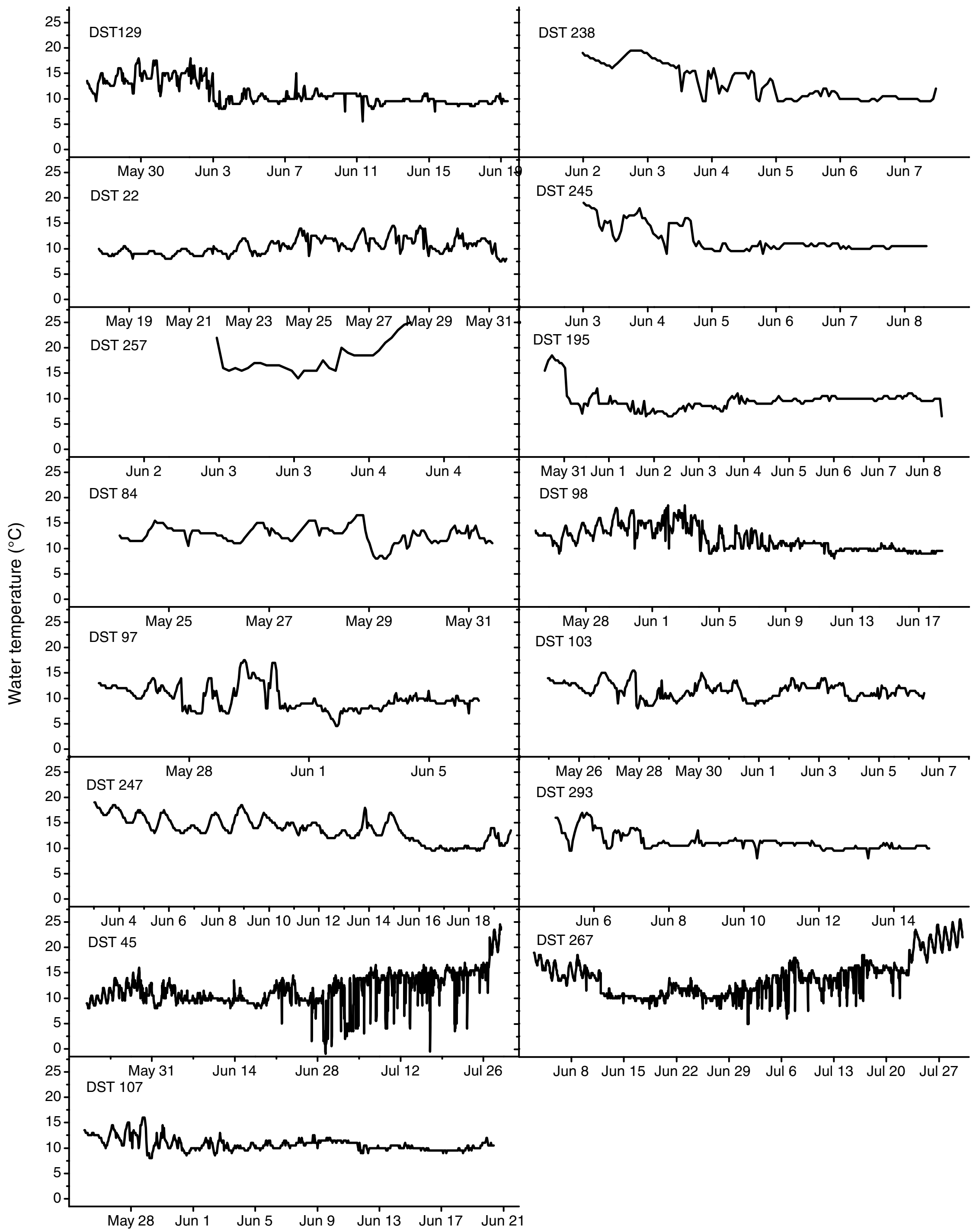

Figure 2

Hourly temperatures and dates recorded by 15 data storage tags attached to Atlantic salmon (*Salmo salar*) postsmolts at Campbellton River, 2002.

ally consistent. The cooler temperatures experienced by the fish during the day indicated that they were deeper in the water column during day than during the night. Diurnal trends in water temperatures also have to be considered because stream temperatures are generally warmer during the day than at night. Warmer temperatures during the day are generally the case for sea temperatures as well (t=5.00, P<0.0001) although less

