

Winter behaviour of riverine anadromous Arctic charr and sea trout in northern Norway

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PREFACE

This study uses two different electronic tracking methods to map the winter migration behaviour of sympatric anadromous Arctic charr and sea trout from northern riverine populations; acoustic telemetry and data storage tags (DST). Originally, the idea was to use only DSTs to map the two species migrations between salt and fresh water. However, as a derivation from a parallel project that aimed to map possible migrations between the River Skibotn and the River Signaldalen for estimation of possible spreading of the parasite *Gyrodactylus salaris* (Rikardsen *et al.* unpubl. data), I was also able to track the migration behaviour of acoustically tagged fish within the Skibotn River parallel to the project using DSTs. In the acoustic tracking project, I concentrated on the migration behaviour of the fish within the river and estuary. There also exist some acoustic data on migrations within the Lyngen Fjord, but these data are not yet completely analysed and are part of another project and therefore not included in the present thesis. The acoustic data obtained from the tracking within the river was used by me in a Degree of Master (one year) of Science in Biology at the University of Gothenburg (Autumn 2007), and is now also accepted for publication in Journal of Fish Biology (“Do northern riverine anadromous Arctic charr and sea trout overwinter in estuarine and marine waters?” by Jensen & Rikardsen). As the data from the acoustic project and the results from the originally planned master project using only DSTs are supplementary to each other, data from both projects are included in this thesis in order to strengthen the documentation of the winter behaviour of the anadromous Arctic charr and sea trout. The use of the acoustic data in the present thesis was also approved by the Norwegian College of Fishery Science. In this thesis, I give more detailed data on the individual’s migration behaviour than was included in the previous thesis and accepted publication.

The wintry west extends his blast
And hail and rain does blaw
Or the stormy north sends driving forth
The blinding sleet and snaw
While, tumbling brown, the burn comes down
And roars frae bank to brae
And bird and beast in covert rest
And pass the heartless day
Robert Burns 1871

Tromsø, May 2008

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SUMMARY

Based on earlier migration studies of lake-dwelling anadromous Arctic charr *Salvelinus alpinus* (L.) and sea trout *Salmo trutta* L. in northern Norway, both species are believed to solely overwinter in fresh water and spend only one to three months in the sea during summer. This is an assumption upon which all current management of the species in the area is based, although no studies have focused on the migration behaviour of the riverine populations of these species in the area. The main objective of the present study was therefore to map the winter migratory behaviour of riverine and sympatric adult anadromous Arctic charr and sea trout in the River Skibotn in northern Norway.

A combination of acoustic telemetry (one year study) and Data Storage Tags (DST) (two year study) were used to track fish migrations between the river, estuary and sea. The acoustically tagged fish were tracked both manually and automatically within the river and estuary, while temperature experienced by the fish were obtained from the recaptured DSTs and used as indicator if the fish had been in fresh or salt water or in the estuary. In total, 30 fish were tagged acoustically and 157 fish tagged with DSTs, where acoustic data was obtained from a total of 9 Arctic charr and 15 sea trout, and temperature preference data from 10 of the recaptured charrs and 22 of the recaptured sea trout.

The results surprisingly showed that large proportions of both the tagged Arctic charr and sea trout descended the river for estuarine and/or marine waters as early as October, with increasing numbers of fish entering the estuary and sea throughout the winter. Both the estuarine and marine waters thus seem to play an important role during overwintering for both species. Fish moved actively between habitats throughout the winter, and there was large individual variation in time of migration and time spent in different habitats. No clear differences between and within species could be detected.

These results thus contradict the earlier assumption that both species solely overwinter in fresh water. The seemingly difference in behaviour between lake-dwelling and riverine populations may be related to the harsh and unstable overwintering conditions within the river (e.g. low water levels and drifting ice) compared to the more stable winter conditions within lakes. The river is regulated for hydropower, which may have affected the behaviour of the fish. However, based on unpublished results from other undisturbed rivers in the area, it is reason to believe that the behaviour observed in the present study may also be common for populations in unregulated rivers. In order to fully verify if this behaviour is common among the northernmost riverine populations, further studies has to be conducted on other northern populations of both species, as well as detailed studies of their habitat use and dispersal at sea during winter.

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1. INTRODUCTION

Seasonal migrations are adaptations to ensure the fine-tuning of growth, survival and reproduction in relation to environmental conditions experienced by the individual (Dodson 1997). Anadromous salmonids are born in freshwater and migrate to sea as juveniles to feed. They achieve the bulk of their growth in the sea, which at high northern latitudes usually has more food resources available than the freshwater habitat where they reproduce (Gross 1987; Thorpe 1994). Three anadromous salmonids are commonly found at high northern latitudes: Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. (hereafter referred to as sea trout) and Arctic charr *Salvelinus alpinus* (L.) (Klemetsen *et al.* 2003). Whereas Atlantic salmon normally makes an oceanic sea migration for 1–5 years before returning to freshwater to spawn (Klemetsen *et al.* 2003), anadromous Arctic charr and sea trout feeds in coastal waters during summer before returning to the freshwater habitat to spawn and overwinter (Berg & Berg 1987; 1988; Johnson 1980; Jonsson 1985; Klemetsen *et al.* 2003; Lyse *et al.* 1998; Pemberton 1976; Rikardsen *et al.* 2000; 2004) or to overwinter as sexually immature individuals (Elliot 1994; Jonsson 1985; Klemetsen *et al.* 2003 Nordeng 1983; Rikardsen *et al.* 1997; 2004).

