

Behaviour of Atlantic salmon (*Salmo salar* L.) recorded by data storage tags in the NE Atlantic – implications for interception by pelagic trawls

by

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Abstract

In a project carried out in the Nordic Seas (Northeast Atlantic) in 2002 - 2004, 413 Atlantic salmon (*Salmo salar* L.) were tagged with data storage tags (DST) either logging temperature and depth (StarOddi, Milli) or just temperature (Dallas semiconductor, iButton). The main aims were to study various marine life history traits of salmon, such as winter habitats, diurnal patterns of vertical migration, feeding activities. Another aim was to collect salmon behaviour data with relevance for issues related to by-catch of salmon in pelagic fisheries. In this paper we focus on possible implications of the diurnal depth distribution of salmon in relation to catchability of salmon in sampling trawls versus commercial fisheries. Five DSTs were returned from fishermen. Four of these were Milli-tags and are used in this presentation. Time from release to capture ranged from 48 - 128 days. The DSTs logged data at alternating intervals of 1, 5, 30, 60 and 120 min. almost 45000 recordings were retrieved. The data records were grouped in different phases: post-release; oceanic feeding & migration; coastal migration; estuarine migration; in-river phase. Salmon stay in the upper 5 m for 60% of the time during the oceanic phase, making deep dives (280 m) in between. The proportion of time the salmon stay at the surface (<2 m) decreases from 5.5 to 2.5% between 9 and 17 h.

Keywords

Atlantic salmon; tagging; archival tags; data storage tags; DST; behaviour; vertical distribution; diurnal depth distribution.

Introduction

Reports of salmon being taken as by-catch during pelagic fishing operations for other species in the Northeast Atlantic have been circulating for some years. However, these reports have been sporadic and often anecdotal in nature and do not provide evidence of any potentially significant by-catch of salmon in these fisheries. A high number of post-smolts (young salmon in their first summer at sea) and mackerel were captured in the Norwegian Sea during Norwegian experimental cruises 1998-2004 further raised this concern (ICES 2004).

An inter-Nordic tagging study including Norway, Faroes and Iceland was carried out in the sea in 2002-2004. The aims were to study various marine life history traits of salmon, such as winter habitats, diurnal patterns of vertical migration and feeding activities.

Data from data storage tags (DSTs) can reveal detailed aspects of diurnal, tidal, and seasonal movement patterns that influence our ability to assess and manage commercial species. Archival tagging data may have uses for fisheries management. For example, daily vertical migration of salmon can influence the availability to trawl surveys, if the trawl survey is carried out with a standard surface salmon trawl, i.e. with a fishing depth from the surface to 7 m below surface. The diurnal vertical migration patterns would influence the proportion of the stock available to the survey and therefore also the effective catchability of the survey.

More important for the management of salmon, however, is the vertical distribution of salmon and their vulnerability for interception by fishing gears intended for other pelagic species. By-catch of salmon in the open ocean in the Norwegian Sea has been mentioned by North Atlantic Atlantic Salmon Conservation Organisation (NASCO) as a potential source of mortality not accounted for in the assessment of salmon (ICES 2005). The NASCO focus has been on the commercial pelagic trawl fisheries. In particular the summer fisheries for mackerel and herring at the surface in the Norwegian Sea have been suspected to be an added source of unaccounted mortality of salmon at sea (ICES 2004).

Data from four salmon tagged with data storage tags (recording depth and temperature) captured and released in the Norwegian Sea in spring 2004 and recaptured a few months later in homewaters in Norway and Sweden, allowed us to extract some important general information on the behaviour of salmon, particularly their diving patterns and depth preferences during day and night during the oceanic phase. We focus here on possible implications of the diurnal depth distribution of salmon in relation to

- 1) the catchability of salmon at various depths (by 5 m depth bins) and possible consequences for being intercepted by a pelagic trawl as by-catch in the fishery for other pelagic species;
- 2) the diel depth distribution of salmon at surface (as the proportion of recordings above 2 m depth by hour) to see whether there are certain periods during the day when salmon would be more vulnerable to a pelagic trawl towed at the surface, and possible consequences for the catchability of a pelagic trawl survey for salmon.

Material and Methods

A specially designed “salmon trawl” with extra flotation on the head line and the wings was used together with a cage for live fish capture (modified from “Fish Lifter”, Holst and McDonald, 2000) attached to the cod end of the trawl. Under moderate wave actions, this technique allows most of the fish to pass through the cod-end of the trawl into the cage with very little external damage, i.e. loss of scales (Holst and McDonald 2000; ICES 2000/ACFM:13). The towing speed was around 4.5-4.8 knots and the wire length was 290–340 m depending on the condition of the waves. The vertical opening of the trawl was estimated to be less than 7 m.

The areas fished are shown in Figure 1, with indications of the location of the tagging of the four salmon recaptured, from which the DSTs were recovered and used in the present analysis.

The catches ranged from nil to 20 salmon per hour with a mean catch rate of 3- 5 salmon, depending on the sea-surface temperature (6-9°C). During the tagging project, from 9 one- or two-week surveys in the period summer 2002 to fall 2004, in total 747 salmon were caught of which 508 were post-smolts (salmon in their first year at sea). 413 salmon were tagged, 299 with StarOddi and 64 with *i*Button DSTs (Table 1).

Post-capture the fish were placed in a recovery tank and observed for 0,5 - 4 h. Fish reacting promptly when tank cover was removed, with unwavering swimming behaviour were chosen for tagging unless smaller than 400g. Fish with scale loss larger than 30% of the integument were in general discarded. The salmon were anaesthetised (Benzocaine- ethyl-p-aminobenzoate) and the tag was placed in the body cavity through a small incision in front of the left pelvic fin, 1-2 cm up the fish’s ventral side (depending on fish size) . An additional bright coloured numbered external T-bar anchor tag was attached under the dorsal fin as secondary tag to facilitate detection by fishermen. A few scales and the adipose fin were removed for biological analyses and length and weight of the fish were recorded. Stomach content of dead fish was removed for further analyses. In 2004, a special trough that could contain 45 fish recovering from anaesthesia, and that could be hoisted over the ship’s side by a crane was used for releasing the fish on the Norwegian ship. The salmon didn’t have to be touched post-operation, which greatly reduced handling stress.