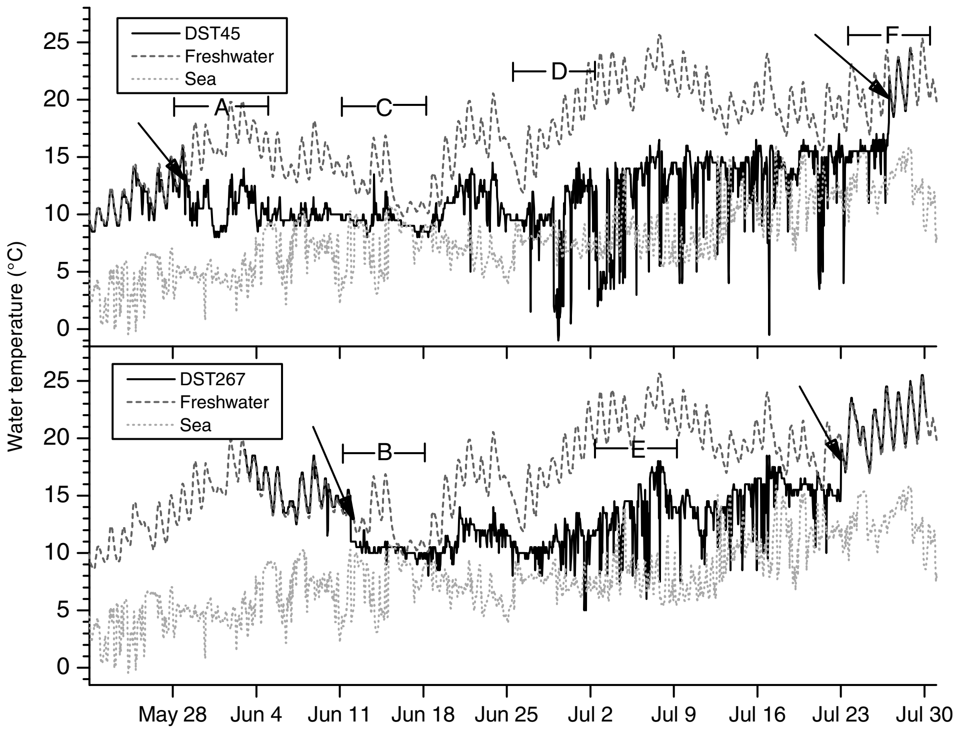

Figure 3

Hourly temperatures recorded by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts versus date for tags 45 and 267 applied at Campbellton River, 2002. Also shown are water temperatures recorded at the trap in the Campbellton River counting fence and in the sea near the Campbellton River estuary, 2002. Arrows indicate time of departure from and entry to freshwater. Periods selected for further analysis are shown and labelled alphabetically from A to F and are shown in detail in Figure 4.

pronounced at greater depths. Because sea temperatures are lower at night than during the day and because the water temperatures experienced by the fish are warmer at night, it is likely that the fish are actively changing depths. Also, there were times when water temperatures declined or increased by 5°C but the temperature of the fish remained steady; this feature would indicate that the fish was actively seeking specific temperatures and changing position in the water column in order to find these temperatures.

The results of the mixed-effects ANOVA with data for weeks 24 to 29 from fish tags 45 and 267 indicated significant differences in temperature for week ($F_{5,1987}$=251.82, P<0.0001) and night-versus-day effects ($F_{1,2393}$=54.53, P<0.0001). Both smolts spent about 90% of the time in water temperatures ranging from 8° to about 15°C. Overall, mean temperature for day activities for both fish combined was 11.6°C and for night it was 12.5°C. Therefore, for all weeks for both fish, temperatures experienced during the day were generally lower than during the night. Whether these differences were due to choice or simply because the fish were in different locations and experiencing local water conditions is unknown.

The frequency distribution of water temperatures while the fish were in the sea showed a wide range, from below 0° to about 20°C (Fig. 6). This distribution was wider and included temperatures that were both colder and warmer than temperatures available in the estuary off Campbellton River at 8 m or at Comfort Cove at 10 m. The warmer temperatures in the estuary than those recorded by the sea recorders are possibly due to the fish being near the surface or shore (or to both factors). The DST temperatures were lower than freshwater temperatures, reflecting the sea temperatures rather than freshwater temperatures. The pattern for each fish presumably reflects a combination of individual preferences and the availability of specific water temperatures depending on the location of the fish at sea. The temperatures recorded by each tag reflect the time (season) of entry into the sea and the time of recapture, especially for those fish caught in fisheries while the fish were still at sea.

Discussion

The transition from freshwater to ocean life for Atlantic salmon (whether as smolts or kelts) can have a serious