However, the duration of the marine residency of sea trout seems to vary at different latitudes. Whereas European anadromous Arctic charr are only found north of 65 °N in Norway (Klemetsen *et al.* 2003), European sea trout express anadromous behaviour from 42 °N to their northern limit at 71 °N (Elliot 1994). The southern sea trout populations seem to be variable in the time they spend in the sea versus freshwater (Elliot 1994; Heuch *et al.* 2002; Jonsson & Jonsson 2002; Limburg *et al.* 2001; Pemberton 1976; Sømme 1941), but average residence time in the sea can generally be said to decrease with increasing latitude (L'Abée-Lund *et al.* 1989). From otoliths readings in some sea trout populations from the Baltic Sea, no evidence of a pure freshwater history at all have been detected, indicating that these populations may in fact spawn in brackish water and does not rely on the freshwater habitat during any part of their life-cycle (Limburg *et al.* 2001). In coastal Skagerrak, sea trout are also frequently found in coastal waters during late autumn and winter (Knutsen *et al.* 2004; Olsen *et al.* 2006), a behaviour most likely explained by sea trout originating from small local streams or creeks with poor overwintering conditions (Jonsson *et al.* 2001; Knutsen *et al.* 2004).

Studies of northern populations generally indicate 2–3 months stay on average at sea for sea trout and 1-2 months for Arctic charr (Berg & Berg 1989; 1993; Dempson & Kristoffersen 1987; Klemetsen *et al.* 2003; Kristoffersen *et al.* 1994; Mathisen & Berg 1986; Nilssen *et al.* 1997; Rikardsen *et al.* 1997; 2000). The Vardnes watercourse (approximately 69° 10'N) is one of few northern system where the migratory behaviour of sympatric sea trout and anadromous Arctic charr has been extensively documented (e.g. Berg & Berg 1987; 1988; 1989; 1993). In these studies, the mean sea residency was 68 days (April - September) for sea trout and 48 days for Arctic charr (May - July). In contrast to sea trout, studies of sea residency of anadromous Arctic charr from other parts of the northern hemisphere all indicate that this species migrate to sea for 1-2 months during summer (reviewed by Klemetsen *et al.* 2003). These studies include watercourses such as the Diseth river system on Svalbard, the Nauyuk system in Arctic Canada and Nain and Tikkoatokak in Labrador.

The low temperature in northern waters restricts heterothermic animals' activity and growth potential during winter, thus making them more vulnerable to predation from homeothermic animals (Knutsen *et al.* 2004). Northern anadromous Arctic charr and sea trout that overwinter under ice cover in freshwater lakes or large pools, usually have stable environmental conditions and are usually exposed for a low risk of predation, and a seawards feeding migration during summer when the growth potential is higher thus seems like a good strategy in order to maximise fitness. Both species are also believed to have low salinity tolerance at low water temperatures (Arnesen 1994; Arnesen & Halvorsen 1990; Berg & L'Abée-Lund 1991; Finstad *et al.* 1988; 1989), further restricting them to residency in freshwater during winter.

Based on these facts, northern sea trout, and especially anadromous Arctic charr, have been assumed to solely overwinter in freshwater. However, recently Rikardsen (2004) and Rikardsen *et al.* (2002; 2006) captured sea trout at sea during winter in two fjords in northern Norway. The fish were captured at full strength seawater (salinity 30 – 32) at temperatures as low as 1 – 2 °C. No such published documentation exists for anadromous Arctic charr, although immature individuals of this species was captured in late September in estuarine marine waters of the River Repparfjord in Northern Norway during a gillnet survey (Rikardsen *et al.* 2002). The authors of these reports hypothesised that these fish may have originated from watercourses without lakes, i.e. having a winter behaviour resembling that of more southern populations of sea trout, although this could not be documented in their studies.

There is thus uncertainty about the winter ecology of the northern populations of both these species, and it can be suspected that at least sea trout from riverine populations might reside in marine waters during winter.

Studies on winter feeding ecology of lake-dwelling anadromous Arctic charr populations have shown that they feed little or not at all during winter after their return to freshwater (Boivin & Power 1990; Dutil 1986; Rikardsen *et al.* 2003; Sprudles 1952). Adult sea trout have also been shown to have less appetite than resident individuals after their return to freshwater (Elliot 1997). Furthermore, a unpublished study conducted in Lake Storvatn (70° 39'N) in the Hals watercourse in Northern Norway has indicated that lake-dwelling sea trout, and especially anadromous Arctic charr, remain mostly immobile during parts of the winter and probably rest at the bottom of the lake during most of the winter (A. Rikardsen *et al.* unpubl. data). The reduced feeding combined with the seemingly immobility indicates a low activity level during winter, which corresponds to the fact that fish are heterothermic and their metabolism and thus their activity is reduced at low temperatures (Knutsen *et al.* 2004). Therefore, we can expect that also riverine populations of both species have a low activity and moves little during the winter, especially since the temperature drops to close to the freezing point in the river during winter.

Based on the previously discussed topics, the behaviour of the northern populations of both species can be suspected to resemble each other. The anadromous life-history, the utilization of similar freshwater habitats, the seemingly low activity and feeding when residing in the freshwater habitat during winter, and the coastal migratory feeding pattern are found in both species (Klemetsen *et al.* 2003). Arctic charr are, however, generally found to have a 1-2 month shorter residency in marine waters than the sea trout found at the same latitudes, and they also feed of different prey compared to sea trout when in marine waters (Dempson *et al.* 2002; Grønvik & Klemetsen 1987; Johnson 1980; Knutsen *et al.* 2001; 2004; Lyse *et al.* 1998; Rikardsen *et al.* 2007a). They also seem to utilize different parts of the fjord during summer (Rikardsen *et al.* 2007a; b). Differences in migratory behaviour are also commonly found between the sexes within salmonid species (Jonsson & Jonsson 1993). In the Vardnes watercourse, female sea trout resided longer in marine waters than the males (69.1 and 66.3 days, respectively), whereas the opposite occurred in Arctic charr (females 45.9 days, males 48.8 days) (Berg & Berg 1989; 1993). In the same studies, the duration of freshwater residency was also found to increase with fish length in both species. Although not studied,

such differences in sex and size can also be expected to occur among riverine populations of these species, both between and within the two species.