Two types of tags were used, an *i*Button tag (Dallas Semiconductor, weighting 1 g in the sea) recording temperature only with memory capacity of approx. 12,000 recordings and a StarOddi depth and temperature recording tag (Star Oddi “Milli”, 38.4 x 12.5 mm, weighing 5g in the sea) with a memory capacity of 21,738 measurements per parameter. The *i*Button tag can be set to record at a fixed measurement interval. The StarOddi tag can be set to log at fourteen sequences with different measurement intervals from seconds to weeks. In this experiment, sequences of 1, 5, 30, 60 and 120 min were used. The tags could record for two years from the time of tagging.

In the releases in April 2004, all tags were set with a starting sequence of 14 days at 60 minute intervals. Thereafter the DSTs were set with different recording protocols depending on the size of the fish to be tagged.

- A) The smallest salmon (0.4 – 1.0 kg) was expected to return to the river more than one year later, had five x 48 hours of recordings at one minute intervals (2880 recordings per sequence) distributed in months 5 (i.e. May), 9, 12 the year of release and, 3 and 6 the following year respectively. The short intervals were alternated by longer periods of 60 and 120 min intervals, while 5 and 30 min were set in between these periods (DST 2, Figure 2e).

- B) Salmon of 1-3 kg, a size group that could stay one or more years at sea, but which also might return the same year (as 1 SW fish or Grilse), received DSTs set with sequences of recordings at 1 minute intervals in month 5, 6, 8, 12, the year of release and 3 and 6 the following year. The dense intervals were alternated with extended periods of 60 and 120 min. intervals (DST 1, Figure 2e).
- C) The largest salmon (>3 kg) expected to return to the home river within two to four months after release were implanted with DSTs with more frequent sequences of 1 and 5 minute recordings. No 120 min. sequences were used in these DSTs (DSTs 3 and 4, Figure 2e).

Handling of tag data

To analyse the depth distribution of salmon in the oceanic phase a complete time series of only one sampling rate is needed to get an unbiased depth distribution in relation to the number of observations of each interval. Therefore, a complete time series of depth and temperature recordings of the 120 min data were extracted, including recordings extracted from the fine scale data (shorter intervals). The full time series of the 120 min data was chosen as being representative for the depth distribution of the fish, while the 1 or 5 min data include only a small and discontinuous fraction of the data from each fish, as well as the 30 and 60 min data.

The 120 min data set was grouped by 5 m depth bins (0-4.9; 5-9.9,...) to represent the depth distribution (% of depth observations) of salmon down to 50 m, and from 50-100 m, and deeper than 100 m (Figure 3).

The diel depth distribution of salmon was calculated as the as the proportion of depth recordings of fish above 2 m depth by hour, i.e. as the proportion of fish at the surface, to see whether there are certain periods during the 24-hour cycle that salmon are more vulnerable to a pelagic trawls towed at the surface. The 2 m limit was chosen to distinguish the surface dwelling behaviour from active diving behaviour. The data was pooled from all four fish and from all 60 min observations, plus resampling the denser sampling rates to obtain 60 min data for those as well, to get a reasonable number of observations (Table 2; Figure 4.)

Results

Altogether five DSTs have been recovered from the releases in the Norwegian Sea: one *iButton* tag returned from River Namsen in mid Norway 2002, and four *StarOddi* tags were returned from River Namsen, Børsa Estuary, River Surna (all mid Norway) and River Ätran in southwest Sweden. The shortest possible direct migration routes of these fish are presented in Figure 1.

The data from the recapture of the *iButton* tagged fish (temperature only) were not used in the present analysis. One salmon from the Faroese tagging in 2003 was reported in September 2004 in the River Urie, Scotland, but unfortunately, only the external secondary tag was recovered.

A summary of the details of the four recaptured fish tagged with *StarOddi* tags is given in Table 2, which shows the release and recapture dates, and also our estimation of the dates indicating the end of the “open” sea phase and estuarine/inshore phase, respectively (in three cases only as one salmon was captured in the estuary).

The number of data recordings by each sampling interval (1, 5, 30, 60, and 120 min, respectively) is also shown in Table 2, indicating the resolution of the available data.. Close to 45,000 recordings have been retrieved altogether .

Data records from these four recaptures (all released and recaptured in 2004) are presented in Figure 2a-d respectively on the time scale 24.04–30.08 2004, which were the dates of the first records after release in the sea and the last record in river/estuary before capture. These graphs show the depth and temperature profiles for each fish with an indication of the estuary/river phase at the end of each time-series. To get an unbiased estimate of the “oceanic” behaviour of salmon, only the data in the sea phase were used in the present analysis omitting the estuary/near shore and river data.

Fish number 1 (Figure 2a) was recovered in River Ätran, Sweden and the track can be described as a post-release period, a probable feeding period with migration activity, a coastal migration (rising temperature), and finally the estuarine dwelling and migration followed by in-river dwelling when the diving activity ceases (marked in the graph).

Fish number 2 (Figure 2b) was recovered in River Surna , mid Norway and the track can be described as a post-release period, a probable feeding period with migration activity, a coastal migration (rising temperature), and finally the estuarine dwelling and migration followed by in-river dwelling when the diving activity ceases (marked in the graph). The River Surna is draining from high mountains and is regulated by power dams. The flushing of water from the dams may have caused the large fall in temperature observed in the graph.

Fish number 3 (Figure 2c) was recovered in River Børsa estuary, mid Norway and the track can be described as a post-release period, a probable feeding period with migration activity, a coastal migration and estuarine dwelling (diving activity ceases and temperature rises) until captured (marked in the graph).