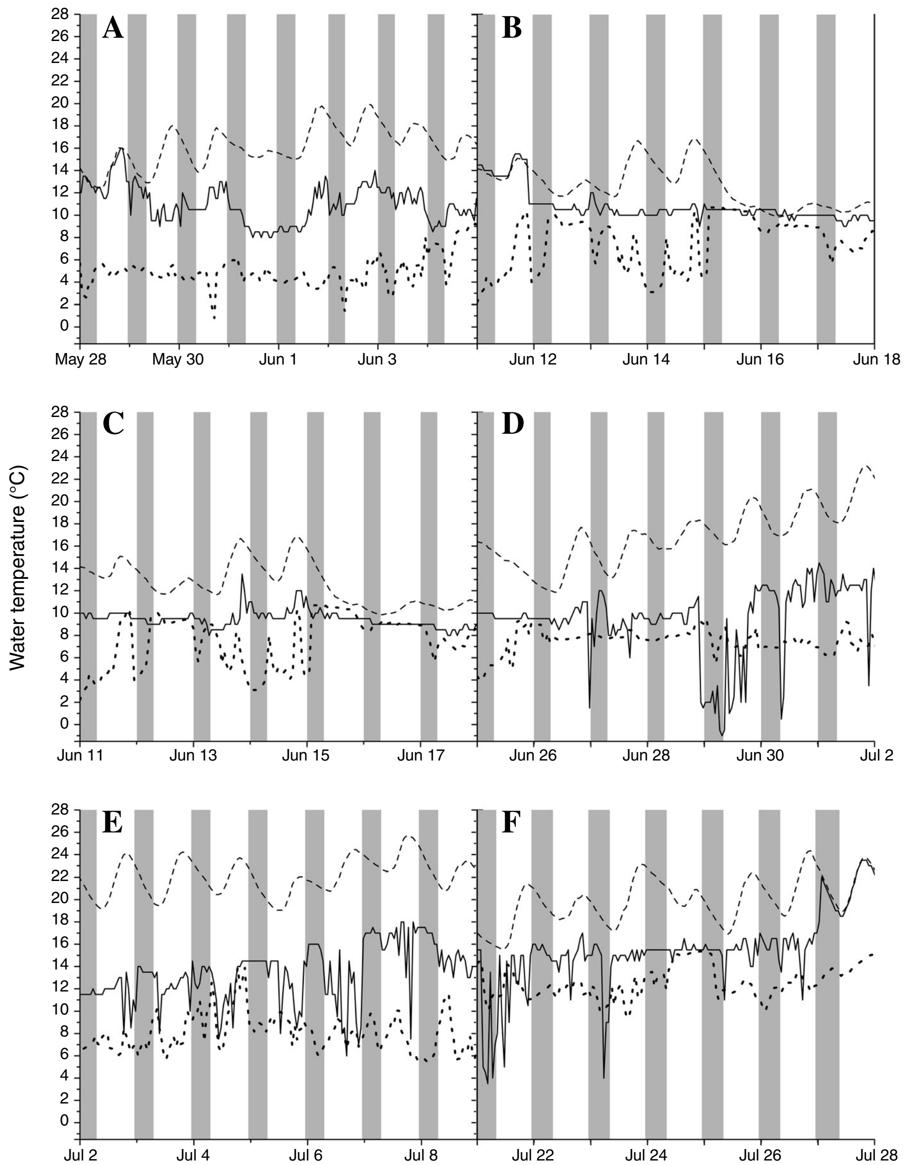

Figure 4

Comparison of day and night temperatures recorded hourly by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts for selected periods of time. Night is shown in grey and day is shown in white. Solid lines are the DST temperatures; the dashed line represents freshwater temperature and dotted line represents sea temperature at 8 m. The periods A to F are shown on Figure 3 for each tag.

consequence for an individual fish, as well as be an important factor controlling year-class strength and abundance at the population level (McCormick and Saunders, 1987, McCormick et al., 1998). The transformation process from freshwater to salt water made by smolts is accompanied by changes in metabolic rate (Hoar, 1988) and increases in energy demands, which explain the need for the fish to immediately begin feeding. Levings (1994) concluded that of all the variables influencing survival of postsmolt salmon, temperature is particularly important. If they are to survive, individuals must quickly adapt to their new physical environment and be able to flee predators and seek prey. In spite of its presumed importance, the ecology of salmon smolts as they enter the marine environment is largely unknown. This article provides the first recorded results of temperatures experienced by salmon smolts as they enter the sea and provides insight into how postsmolts adapt to life at sea based on ambient temperature ranges and temperature choices made by the postsmolts. The