While previous studies have focused on the ecology of anadromous Arctic charr and sea trout during the parr stage (e.g. Elliott 1994; Jonsson & Jonsson 1993; Rikardsen & Elliott 2000) and the marine feeding phase during summer (i.e. Berg & Berg 1987; 1989; Finstad & Heggberget 1993; Rikardsen *et al.* 2007a), very few studies has focused on the winter ecology of adult sea trout (Knutsen *et al.* 2004; Olsen *et al.* 2006; Rikardsen *et al.* 2006) and, to my knowledge, no published study exist regarding the winter ecology and behaviour of adult European anadromous Arctic charr. Furthermore, almost all studies of the northern anadromous Arctic charr and sea trout has been done on population that originate from watercourses including lakes, despite the existence of several riverine populations of these species in the area.

Huusko *et al.* (2007) recently reviewed the winter ecology of stream salmonids, and state that “despite the common view that conditions in winter strongly influence survival and population size of fish, the ecology of salmonids has not been as extensively studied in winter as in other seasons”, and also that “Investigations in large rivers, regulated and dredged rivers, and under conditions of different ice formations are almost totally lacking”. The finding of sea trout in the marine habitat during winter (Rikardsen 2004; Rikardsen *et al.* 2002; 2006) is surprising and contradicts the earlier studies from the area (e.g. Berg & Berg 1987; 1989; Klemetsen *et al.* 2003; Rikardsen *et al.* 2007a). There is obviously a lack in knowledge on the winter behaviour of these northernmost populations of anadromous Arctic charr and sea trout. While it is now evident that at least some northern populations of sea trout can be found in marine waters during winter and that the species thus have a more complex and flexible marine life history pattern than previously believed, no information exists on the duration of these marine winter migrations, what proportion of individuals within a population migrate, where in the sea the fish resides, and the origin of and reason for migrations to marine waters during winter (Rikardsen *et al.* 2006). No such information exists on Arctic charr during winter. However, if the marine winter migrations of northern sea trout are related to harsh overwintering conditions in the riverine habitat, as suggested by Rikardsen *et al.* (2002; 2006), riverine populations of anadromous Arctic charr could also be expected to be exposed to the same environmental conditions in the riverine habitat, thus affecting their overwintering behaviour.

The aim of this study was therefore, for the first time, to document the seasonal migratory behaviour, and then especially the winter behaviour, of sympatric adult riverine anadromous Arctic charr and sea trout. Both migrations within the river in order to determine behaviour and activity in this habitat, and possible migrations to marine waters were of interest. The River Skibotn in northern Norway house sustainable populations of both anadromous Arctic charr and sea trout, where the anadromous fish has no access to lakes and are regarded as purely riverine populations (Kristoffersen *et al.* 2005). By use of acoustic telemetry and data storage tags that recorded temperature, the following null hypotheses were tested:

H0₁: Both riverine populations of anadromous Arctic charr and sea trout overwinter in the river and migrate to sea during summer

H0₂: The fish has low activity and remains stationary during winter.

H0₃: There is no difference in the seasonal migration behaviour between the two species, as well as between sex and size classes within the species.

2. STUDY AREA

The River Skibotn is located Troms County in northern Norway (69° 19'N; 20 °21'E) (Fig. 1), and has a catchment area of approximately 784 km² with a mean annual flow of about 1800 ls-1. Anadromous fish can migrate about 20 km upstream, were further movement is prevented by several waterfalls (Berg 1964) (Fig. 1). The river has been infected with the parasite *Gyrodactylus salaris* Malmberg since 1979 and Atlantic salmon are to date only occasionally captured in the river (Winger *et al.* in press). The river is dominated by sea trout, but also inhabits a sustainable population of Arctic charr. These species are also found in low numbers in their resident form, and in addition sticklebacks (*Gasterosteus aculeatus* L.), flounder (*Platichthys flesus* (L.)), eel (*Anguilla anguilla* (L.)) and burbot (*Lota lota* (L.)) also inhabit the river (Winger *et al.* in press).