Fish number 4 (Figure 2d) was recovered in the Namsen fjord (estuary), mid Norway. and the track can be described as a post-release period, a probable feeding period with migration activity, a coastal/fjord migration (rising temperature and ceasing diving activity) until the fish was captured in a bag net in the fjord (marked in the graph).

When analysing the DST data care had to be taken to the number of available data in each sampling interval, as the tags were set to record with various recording intervals in different periods. For fish number 1 and 2, half of the period was logged with 120 min intervals, the rest with a mixture of periods of 60, 30, 5 and 1 min intervals; for tag number 3 and 4 around half of the time consisted of 60 min intervals while the rest was a mixture of 30, 5, and 1 min intervals (Figure 2e).

From the grouped depth distributions in Figure 3 we may deduce that salmon occupy the upper 5 m water column in nearly 60% of the time during the oceanic feeding and early homeward migration phase.

In total 5574 observations of 60 min data were available for the analyse of the diel distribution (Table 2; Figure 4). Of these 28.5% were above 2 m depth, which were grouped by each hour during the day. The 120 min data were excluded in this analysis (1534 observations).

The results show that the proportion of time spent at the surface by the salmon decreases from 5.5% to 2.5% by hour during the daylight hours, i.e. between 9 to 17 hours (Figure 4).

Discussion

The difference in tag recapture rates between the releases made in late autumn/winter (1 of 304 tagged) and in spring/summer (5 of 109 tagged, see Table 1) makes us assume that the harsh weather conditions at capture during late autumn/winter has gravely affected the condition of the fish used for tagging. The mean scale loss for the former releases 15.6, while it was 10.0 for the latter releases. In addition the winter habitats are thought to be strenuous for salmon in the Nordic seas (Friedland *et al.* 2000), and surely have added to the post-tagging trauma and resulted in a higher tagging mortality. Several other explanations are possible to make up or add to the observed differences. Such are: the longer time lapse from the autumn release at sea until the salmon appear in the fisheries may have caused loss of external tags making the tagged fish less identifiable for fishermen; or the DSTs might have grown out through the body wall and lost (Nielsen, pers. com). Differences in handling at tagging and release may also cause varying survival rates, but on the other hand the tagging both in spring and autumn 2004 was performed by the same person leaving the winter conditions as the dominant cause for the difference.

The area around 2° E between 65-68°N (Figure 1) where the 5 recaptured DST fish had been tagged seems to be an area of feeding/ passage of both young (1 Sea Winter) and older (2 Sea Winters) salmon from the mid Norwegian rivers. The CPUE for this area was 4.5 salmon h⁻¹ and four out of the five DSTs were retrieved in mid Norway.

The diving patterns of the four salmon vary considerably, and differences in the recording protocols for the DSTs make comparison between individuals difficult. The large variety in the individual behaviours is a general observation from many DST studies. However, in spite of these shortcomings, some general patterns can be discerned in our data: A phase of post-tagging recovery, an active feeding and migration phase in the ocean (deduced from the amplitude of the depths recorded, Figures 2a-d). Then a gradual rise in logged temperatures combined with smaller amplitudes in depth recordings can be seen, indicating a phase of more close-to-coast movement. Lastly a phase of very varying length of clearly estuarine or in-river dwelling prior to capture. Within each phase there are individual variations in diving depths, probably resulting from availability of food and/or the hydrography in the area of residence.

The behaviour of a fish in relation to the fishing gear will determine whether it will be captured or not. However, so far little has been known of the behaviour of salmon at sea. By direct observations from sonic tracking (Jákupsstovu 1988; Sturlaugsson and Thorisson 1996) and indirectly through their selection of prey (Jacobsen 2001), the salmon are assumed to be surface dwellers performing occasional dives a behaviour that also has been observed for post smolts in fjords (Holm et al 2000). Our data strongly support the surface dwelling thus protecting them from some of the pelagic fisheries activities. But although the fish stay in the upper 0-5 m in around 60 % of the time (Figure 3) the relatively frequent dives below 20 – 50m (Figures 2a-d and 3) might make the salmon more vulnerable to interception by mid-water trawls in some areas than previously thought. This diving behaviour for feeding and / or orientation could explain why occasionally there are reports of considerable numbers of adult salmon taken in pelagic catches as the salmon seem to be distributed in scattered shoals both at feeding and migration (Jacobsen 2000; Hansen and Jacobsen 2003).

The observed difference between the number of observations of salmon at the surface during daylight and darker periods (Figure 4), would imply, at daylight hours, less salmon are available for e.g. the special salmon sampling trawl (sampling at 0 to \approx 7 m depth) resulting in an increased vulnerability to interception by commercial midwater trawls. At darker hours however, our data imply that the opposite could be the result, i.e. reduction in vulnerability to midwater trawls and increased availability of salmon for the sampling trawl. Unfortunately, neither research fishing nor commercial fishing data exist to support or reject this observation. In the spring 2004 the salmon trawl could only be operated between 05 and 23 h due shortage in scientific personnel and the research ship's fishing crew. In late April it is entirely dark only for around 2 hours at latitudes around 66°N. The whole six hour trawl watch was omitted because, from earlier experience, this would be the time when large by-catches of herring could be expected (Holm, Holst and Jacobsen pers. obs.) resulting in extra workloads for the personnel. There is insufficient information on the time of capture from the very limited official records of salmon being taken in the commercial fisheries, and consequently no conclusions can be drawn from these data.

With the results at hand, we propose that clusters with frequent recordings with maximum 10 min intervals registering behaviour in detail at the different time periods from tagging onwards would yield the most valuable results with respect to understanding salmon migration. We are also inclined to propose that DSTs having large memory capacity and advanced technical performance, with ability to record large amounts of data for several parameters in the long run would be more useful tools regardless of the higher costs involved. DSTs with depth, temperature and salinity as a minimum requirement, and geolocation as a preference would provide direct information on where the salmon have been and what environments they have encountered. Each retrieved DST would then be a valuable addition to the base knowledge needed to understand how and why the salmon react in different man made or natural situations the fish experience at various parts of their maritime habitat.