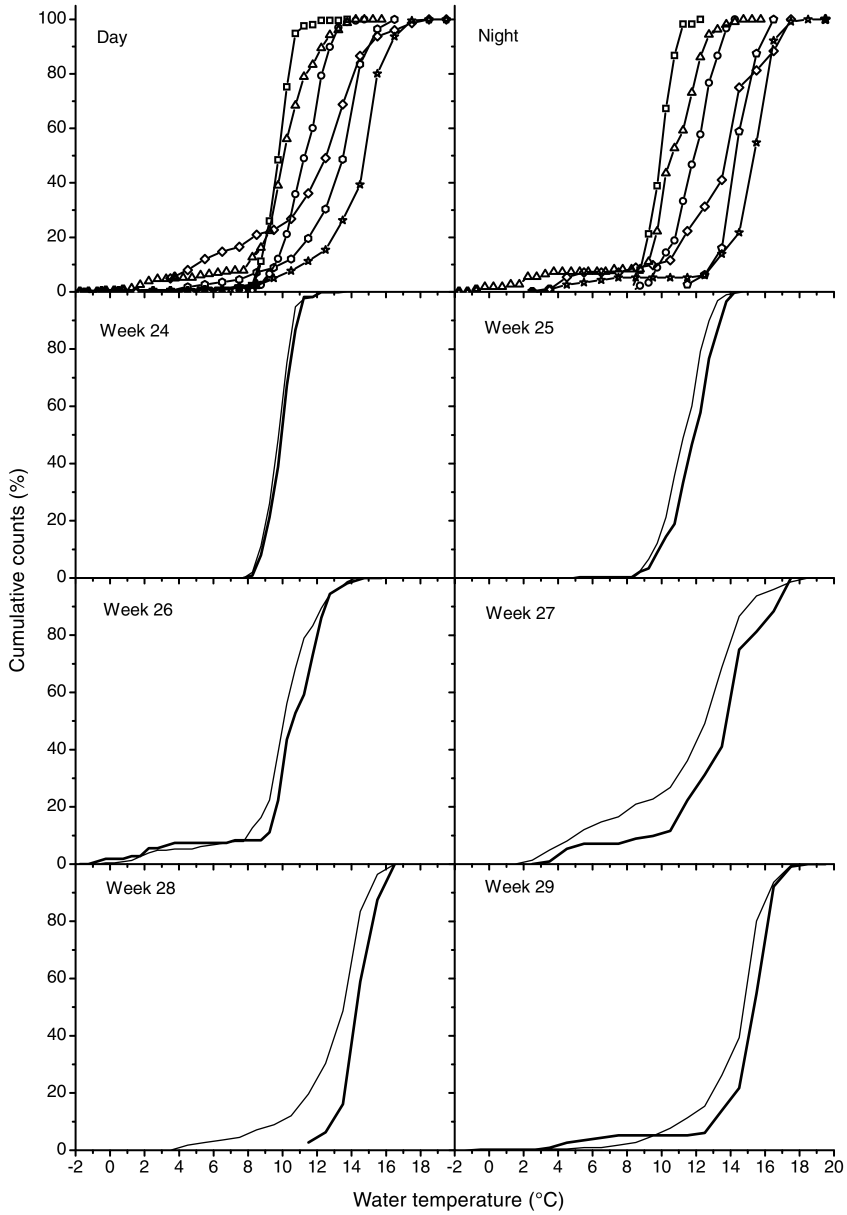

Figure 5

Difference between night and day temperatures recorded hourly by data storage tags and expressed as cumulative counts for weeks 24 to 29 from Campbellton River, 2002. Water temperatures are shown for six periods and for all day and night temperatures. Thin solid line is for daytime temperatures and thick line is for night time temperatures. In the multi-line graphs labelled "day" and "night," the square=week 24, the circle=week 25, triangle=week 26, polygon=week 27, dark pentagon=week 28 and the star=week 29.

temperature profiles collected by these data storage tags provide detailed information on the thermal habitat experienced by 15 Atlantic salmon postsmolts for periods ranging from a few days to about two months at sea. Temperatures recorded ranged from below 0° to nearly 20°C, although most of the time was spent in water from 8° to 15°C, probably near the surface.

Sigholt and Finstad (1990) and Handeland et al. (2003) reported that lethal sea water temperatures for both wild and farmed salmon smolts adapting to seawater occurred at very low and very high temperatures. At the lower end of the range in temperatures, some mortalities occurred at sea temperatures of 6–7°C, whereas at the higher end, mortalities occurred at temperatures over 14°C, indicating that there may be environmental windows for successful transition of smolts into the sea at locations other than at the extreme edges of the temperature ranges documented by Power et al. (1987). Reddin and Friedland (1993) noted that during colder years with heavy ice flows along the northeast coast of Newfoundland, commercial catches and returns of salmon to rivers were lower, even though freshwater warming was occurring normally and they also noted that these low catch rates and returns may have been due to the mortality of postsmolts early in the marine phase. Our results from DSTs applied to Campbellton River smolts indicated that temperature-related mortalities, at least in 2002, were unlikely because the smolts spent little time in water colder than 7°C. Furthermore, because the only colder water present was deeper in the water column, salmon postsmolts were able to avoid it by remaining in the warmer surface waters. In 2002, there was little or no inshore ice at the time of the Campbellton River smolt migration as is sometimes present in other years when mortalities from cold water temperatures could occur.

It is interesting to note that temperatures recorded by the DSTs for the first few weeks after the smolts entered the sea were very similar to that experienced by salmon kelts tagged with DSTs also from Campbellton River (Reddin et al., 2004). In addition, the temperatures from tagged kelts when compared to temperatures from tagged smolts showed similar periods of stability just after entry of the salmon into the sea, as well as abrupt changes in temperatures consistent with deep diving activities. Although we did not know the precise geographic location of either group of fish, it appears that kelts and postsmolts are found initially in water of similar temperatures and behave in similar ways with respect to temperature. Because neither the postsmolts nor kelts started their deep diving activities for four weeks after sea entry, it may be that they were recovering from the transition process or that they may have been near shore where deeper depths are not available (or both these reasons may apply). Resolution of these questions will have to await the results from application of geolocation and depth-sensing tags.