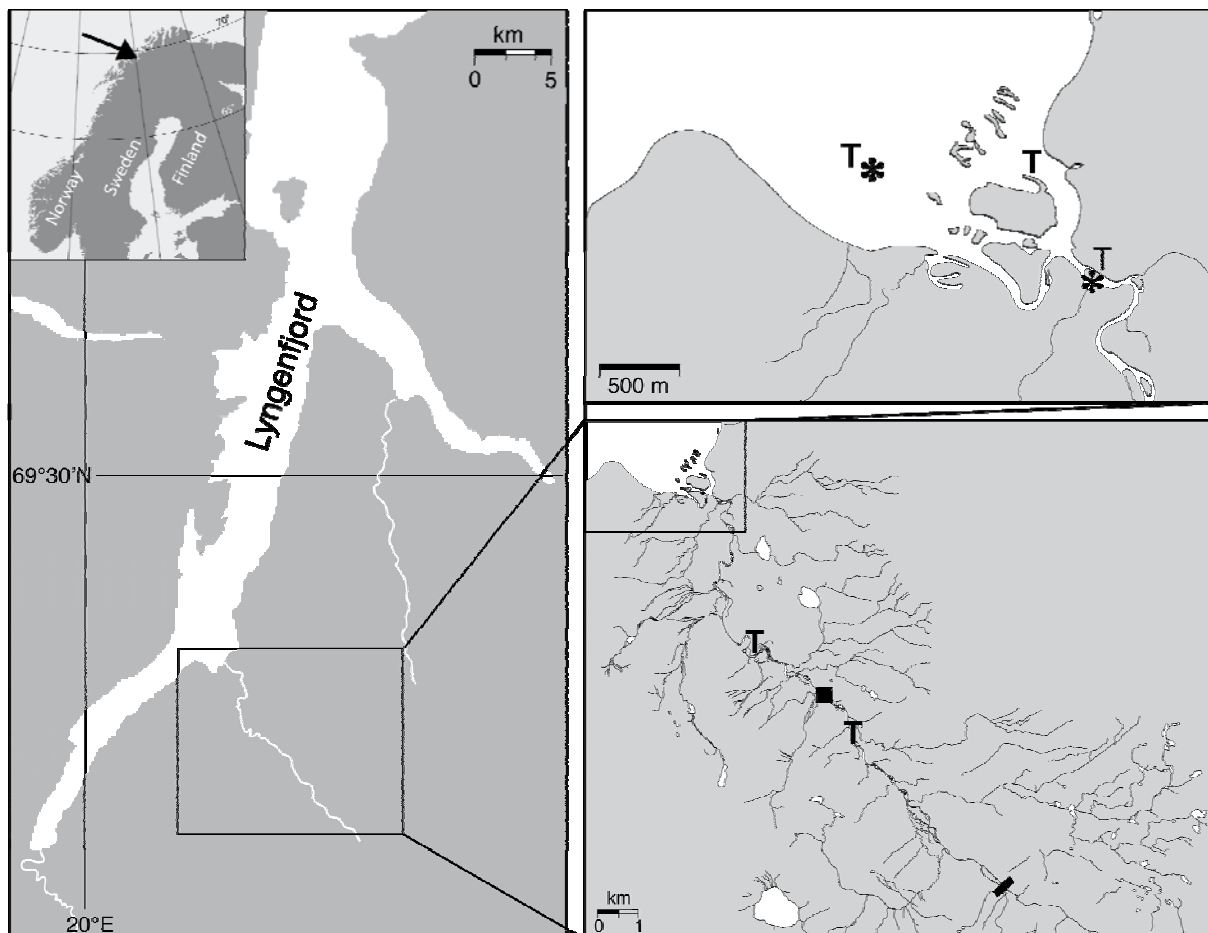


FIG. 1. Map of the study area with the position of the automatic listening stations (*), the positions of temperature loggers (T), the location of the power plant outlet (■) and the migratory barrier (—).

The river is influenced by saltwater about 1.5 km upstream from the seawards boundary at normal tides, and this saltwater influenced area is here defined as the estuary. The depth in the estuary ranges between one and three metres at low tide. The depth increases rapidly outside the estuary. Approximately 100 m from the estuary the depth in the fjord is 50 m, and about 800 m further offshore the fjord has reached its average depth in the area of about 100 m. The first 1.5 km of river upstream from the estuary has fine grained substratum which makes it unsuitable for spawning, while the remaining part of the anadromous stretch of river has substratum consisting of bigger rocks and gravel. There are several pools of different sizes up to maximum 300 m in length and 5 m depth.

The river has been regulated for hydropower since 1980, and the outlet is located about 10 km upstream from the estuary (Fig. 1). Water is led to the power plant from lakes located upstream from the anadromous stretch of the river, leaving the area upstream from the power plant outlet with a reduced discharge. The power plant also influences the temperature and ice regime of the river by releasing water that is warmer (fluctuated from 0–2 °C during winter 2005–2006) than in the main river upstream from the power plant (0 °C). The river below the power plant is thus mixed with slightly warmer water from the power plant and therefore remains partly ice free during winters with average seasonal temperatures. The River Skibotn drains into the Lyngenfjord (Fig. 1), which also house two other rivers of similar size as the River Skibotn; the River Signaldal in the bottom of the Lyngenfjord (about 30 km south of River Skibotn), and the River Mandal (about 40 km north east of River Skibotn), in addition to multiple rivers of smaller size.

The temperature in the river and sea was continuously recorded throughout the two year study period by placing temperature loggers (iB-tags, see chapter 3.1) set to record temperature every fourth hour in the different habitats. Temperature was recorded upstream (Upper River) and downstream (Main River) from the power plant in the river (Fig. 1), and on several locations from the innermost to the outermost parts of the fjord. The temperature in the river above the power plant was stable around zero degrees from October to April (Fig. 2), and also completely covered with ice during this time. The temperature beneath the power plant fluctuates in relation to the regime of the power plant. River temperature was measured about 7 kilometres upstream from the estuary from the beginning of October 2005 to mid September 2006 and about 300 m upstream from the estuary from mid September 2006 to the end of August 2007. The river temperature beneath the power plant was lower during the second

year (Fig. 2), possibly due to the location of the temperature recordings. Ice conditions beneath the power plant were monitored during winter from 2006-2007, and during this period no complete ice cover was observed from the power plant outlet and about 4 km downstream, and the entire stretch beneath the power plant remained open until end of January. Ice formed in non-rapid stretches of river from 4 km downstream from the power plant to the estuary in the beginning of February, and remained until mid March. The Sea temperatures measured at different locations in the fjord correlated well to the temperature measured in salt water at three metres depth approximately 100 m outside the estuary, and were higher than the temperature in the river from November to April (Fig. 2).