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References

- Friedland, K.D., Hansen, L.P., Dunkley, D.A. & MacLean, J.C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES Journal of Marine Science 57 (2): 419-429.
- Hansen, L.P. & Jacobsen, J.A. 2003. Origin, migration and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES Journal of Marine Science 60 (1): 110-119.
- Holm, M., Hansen, L.P., Holst, J.C. & Jacobsen, J.A. 2004. Atlantic salmon (*Salmo salar* L.). In The Norwegian Sea Ecosystem (Skjoldal, H.R., ed.), pp. 265-303, Tapir Academic Press, Trondheim.

Holm, M., Holst, J.C. & Hansen, L.P. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES Journal of Marine Science 57 (4): 955-964.

Holst, J.C. and McDonald, A. 2000. FISH-LIFT: A device for sampling live fish with trawls. Fisheries Research, 48:87-91.

ICES 2004. Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries. ICES CM 2004 (I:01), 65 pp.

ICES 2005. Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries (SGBYSAL). ICES CM 2005 (ACFM:13), 41 pp.

ICES 2006. Report of the Working Group on North Atlantic Salmon (WGNAS). ICES CM 2006 (ACFM:23), 254 pp.

Jacobsen, J.A. 2000. Aspects of the marine ecology of Atlantic salmon (*Salmo salar* L.). Ph. D. thesis at the University of Bergen, May 2000.

Jacobsen, J.A. & Hansen, L.P. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. ICES Journal of Marine Science 58 (4): 916-933.

Jákupsstovu, S.H.í. 1988. Exploitation and migration of salmon in Faroese waters. In Atlantic Salmon: Planning for the future (Mills, D. & Piggins, D., eds.), pp. 458-482, Croom Helm, London, 587 pp.

Sturlaugsson, J. & Thorisson, K. 1996 Depth movements of homing Atlantic salmon (*Salmo salar* L.) in coastal waters W. Iceland, in relation to environmental factors. In : Book of Abstracts, Fifth European Conference on Wildlife Telemetry, Strasbourg, France, 25-30 Aug. 1996. 1pp.

Table 1. Total number of salmon caught and number of fish tagged (and released) in 2002 - 2004.

Survey	Area	Year	Period	Salmon caught (postsmolts/adults)	Number tagged (StarOddi/iButton)
Norway	Norwegian Sea	2002	20/6 - 4/7 2002	17 (0/17)	4 (3/1*)
Faroe Islands	North of the Faroes	2002	16 - 23/10 2002	190 (185/5)	112 (62/50)
Iceland	South & west of Iceland	2002	12/11-09/12 2002	6 (4/2)	5 (5/0)
Iceland	East of Iceland	2003	10 - 23/1 2003	22 (21/1)	6 (6/0)
Norway	Norwegian coast	2003	17 - 24/5 2003	45 (0/45)	11 (11/0)
Norway	Norwegian Sea	2003	17/6 - 8/7 2003	27 (0/27)	7 (7/0)
Faroe Islands	North of the Faroes	2003	22 - 29/10 2003	177 (173/4)	116 (95**/21)
Norway	Norwegian Sea	2004	21 - 30/4 2004	136 (0/136)	87 (61***/26)
Faroe Islands	North of the Faroes	2004	3 - 10/11 2004	127 (125/2)	65 (49/16)
Total				747 (508/239)	413 (299/64)

* One iButton tag recovered from the Namsen fjord, Norway.

** One external tag recovered from the River Urie, Scotland, the DST was not recovered.

*** Four StarOddi tags recovered, three from Norway; one from Sweden: See Table 2.

Table 2. Summary table with details of the four recaptured fish with data storage tags (DST). The recapture dates are shown in bold, the other dates indicate the end of the “open” sea phase and estuarine/inshore phase, respectively. In addition one salmon was recovered on 17th July in River Namsen, the fish was tagged with an *iButton* (temperature only) tag, and one salmon from the Faroese tagging in 2003 was recovered in September 2004 in River Urie, Scotland, but unfortunately the DST was not recovered.

Fish Number	Tagging dates	Release		Recapture dates (bold)			Recapture		1 min data			5 min data			30 min data			60 min data			120 min data		
		L	W	Sea	Estuary	River	L	W	Sea	Est.	River	Sea	Est.	River	Sea	Est.	River	Sea	Est.	River	Sea	Est.	River
1	24-04-2004	49	1.11	19-07-2004	08-08-2004	30-08-2004	54	1.45	5762	0	4321	0	0	0	0	0	0	1201	0	0	384	235	235
2	25-04-2004	46	0.93	07-08-2004	14-08-2004	22-08-2004	50	1.5	1501	0	0	5759	0	0	1441	0	0	278	0	0	497	86	97
3	29-04-2004	75	4.42	12-06-2004	14-06-2004	15-06-2004	74	4	5822	0	0	2881	0	0	481	0	0	479	57	27	0	0	0
4	29-04-2004	71	3.185	10-07-2004	12-07-2004		74	4.3	5822	0		5762	0		481	0		908	57		0	0	
Total									18907	0	4321	14402	0	0	2403	0	0	2866	114	27	881	321	332