Colbourne et al.[16], Friedland et al. (2003), Beamish and Bouillon (1993), and Downton and Miller (1998) and many others have examined relationships between environmental variables and the abundance of Pacific and Atlantic salmon and other fish species with a view of providing forecasts of future abundance but without any knowledge of what thermal regimes the fish actually use. Colbourne et al.[14] indicated that the goal of searching for relationships is important in order that influences of the physical ocean environment can be used to provide more accurate forecasts of stock abundance and ultimately so that they can be used to create management plans for various fisheries (Bisbal and McConnaha, 1998; Friedland, 1998). These predictions are currently used for both North American and European Atlantic salmon, for which abundance has been forecasted partly on the basis of environmental information (Anon.[8]). Physical conditions in the ocean have been shown to be related to mortality and growth of some other species (Brander, 1995; Dutil et al., 1999; Watanabe and Yatsu, 2004). Blackbourn (1993) and Downton and Miller (1998) have suggested that freshwater survival rates for some species of Pacific salmon are even related to SSTs experienced by potential spawners while still at sea, shortly before their return to freshwater. These studies and their importance clearly show the need for studies on the physical oceanography and ecology of fish at sea. For Atlantic salmon, Reddin and Friedland (1993) created a profile of sea temperatures, based on research vessel catch rates, that indicated that Atlantic salmon were commonly found in water at temperatures from 4° to 10°C. Reddin et al. (2004)

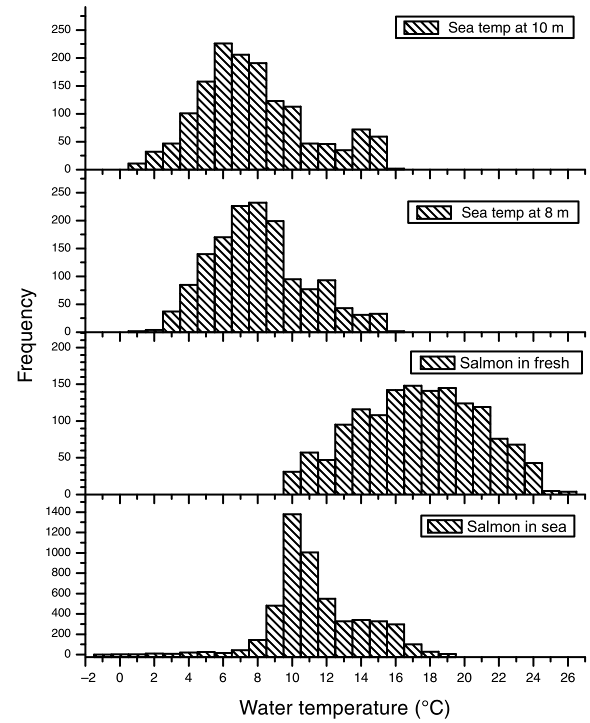

Figure 6

Frequency distributions for all temperatures recorded hourly at sea at 10 m depth (Sea temp at 10 m) and at 8 m depth (Sea temp at 8 m), and for salmon in freshwater from the DSTs (Salmon in fresh), and for salmon from DSTs while in the sea (Salmon in sea). All sea temperatures from the DSTs were used and the freshwater and marine temperatures are for the same time periods that the DST-tagged fish were in the sea.

[16] Colbourne, E. B., E. G. Dawe, D. G. Parsons, E. F. Murphy, W. R. Bowering, E. L. Dalley, J. T. Anderson, J. B. Dempson, D. Orr, D. E. Stansbury, and G. P. Ennis. 2002. A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. NAFO SCR Doc. 02/34, 21 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

indicated that Atlantic salmon kelts tagged with DSTs were found where temperatures ranged from a low near 0° to over 25°C, although most of their time was spent in water of 5° to 15°C. This finding was similar to that for adults by Sturlaugsson[1] and Karlsson et al.[17] The present study indicates that salmon postsmolts are located mostly near the surface in water temperatures ranging from 8° to about 15°C. Because the temperatures experienced by kelt are somewhat warmer then those used in correlation studies of salmon growth and survival, it may be that our results will encourage other researchers to review the temperatures they use in such studies.

Prey items in the diet of adult Atlantic salmon are fairly well known revealing that Atlantic salmon are opportunistic feeders, feeding on whatever is abundant in the area (Reddin, 1988; Hislop and Shelton, 1993). Although food resources are still unknown for some regions, the prey species of smolts and postsmolts at sea has recently become an important area for research in the northeast Atlantic (Andreassen et al., 2001; Salminen et al., 2001; Rikardsen et al., 2004). Rikardsen et al.'s (2004) extensive analysis of postsmolt diet in eight fjords in Norway revealed extensive feeding on pelagic larval fish species and crustaceans, as well as substantial geographic and annual variation in prey diversity and feeding intensity. Furthermore, Levings (1994) summarized the diet of smolts and postsmolts in the estuarine and near-shore environments from publications by Power and Shooner (1966), Dutil and Coutu (1988), and Hvidsten et al.[18] which shows postsmolts feeding on gammarid amphipods and intertidal and land-based insects. Although diet information exists for postsmolts, the feeding mechanisms of postsmolts are unknown because there are few, if any, tracking studies in estuaries and the coastal areas. However, the new data on postsmolts early in their marine life that we have collected using DSTs can help us infer this information and the diet studies, although not specific to Newfoundland waters, indicate that salmon prey on pelagic fish larvae and crustacean species, some of which inhabit the deeper waters of the water column. Thus, it would appear that postsmolts in the present study and the kelts in a previous study (Reddin et al., 2004) were diving from surface waters to greater depths to obtain prey. The temperature profiles from the DSTs, compared to oceanographic data available from other studies (Colbourne[14]; Colbourne and Fitzpatrick[19]), indicate that these dives may be anywhere from 25 to 50 m in depth.