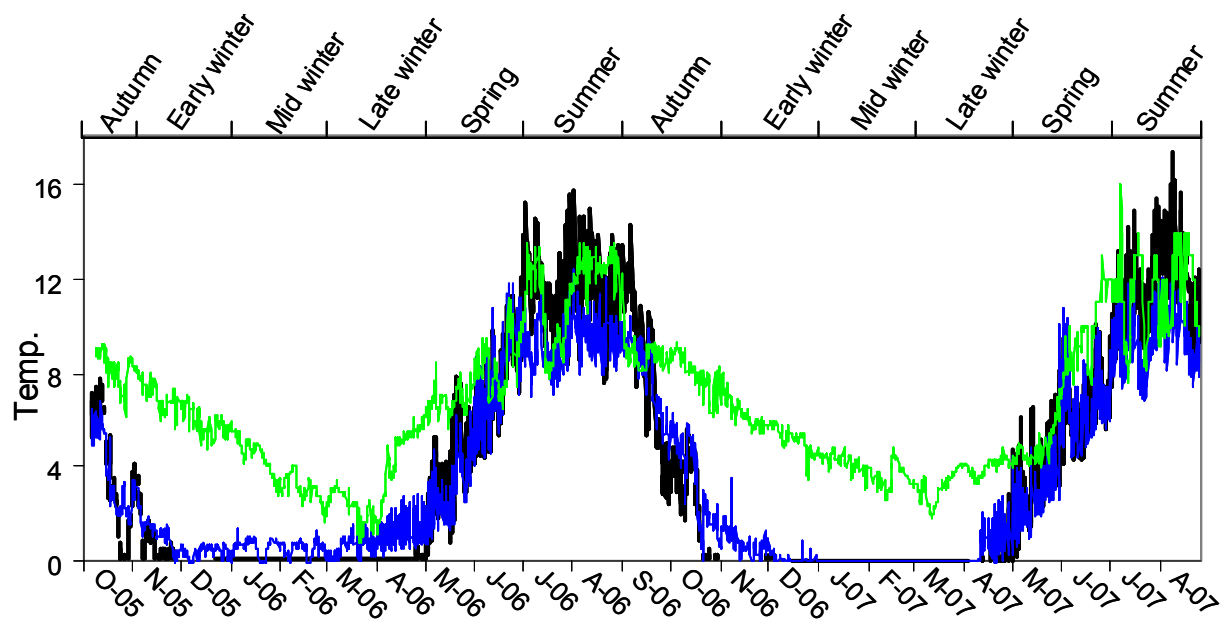


FIG. 2. Temperature recordings in the upper river (—), the main river (—), and the sea (—) from October 2005 to August 2007, also showing the definitions of seasons used in the present study.

The different seasons were defined according to time of spawning and also to the temperature in the river and sea. *Autumn* was defined to be the time when fish spawned (September and October), *winter* as the months when the temperature in the river above the power plant was close to zero (November to April), *spring* as the period with increasing temperature in all habitats (May and June) and *summer* as the months with the highest temperature in all habitats (July and August). In addition, the winter was divided into *early winter* (November and December), *mid winter* (January and February) and *late winter* (March and April) to simplify discussions on winter behaviour (Fig 2).

In the estuary, temperature (measured about 900 m from the seawards boundary) was recorded from the beginning of October 2006 to the end of August 2007. The water

temperature in this area was measured at the river bed and fluctuated according to the tide. It corresponded well to the river temperature at low tide and sea temperature at high tide (Fig. 3). Except for three brief periods with spring tides in early and mid winter, there was a diurnal influx of saltwater in the area (Fig. 3). The bottom of the estuary is thus clearly dominated by saltwater twice a day at high tides and freshwater at low tides. Salinity was also measured once about 100 m outside the estuary at high tide in mid October 2006, where the surface water was found to have a salinity of 23.9, while the salinity was 32.6 from 1 to 15 m measured with 1 m intervals. Since the power plant is generally run at a low discharge during the winter months, the conditions in the estuary are here supposed to resemble the ones measured in mid October throughout the winter.

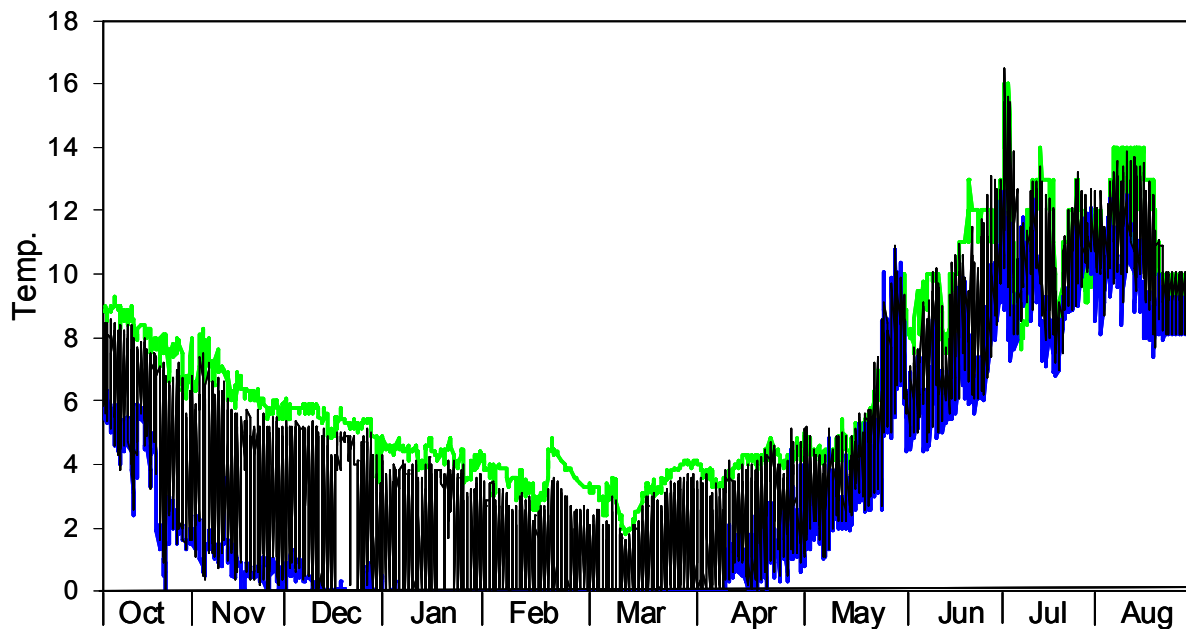


FIG. 3. Temperature recorded in the tidal-zone (—) in relation to the temperature in the main river (—) and sea (—) from October 2006 until August 2007.