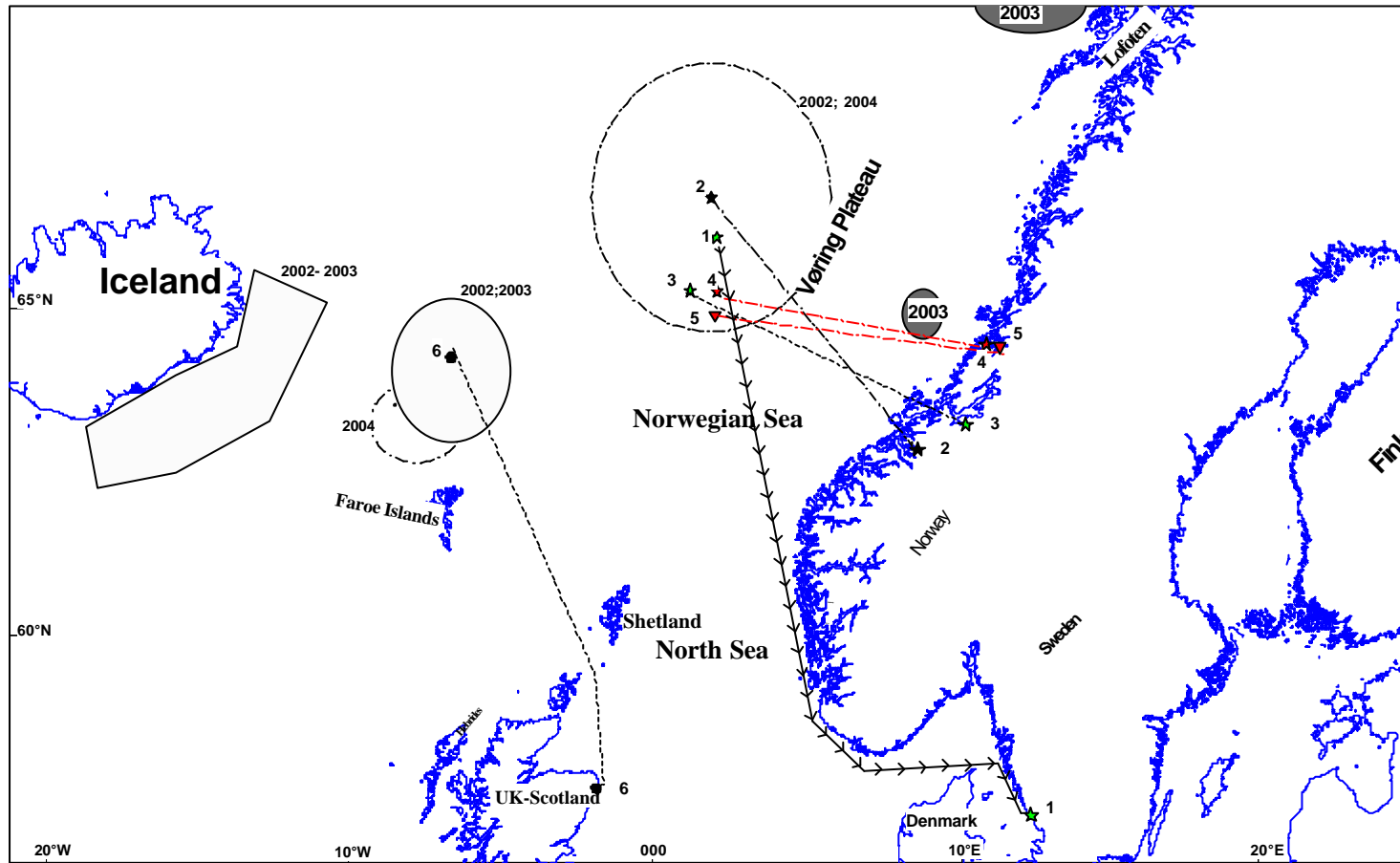


Fig. 1. Areas of capture and release of DST tagged salmon in 2002-2004. Numbers refer to recaptures listed in table 2. Only DSTs 1- 4 yielded data that are used in the present paper. Encircled areas represent areas fished during the different years (legends in the figure).

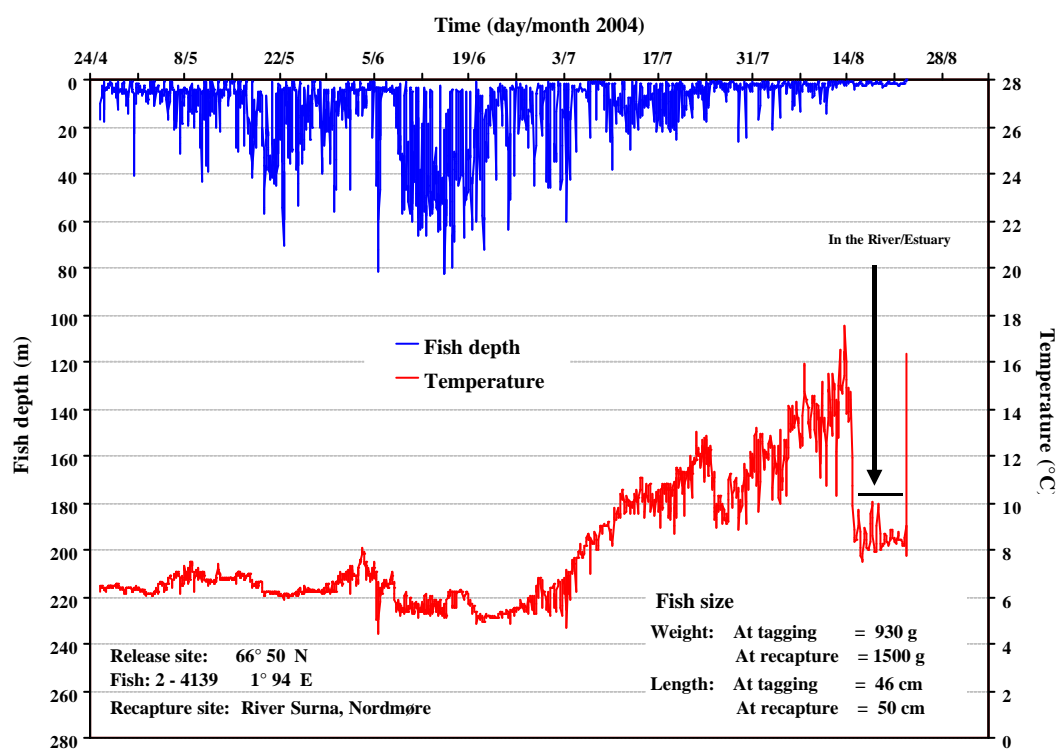
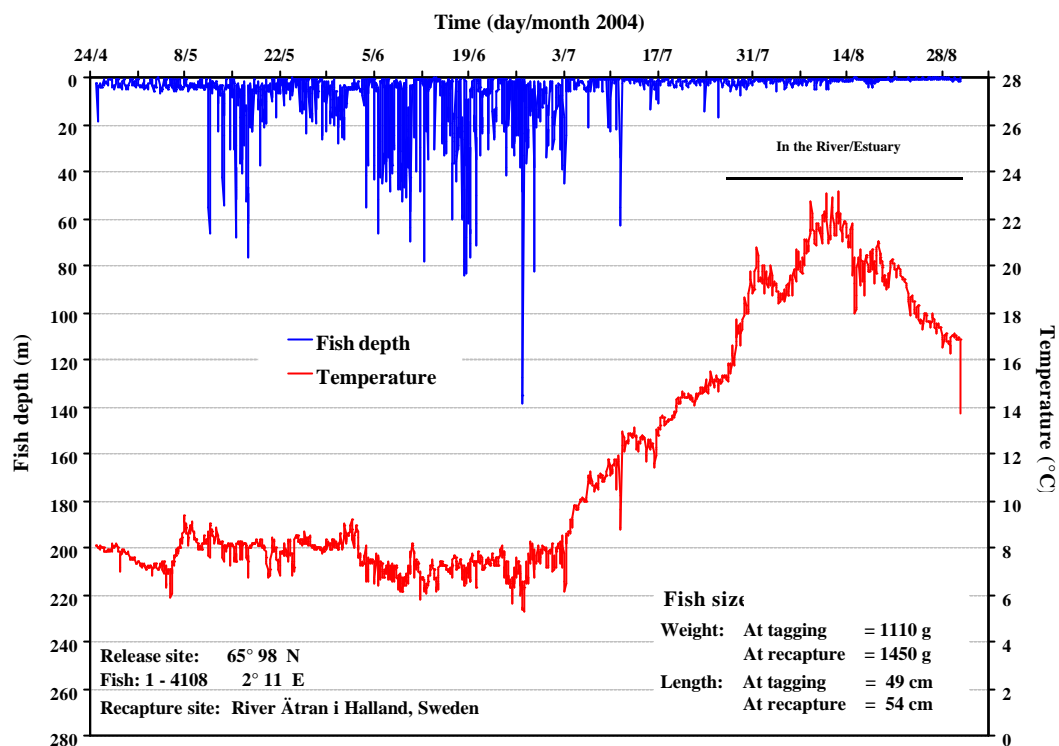