There is a tendency for postsmolts to be caught in the upper part of the water column, as evidenced by trawling for postsmolts at sea (Shelton et al., 1997; Holm et al., 2000; Rikardsen et al., 2004), by acoustic tracking of postmolts in fjords (Holm et al., 2000; Moore et al.[20]), and by net catches in surface waters (Dutil and Coutu, 1988; Reddin and Short, 1991; Thorisson and Sturlaugsson[21]). The temperature profiles from our DST-tagged postsmolts indicate that although most of their time is spent near the surface (and nearer the surface at night), salmon postsmolts undergo deeper dives, probably in search of prey. Deeper diving activities have been reported previously for salmon kelts also from Campbellton River by Reddin et al. (2004). The present study demonstrates that postsmolts also show the same type of behavior although the frequency of dives varies somewhat from fish to fish. Holm[22] et al. (2000) noted that salmon postsmolts caught in pelagic trawls in the Norwegian Sea were all caught during surface trawls; none were caught at deeper depths. Westerberg (1982) during coastal tracking studies noted that salmon made dives of short duration to greater depths; his results are similar to the results shown in our study.

Wada and Ueno (1999) listed three hypotheses to explain diving behaviour in Pacific salmon, viz. the salmon are making orientation for homing migration, for feeding, and for controlling body temperature. Reddin et al. (2004) suggested a fourth hypothesis: that the salmon are diving to avoid predators. Our conclusion is that the deep diving activities of salmon postsmolts (to as deep as 50 m) recorded by the DSTs, because of their frequent nature, are probably related to prey seeking and feeding. Reddin et al. (2004) further pointed out that there may be an energetic advantage for salmon to seek prey in cooler, deeper waters where prey are more abundant and then to return to warmer surface waters where their food can be digested more rapidly.

Ecological information can also be discerned from the temperature patterns provided by the DSTs. Ogura and Ishida (1995), Wada and Ueno (1999), Walker et al. (2000) and Reddin et al. (2004) all noted a period of more stable temperatures experienced at both the beginning and at the end of the temperature time series from the DSTs and concluded that the fish remained at the same

[17] Karlsson, L., E. Ikonen, H. Westerberg, and J. Sturlaugsson. 1996. Use of data storage tags to study the spawning migration of Baltic salmon (*Salmo salar* L.) in the Gulf of Bothnia. ICES C.M. (council meeting) 1996/M: 9, 15 p.

[18] Hvidsten, N. A., B. O. Johnsen, and C. D. Levings. 1993. Behaviour and feeding of emigrating salmon smolts in Trondheimfjord. Res. Rep. no. 164, 17 p. [In Norwegian.] Norwegian Institute for Nature Research, Trondheim, Norway, Tungasletta 2, 7485 Trondheim, Norway.

[19] Colbourne, E. B., and C. Fitzpatrick. 2003. Physical oceanographic conditions in NAFO subareas 2 and 3 on the Newfoundland and Labrador Shelf during 2002. NAFO (North Atlantic Fisheries Organization) SCR Doc. 03/14, 57 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

[20] Moore, A., I. C. Russell, M. Ives, E. C. E. Potter, and C. P. Waring. 1998. The riverine, estuarine and coastal migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts. ICES CM 1998/N: 16, 11 p.

[21] Thorisson, K. and J. Sturlaugsson. 1995. Postsmolt of ranched Atlantic salmon (*Salmo salar* L.) in Iceland: IV. Competitors and predators. ICES C.M. 1995/M: 12, 9 p.