3. METHODS

In order to map the migration behaviour of fish, a combination of data storage tags (DSTs) and acoustic telemetry were used during the period from 2005-2007. The acoustically tagged fish were tracked both manually and automatically within the river and estuary, while temperature experienced by the fish were obtained from the recaptured DSTs and used as indicator if the fish had been in fresh, brackish or salt water throughout the year.

3.1 Telemetric methods and tag specification

Telemetry is an excellent method to study individual migration behaviour of animals in their natural environment with no need of handling or visual recognition during data sampling, thus with no or minimal influence on the animal's behaviour (Cooke *et al.* 2004). In the present study, two different methods of telemetry were used, acoustic telemetry and data storage tags (DST). In acoustic telemetry, the tags attached to the animal send out individually coded acoustic signals at defined intervals that can be detected with the manual or automatic listening devices that make it possible to locate the position of the individual within a certain range (usually maximum 500-600 m in saltwater depending of transmitter signal strength and environmental parameters (Thorstad *et al.* 2000)). In this study, the acoustic tag only gave the horizontal distribution of the fish. Although not used in the present project, some acoustic tags can in addition also give information on other parameters, like depth, hart rate, body temperature etc. (Cooke *et al.* 2004), but such tags were not used in the present study.

The acoustic tags used in this study were in two sizes; 9 x 23.5 mm (type MP9 long, www.thelma.com) with a mass of 5 g in air (3 g in water), and 13 x 26 mm (type MP13) with a mass of 9 g in air (6 g in water). The lifetime of the battery of the tags was guaranteed for 359 and 625, respectively. The tags send out individually coded signals at random intervals ranging between 20 and 60 s, to avoid code collisions when more than one fish were within the range of a receiver. Acoustically tagged fish were manually tracked from the outlet of the power plant to the estuary by drifting down the river in a rubber boat equipped with an acoustic receiver (VR60, www.vemco.com). This was done approximately every third week from early October to mid-November (after spawning) and once a month during most of the period from mid-November to the beginning of May. However, due to an unusually cold February (average temperature 6.2 °C lower than the average temperature during the previous 10 years calculated from data at www.met.no) during the study period, the lower parts of the

river was partially covered with ice from late January to mid March, and the tracking was postponed in areas that could not be reached.

The riffles between the pools prevented the echo of the tag to be detected below or above the pools, which made it possible to determine the exact pool where the fish was located. Upstream from the power plant tracking was performed from the river bank prior to and after ice formation. Tracking was also performed once in January under the ice in the deepest pools in the area upstream from the power plant by use of an ice drill. In order to continuously track fish movement in and out of the river, one automatic listening station (ALS) (VR2, www.vemco.com) was placed about 1.8 km upstream from the outer boundary of the estuary, with a second one in salt water about 100 m outside the estuary

In contrast to the acoustic tags, the DSTs records one or several parameters (e.g. temperature, depth, salinity, light etc.) which are stored within the tag as a function of time (Cooke *et al.* 2004). When a tag is recaptured, the data can be downloaded. In this study, the main parameter recorded by the DST was temperature. Since the temperature usually differs in fresh and marine waters (Fig. 2), the temperature stored in the tag attached to the fish could be used to estimate which of the two habitats the fish had used over time. In order to verify this, some fish were also tagged with DSTs that in addition to recording temperature, also recorded depth and salinity (CTD-tags) preference by the fish. However, these tags were mainly used to test the salinity preference of Arctic charr related to another ongoing project. Therefore, the temperature recordings from that study are included in this study, whereas the salinity recordings are merely used as a demonstration that the temperature recorded by the individual fish in fresh, brackish and salt water is in fact related to actual shifts between habitats estimated from the temperature profiles (appendix I). The DSTs used in this study were mainly of the type *iBCod* (44 x 12 mm with a mass of 11 g in air [-5.4 g in water], www.alphamach.com) and *iBBass* (29 x 18 x 8 mm with a mass of 4.7 g in air [-1 g in water]), programmed to record temperature every 4 h. In addition, 47 CTD-tags (15 x 46 mm with a mass of 19 g in air [12 g in water], www.star-oddi.com) were used to record temperature, depth and salinity every 30 min. Tags were calibrated prior to tagging and after recapture by placing them for 24 h set to record every 10 min in a mixture of water and ice (0 °C).

The benefit of using DSTs that measure only temperature is that these tags are inexpensive (c. 400 NOK) compared to the more expensive DSTs that measures several parameters (usually

2000 – 6000 NOK), as well as the acoustic tags (1500-2500 NOK) that in addition needs expensive receivers.

3.2 Tagging

3.2.1 Fish capture

Fish were caught in pools in the River Skibotn using a combination of snorkelling and multifilament gillnets (mesh size 35-60 mm). After the fish was observed by snorkelling, the gillnet was stretched across the river by two persons and slowly drifted downstream. At the outlet of the pool one person crossed the river and the fish were caught in a loop that was dragged close to land. The net was thus used as a dragnet. The fish were gently removed from the net and placed in a cage. Fish were caught during or close in time to spawning when the skin of anadromous salmonids is thick (Stoklosowa 1970), and few physical damages due to the gillnets were observed. The fish were stored in cages and the capture procedure was often repeated until few or none fish were caught in the pool, to prevent tagged fish from being entangled in the net after release.