Fig. 2a-b. Depth (upper line/left axis) and temperature (lower line/right axis) profiles for fish number 1 (a) and 2 (b) with indication of Sea and Estuary/River phase.

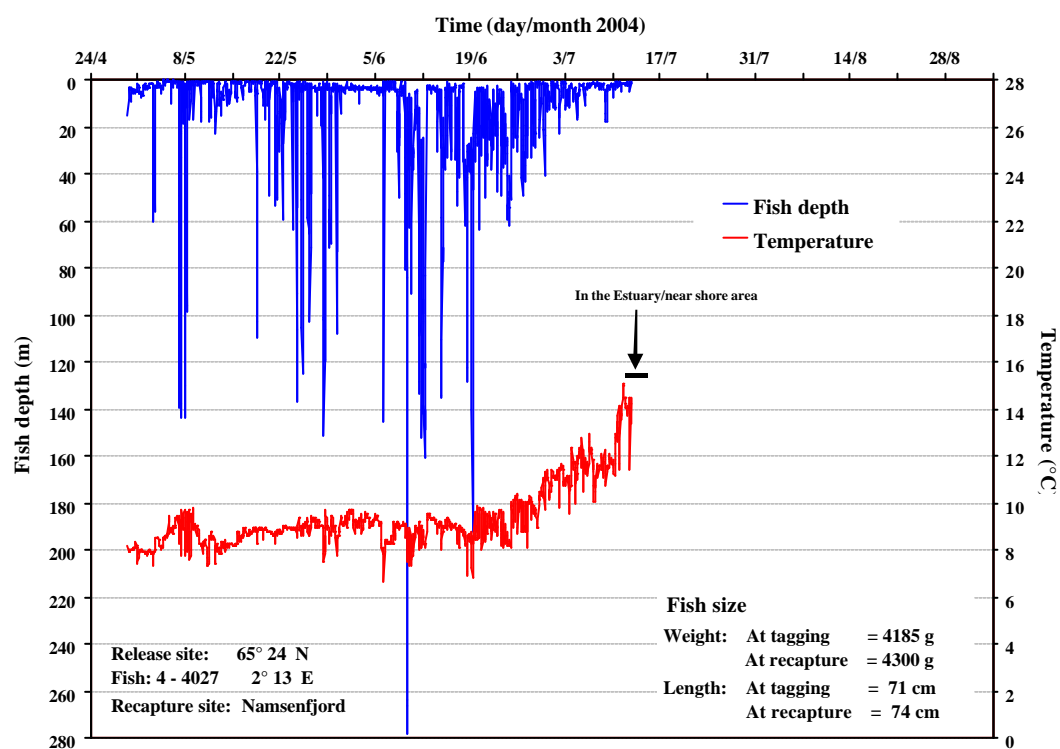
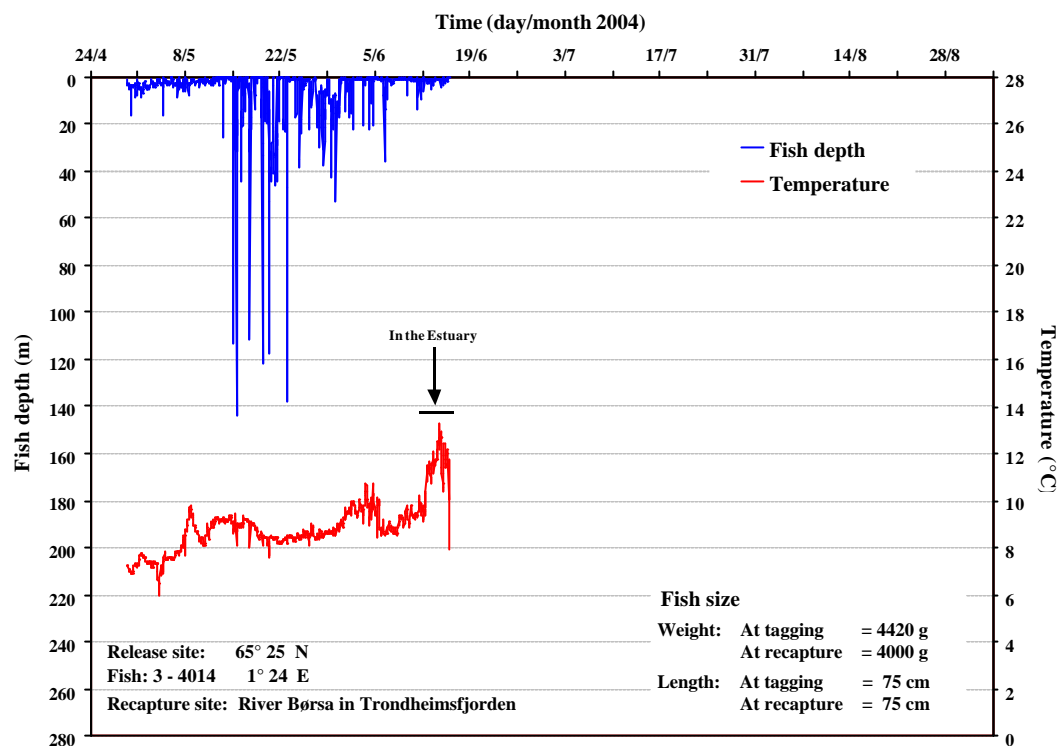