[22] Holm, M., I. Huse, E. Waatevik, K. B. Døving, J. Aure. 1982. Behaviour of Atlantic salmon smolts during the seaward migration. I. Preliminary report on ultrasonic tracking in a Norwegian fjord system. ICES CM 1982/M:7, 10 p.

location in the water column for some period of time, perhaps adjusting to the presence of the tag or to life in the sea (or to both). Furthermore, Reddin et al. (2004) noted that this period of temperature stability could be also due in some instances to the fish being near shore in shallow water where large scale vertical movements and their concomitant changes in temperature were not possible. This period of restricted vertical activity seemed to cease as the fish made its return migration towards freshwater. Our study indicates that in freshwater the water temperature recorded at the trap corresponds closely to the temperature recorded by the DST on the fish on its departure from the river and at its return. DST temperatures in freshwater follow the diurnal rhythm of warming and cooling of the river. In the sea, there is a period of stable temperatures with a diurnal rhythm that follows the daily warming and cooling. Next, the smolts began a period of fairly rapid descents and ascents in the water column during which temperatures rose and fell much more quickly then during the natural daily cycle. Also, night temperatures were warmer than day temperatures, in contrast to the daily warming and cooling cycle of the sea, indicating that smolts were higher in the water column at night then during daylight hours. The differences in temperatures between day and night may reflect avoidance of avian predators as suggested by Reddin et al. (2004) and Montevecchi et al. (2002). This finding is similar to that shown for adult chum salmon by Friedland et al. (2001) but contrasts with that reported by Shelton et al. (1997) who reported that no catches of postsmolts occurred at night during surface trawling in the northeast Atlantic. Because the records of trawling at night are sparse, we recommend that more effort should be put into night trawling in light of the information from our DST-tagged postsmolts.

In terms of our objectives, we have shown that Atlantic salmon smolts can carry DSTs, and that a sufficient number of tags with useful data on thermal ecology can be successfully recovered. The return rates were low and validated the preliminary use of the less expensive DSTs but were high enough that these experiments could be repeated elsewhere. The use of more expensive DSTs with geoposition and more environmental sensors will require methods to recover them at sea if sufficient tags are to be available to provide meaningful results. The thermal habitat used by Atlantic salmon is shown; postsmolts are found in water with temperatures ranging from 8° to about 15°C in the spring. Lastly, although we show from the water temperature records that salmon postsmolts are frequently found near the surface, it is also evident that they make frequent deep dives of short duration. We hypothesize that these deep dives may be directly related to feeding or to evasion from predators (or to both), as has been observed for kelts by Reddin et al. (2004).

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Literature cited

Allan, I. R. H., and J. A. Ritter.
1977. Salmonid terminology. J. Cons. Int. Explor. Mer 37:293–299.

Andreassen, P. M. R., M. B. Martinussen, N. A. Hvidsten, and S. O. Stefansson.
2001. Feeding and prey selection of wild Atlantic salmon post-smolts. J. Fish Biol. 58:1667–1679.

Beamish, R. J., and D. R. Bouillon.
1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50:1002–1016.

Bisbal, G. A., and W. E. McConnaha.
1998. Consideration of ocean conditions in the management of salmon. Can. J. Fish. Aquat. Sci. 55:2178–2186.

Blackbourn, D. J.
1993. Sea surface temperature and the subsequent freshwater survival rate of some salmon stocks: a surprising link between the climate of land and sea. *In* Proceedings of the ninth annual Pacific Climate (PACLIM) Workshop, 21–24 April 1992 (K. T. Redmond, and V. L. Tharp, eds.), Tech. Rep. no. 34, p. 23–32. California Department of Water Resources, Interagency Ecological Studies Program, Pacific Grove, CA.

Boehlert, G. W.
1997. Application of acoustic and archival tags to assess estuarine, nearshore, and offshore habitat utilization and movement by salmonids. NOAA Technical Memo. NMFS-SEFSC-236, 62 p.

Brander, K. M.
1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. 52:1–10.

Downton, M. W., and K. A. Miller.
1998. Relationships between Alaskan salmon catch and North Pacific climate on interannual and interdecadal time scales. Can. J. Fish. Aquat. Sci. 50:1002–1016.

Dutil, J.-D., and J.-M. Coutu.
1988. Early marine life of Atlantic salmon, Salmo salar, postsmolts in the northern Gulf of St. Lawrence. Fish. Bull. 86:197–212.

Dutil, J.-D., M. Castonquay, D. Gilbert, and D. Gascon.
1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 56:1818–1831.

Friedland, K. D.
1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Can. J. Fish. Aquat. Sci. 55:119-130.

Friedland, K. D., D. G. Reddin, J. R. McMenemy, and K. F. Drinkwater.
2003. Multidecal trends in North American Atlantic salmon (Salmo salar) stocks and climate trends relevant to survival. Can. J. Fish. Aquat. Sci. 60:363–383.

Friedland, K. D., R. V. Walker, N. D. Davis, K. W. Myers, G. W. Boehlert, S. Urawa, Y. Ueno.
2001. Open-ocean orientation and return migration routes

of chum salmon based on temperature data from data storage tags. Mar. Ecol. Prog. Ser. 216:235–252.

Godø, O. R. and K. Michalsen.
2000. Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. Fish. Res. 48: 127–140.

Handeland, S. O., B. T. Bjornsson, A. M. Arnesen, and S. O. Stefansson.
2003. Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. Aquaculture 220:367–384.

Hislop, J. R. G., and R. G. J. Shelton
1993. Marine predators and prey of Atlantic salmon (*Salmo salar* L.). *In* Salmon in the sea and new enhancement strategies (D. Mills, ed.), p. 104–118. Fishing News Books, Oxford, UK.