3.2.2 Tagging procedure

The acoustic tags were surgically implanted into the body cavity after a method previously described in e.g. Jepsen *et al.* (2002) and Rikardsen & Thorstad (2006). During tagging, the fish was placed with the ventral side up in a tube and was partially submerged during operation. An incision just large enough to pass the transmitter, approximately 1.5 cm long, was made on the ventral surface halfway between the pectoral and pelvic fins using a scalpel. The tag was inserted into the body cavity through the incision, and the wound was closed by two or three independent un-dissolving sutures (Eticon 2-0, Belgium). In order to identify the tagged fish, they were also tagged externally with a modified Carlin tag (www.floytag.com) with an individual number and address. These tags were attached by pushing two hollow needles through the dorsum of the fish 1-2 cm below the dorsal fin. The attachment wire was pushed through the needles and twisted to closure on the opposite side after removal of the needles. Fish less than *c.* 1000 g were equipped with MP 9L tags, while larger fish were equipped with MP 13S.

In 2005, all DSTs were attached externally to the fish by pushing two hollow needles through the dorsum of the fish 1-2 cm below the dorsal fin. The spacing between the needles matched

the length of the tag. The attachment wire was pushed through the needles and twisted to closure on the opposite side after removal of the needles. A plastic plate was used on the opposite side of the tag to prevent erosion of the flesh by the attachment wire. In 2006 the iB-tags were surgically implanted in the body cavity after the method previously described, while the CTD-tags were externally attached to the fish.

All fish was anaesthetised prior to tagging by the use of 2-Phenoxyethanol (Sigma-Aldrich) and length, weight, sex and sexual maturation was determined. After tagging, the fish was returned to the river and monitored until seemingly normal behaviour and then released. Total handling time, including anaesthesia, was 5-9 minutes for internal tagging and 4-6 minutes for external tagging. Recovery to seemingly normal behaviour took 2-10 minutes. Prior to each tagging, surgical equipment was rinsed in 96 % ethanol. The mass of the tag in air was less than two percent of the mass of the fish, a value that has generally been used as a rule of thumb not to have any big impact on the fish behaviour (Cooke *et al.* 2004; Jepsen *et al.* 2002; 2004).

3.3 Material

The fish were captured and tagged on spawning areas close in time to spawning. Females and males seemed to differ in the timing of migration to spawning areas, and there was therefore a skewed distribution in number of females versus males tagged. In total, more female than male sea trout were tagged, whilst more male than female Arctic charr were tagged (Table 1).

3.3.1 Acoustically tagged fish

Sixteen sea trout [mean fork length 597 mm (298 – 820 mm), mean mass 3300 g (300 – 6900 g)] and fourteen Arctic charr [mean fork length 432 mm (375 – 501 mm), mean mass 1120 g (570 - 1370 g)] were tagged with acoustic transmitters between 15 September and 11 October 2006 (Table 1). In total, 15 (94 %) of the 16 tagged sea trout and 9 of the 14 (64 %) tagged Arctic charr were detected on multiple occasions during the manual and automatic tracking. Two tags from Arctic charrs were recorded but remained stationary during the study period. The two locations were checked by snorkelling and no fish were found. These two fish and three other Arctic charr and one sea trout that were never registered were deleted from the study.

TABLE I. Different characteristics of the acoustically tagged fish; including sexual maturity at tagging (status), fork length (L_F) and mass at tagging, # dist. = distance (km) from outer boundary of the estuary to the tagging location. Fish without individual number were never recorded during the study period after tagging.

Species	Fish no.	Sex	Status	L_F (mm)	Mass (g)	Tagging date	# dist.	
Trout	1		Immature	298	300	17.9.2006	9.3	
	2		Immature	810	6780	17.9.2006	9.3	
	3		Immature	600	2820	17.9.2006	9.3	
	4	Female	Mature	685	4100	17.9.2006	10.1	
	5	Female	Mature	622	3060	17.9.2006	9.3	
	6	Male	Mature	580	3360	17.9.2006	9.3	
	7	Female	Mature	613	2360	17.9.2006	9.3	
	8	Female	Mature	670	3740	17.9.2006	9.3	
	9	Male	Mature	703	4170	17.9.2006	10.1	
	10	Female	Mature	600	2450	15.9.2006	14.2	
	11	Female	Mature	565	2150	15.9.2006	14.2	
	12	Male	Mature	480	1380	17.9.2006	9.3	
	13	Male	Mature	550	1900	15.9.2006	14.2	
	14	Male	Mature	413	830	15.9.2006	14.2	
	15	Male	Mature	538	1720	15.9.2006	14.2	
		Female	Mature	820	6900	16.9.2006	14.2	
Charr	16		Immature	410	750	11.10.2006	7.3	
	17		Immature	405	630	12.10.2006	7.3	
	18	Female	Mature	410	840	18.9.2006	8.6	
	19	Male	Mature	379	580	15.9.2006	14.2	
	20	Male	Mature	375	570	15.9.2006	14.2	
	21	Male	Mature	501	1370	18.9.2006	8.6	
	22	Female	Mature	405	760	18.9.2006	8.6	
	23	Male	Mature	500	1240	18.9.2006	8.6	
	24	Male	Mature	487	1120	19.9.2006	8.6	
			Female	Mature	425	790	15.9.2006	14.4
			Male	Mature	412	690	15.9.2006	14.2
			Male	Mature	475	1240	18.9.2006	8.6
			Female	Mature	395	690	18.9.2006	8.6
		Male	Mature	465	960	18.9.2006	14.2	

3.3.2 Fish tagged with data storage tags

Fifty seven sea trout were tagged with DSTs between 25 September and 8 October in 2005, and 39 sea trout between 15 September and 11 October in 2006. Thirty eight of the tags used in 2005 were iB-tags, whereas nineteen of the tags were CTD-tags. All tags used to tag sea trout in 2006 were iB-tags (Table 2). Twenty six Arctic charr were tagged with DSTs between 25 September and 8 October in 2005 and 35 between 15 September and 11 October in 2006. Six iB-tags were used in 2005, whereas 20 of the tags were CTD-tags. In 2006, 27 iB-tags and eight CTD-tags were used to tag Arctic charr (Table 2).