Fig. 2c-d. Depth (upper line/left axis) and temperature (lower line/right axis) profiles for each fish number 3 (c) and 4 (d) with indication of Sea and Estuary/River phase.

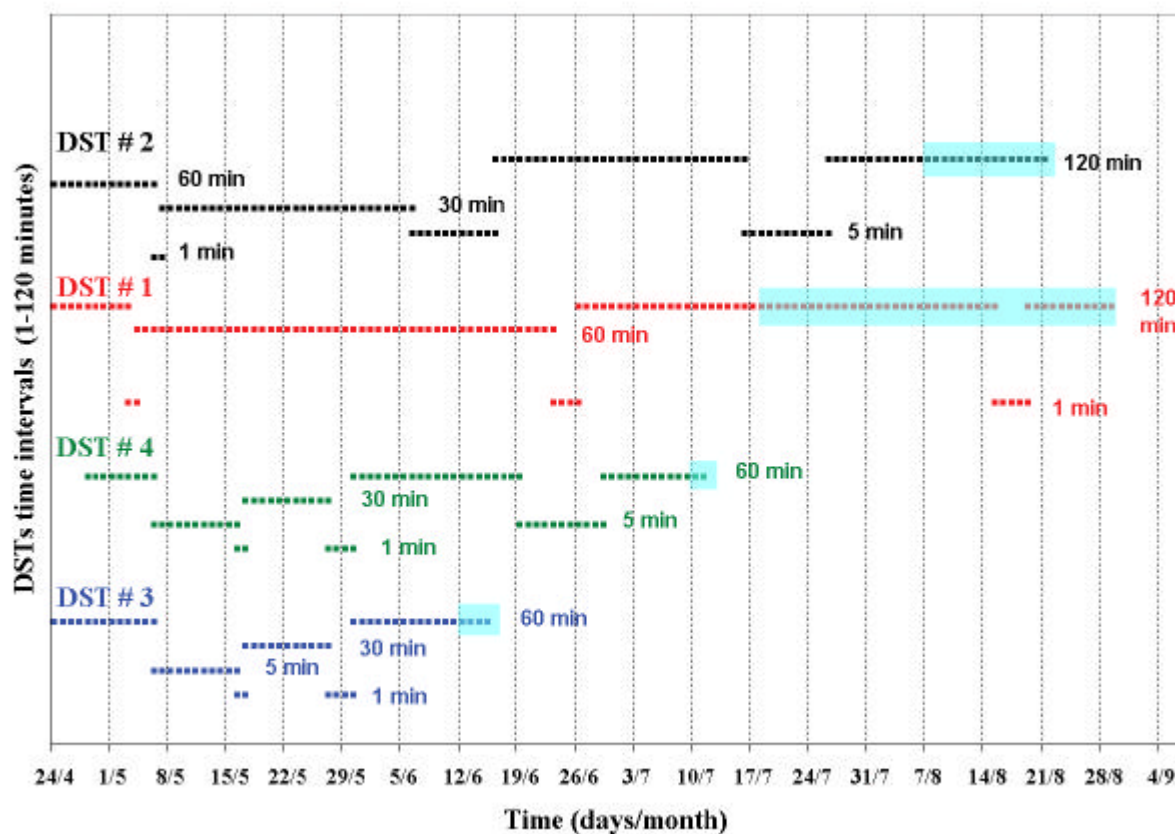


Fig. 2e. Sampling history for each fish, indicating sampling periods with recording rates of 1, 5, 30, 60, and 120 min in the DSTs. The time periods shaded (in light blue) at the end of the timeline of each fish indicates data not used in the present analyses, i.e. data from the coastal/estuary and river phase.