Hoar, W. S.
1988. The physiology of smolting salmonids. *In* Fish physiology, vol. XIB (W. S. Hoar, and D. J. Randall, eds.), p. 275–343. Academic Press, New York, NY.

Holm, M., J. C. Holst, and L. P. Hansen.
2000. Spatial and temporal distribution of post-smolts of Atlantic salmon. ICES J. Mar. Sci. 57:955–964.

Jacobsen, J. A.
2000. Aspects of the marine ecology of Atlantic salmon (*Salmo salar* L). Ph.D. diss., 51 p. Univ. Bergen. Bergen, Norway.

LaCroix, G. L., and P. McCurdy.
1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. J. Fish Biol. 49:1086–1101.

Levings, C. D.
1994. Feeding behaviour of juvenile salmon and significance of habitat during estuary and early sea phase. Nordic J. Freshw. Res. 69:7–16.

McCormick, S. D., and R. L. Saunders.
1987. Preparatory physiological adaptions for marine life in salmonids: osmoregulation, growth, and metabolism. Am. Fish. Soc. Symp. 1:211–229.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders.
1998. Movement, migration and smolting of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. (suppl. 1) 55:77–92.

Mills, D. H.
1989. Ecology and management of Atlantic salmon, 351 p. Chapman and Hall, London, UK.

Montevecchi, W. A., D. K. Cairns, and R. A. Myers.
2002. Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 59:602–612.

Ogura, M. and Y. Ishida.
1995. Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus* spp.) in the central Bering Sea. Can. J. Fish. Aquat. Sci. 52:532–540.

Power, G., and G. Shooner.
1966. Juvenile salmon in the estuary and lower Nabisipi River and some results of tagging. J. Fish. Res. Board Can. 23:947–961.

Power, G., M. V. Power, R. Dumas, and A. Gordon.
1987. Marine migrations of Atlantic salmon from rivers of Ungava Bay, Quebec. *In* American Fisheries Society symposium on common strategies in anadromous/catadromous fishes 1:262–275. Am. Fish. Soc., Bethesda, MD.

Reddin, D. G.
1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. Chapter 26, *in* Atlantic salmon: planning for the future (D. H. Mills, and D. J. Piggins, eds.), p. 483–511. Proceedings of the third international Atlantic salmon symposium, Biarritz, France, 21–23 October 1986. Croom Helm, London.

Reddin, D. G., and K. D. Friedland.
1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. *In* Salmon in the sea and new enhancement strategies (D. Mills, ed.), p. 79–103. Fishing News Books, Oxford, UK.

Reddin, D. G., K. D. Friedland, P. Downton, J. B. Dempson, and C. C. Mullins.
2004. Thermal habitat experienced by Atlantic salmon kelts (*Salmo salar* L.) in coastal Newfoundland waters. Fish. Oceanogr. 13:24–35.

Reddin, D. G., J. Helbig, A. Thomas, B. G. Whitehouse, and K. D. Friedland.
2000. Survival of Atlantic salmon (*Salmo salar* L.) and its relation to marine climate. *In* Managing wild Atlantic salmon: new challenges—new techniques; proceedings of the fifth international Atlantic salmon symposium held at Galway, Ireland, 1997 (F. G. Whoriskey, and K. E. Whelan, eds.), pp. 24–49. The Atlantic Salmon Federation, St. Andrews, News Brunswick, Canada.

Reddin, D. G., and P. B. Short.
1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. Can. J. Fish. Aquat. Sci. 48:2–6.

Rikardsen, A. H., M. Haugland, P. A. Bjorns, B. Finstad, R. Knudsen, J. B. Dempson, J. C. Holst, N. A. Hvidsten, and M. Holm.
2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. J. Fish Biol. 64:1655–1679.

Salminen, M., E. Erkamo, and J. Salmi.
2001. Diet of post-smolt and one-sea-winter Atlantic salmon in the Bothnian Sea, northern Baltic. J. Fish Biol. 58:16–35.

Shelton, R. G. J., J. C. Holst, W. R. Turrell, J. C. MacLean, I. S. McLaren, and N. T. Nicoll.
1997. Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fish. Res. 31:159–162.

Sigholt, T., and B. Finstad.
1990. Effect of low temperature on seawater tolerance in Atlantic salmon (*Salmo salar* L.) smolts. Aquaculture 84:167–172.

Walker, R. V., K. W. Myers, N. D. Davis, K. Y. Aydin, K. D. Friedland, H. R. Carlson, G. W. Boehlert, S. Urawa, Y. Ueno, and G. Anma.
2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9:171–186.

Watanabe, C., and A. Yatsu.
2004. Effects of density-dependence and sea surface temperature on interannual variation in length-at-age of chub mackerel (*Scomber japonicus*) in the Kuroshio-Oyashio area during 1970–1997. Fish. Bull. 102:196–206.

Westerberg, H.
1982. Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.) – II. Swimming depth and temperature stratification. Drottingholm Report 60:102–120.