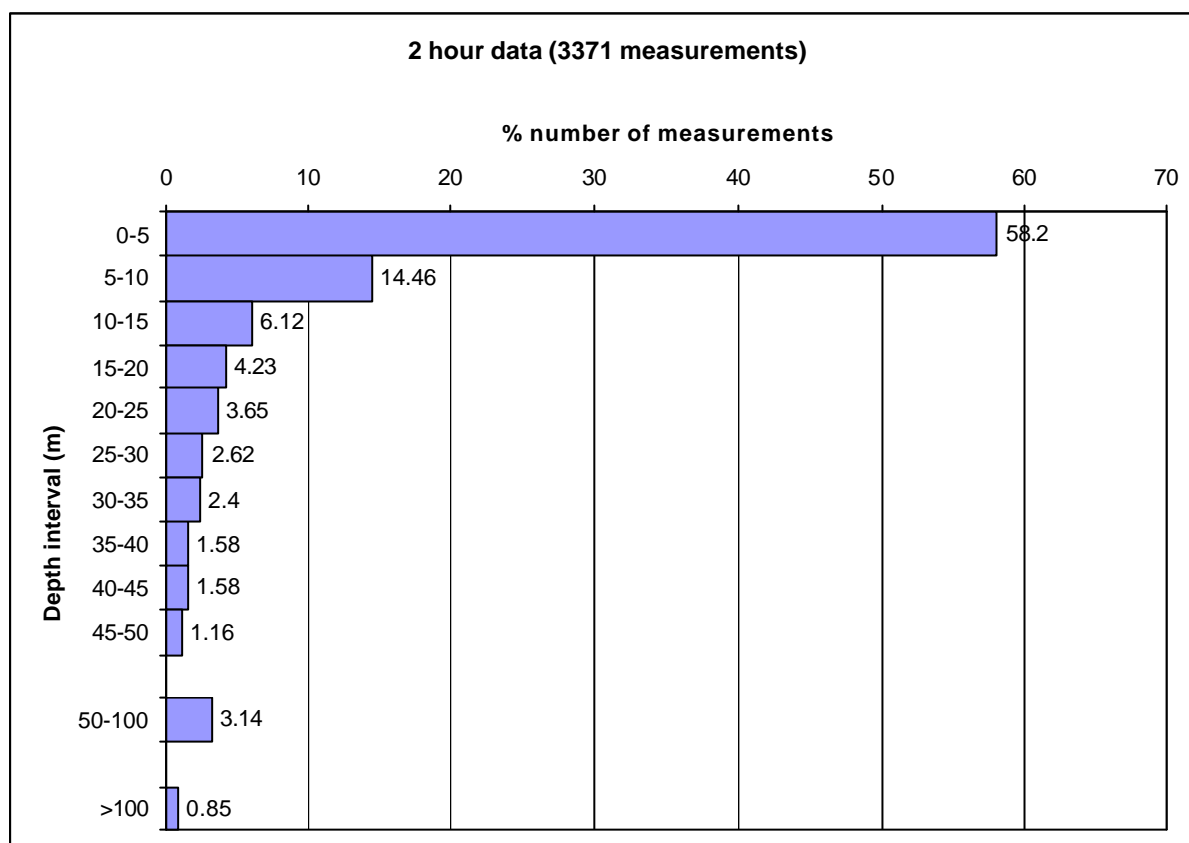


Fig. 3. Depth distribution (% of depth observations) of salmon during sea phase by 5 m intervals down to 50 m, and 50-100 m and deeper than 100 m. Data pooled from all four fish, and from all 120 min observations plus a resampled set from the denser recording intervals to obtain 120 min data, thus obtaining a continuous data series of each fish for their entire oceanic period of liberty (refer to the text and Fig. 2e for a timeline of the various sampling rates).

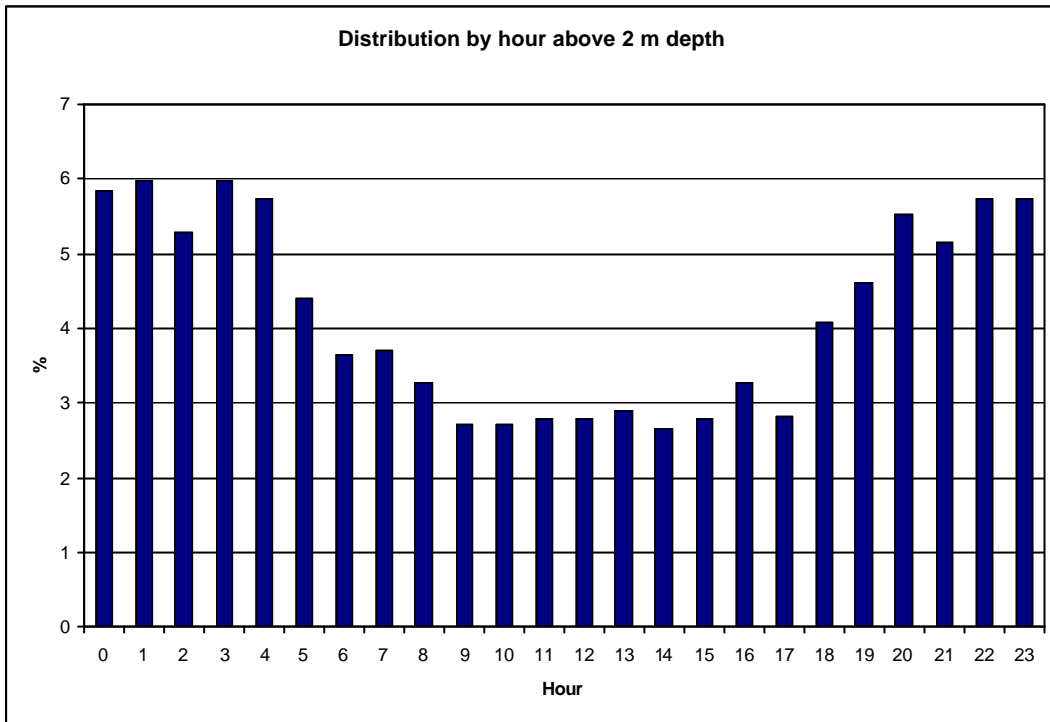


Fig. 4. Diurnal variation (by hour) in the proportion of depth recordings in the upper 2 m. Data pooled from all four fish and from all 60 min observations, and a resample from the denser recording intervals to obtain 60 min data for those as well, but omitting the 120 min data (see Fig. 2e).