TABLE 2. Fish tagged with DSTs in 2005 and 2006, including type of tag (iB & CTD), number of tagged fish in each category, average fork length LF with s. d., sex (♀ & ♂) and sexual maturity (∞ are immature, remaining mature).

		Trout				Charr			
		iB		CTD		iB		CTD	
		No. tagged	$LF \pm$ s.d. (mm)	No. tagged	$LF \pm$ s.d. (mm)	No. tagged	$LF \pm$ s.d. (mm)	No. tagged	$LF \pm$ s.d. (mm)
2005	♀	21	620 \pm 9.2	8	675 \pm 10.1	3	411 \pm 4.0	9	486 \pm 5.1
	♂	11	565 \pm 12.3	11	694 \pm 10.4	3	396 \pm 0.5	11	452 \pm 4.7
	∞	6	468 \pm 2.7						
	Tot.	38	580 \pm 10.8	19	686 \pm 10	6	404 \pm 2.7	20	467 \pm 5.1
2006	♀	19	664 \pm 9.2			2	492 \pm 13.9	1	425
	♂	12	581 \pm 9.2			24	412 \pm 4.3	6	473 \pm 2.6
	∞	8	571 \pm 11.6			1	292	1	439
	Tot.	39	619 \pm 10.4			27	414 \pm 5.8	8	463 \pm 3.0

The DST-tagged fish were recaptured by use of two methods; by returns from local fishermen and anglers and by gillnetting in the river the following autumn. Returns of tags were rewarded with 500 NOK. Length, weight, sex, degree of maturation and age (estimated from otoliths) were recorded whenever possible. However, many of the fish recaptured by local anglers were gutted or eaten before reported as recaptured. In addition, two tags were found on the river beach with bite marks indicating predation by European otter *Lutra lutra* (L.). Estimation of growth, diet and maturity at recapture could thus not be performed. Twenty one out of the 58 trout tagged in 2005 (36%) and 11 out of the 39 trout tagged in 2006 (35%) were recaptured, leaving a total of 33% recaptures during the two year study period. The corresponding numbers for Arctic charr were 8 out of 26 for fish tagged in 2005 (31%) and 14 out of 35 for fish tagged in 2006 (40%), in total 36% during the study period. Four recaptured tags malfunctioned for fish tagged in 2005 (three trout and one charr) and four tags for fish tagged in 2006 (only trout). In addition, two recaptured sea trout and ten Arctic charr rejected the tags through the incision wound or through the flesh on the ventral surface of the belly. This left us with data from a total of 18 sea trout in 2005 (31% out of the tagged trout), four sea trout in 2006 (10% out of the tagged trout), seven Arctic charr in 2005 (27% out of the tagged charr) and four Arctic charr in 2006 (11% out of the tagged charr). One of the charr recaptured in 2007 (Charr no. 2289) were however excluded from the results, as it was recaptured in late August and was very skinny and heavily infected with fungus. The tag showed that the fish had spent the whole winter, spring, and most of the summer in the river. Data could thus be retrieved from 23% of the tagged sea trout and from 16% of the Arctic charr. Characteristics of recaptured fish and tag fate are given in Table 3.

TABLE 3. Characteristics of the recaptured fish, including sexual maturity (status), fork length (L_F) and mass at tagging

Species	Fish no.	Tagging date	Method	Recapture date	Recapture method	Tag/data fate	Sex	Status	L_F (mm)	Mass (g)	
Charr	18	25.09.2005	Externa	03.09.2006	Fieldwork	Recovered	Male	Spent	391	605	
	23	25.09.2005	Externa	08.10.2006	Fieldwork	Recovered	Male	Mature	433	728	
	56	18.09.2006	Internal	10.06.2007	Rod	Recovered	Male	Mature	487	1115	
	74	18.09.2006	Internal	23.06.2007	Rod	Recovered	Male	Mature	405	504	
	2289	08.10.2005	Externa	31.07.2006	Rod	Recovered	Female	Spent	460	770	
	2375	25.09.2005	Externa	15.07.2006	Rod	Recovered	Female	Spent	467	917	
	2385	25.09.2005	Externa	20.05.2006	Predation	Recovered	Male	Spent	395	641	
	2388	25.09.2005	Externa	23.06.2007	Rod	Recovered	Male	Spent	500	1255	
	2396	25.09.2005	Externa	02.09.2006	Fieldwork	Recovered	Male	Spent	515	1348	
	3073	11.10.2006	Externa	19.06.2007	Rod	Recovered	Male	Spent	470	986	
	3084	11.10.2006	Externa	14.05.2007	Rod	Recovered	Male	Spent	465	869	
	-	25.09.2005	Externa	27.07.2006	Rod	Malfunction	Male	Spent	396	632	
	-	18.09.2006	Internal	10.09.2007	Fieldwork	Rejected	Male	Mature	475	1236	
	-	18.09.2006	Internal	01.06.2007	Rod	Rejected	Male	Mature	388	547	
	-	18.09.2006	Internal	15.09.2007	Fieldwork	Rejected	Male	Mature	371	524	
	-	18.09.2006	Internal	15.09.2007	Fieldwork	Rejected	Male	Mature	400	-	
	-	18.09.2006	Internal	29.07.2007	Rod	Rejected	Male	Mature	397	-	
	-	18.09.2006	Internal	08.07.2007	Rod	Rejected	Male	Mature	355	-	
	-	18.09.2006	Internal	03.06.2007	Rod	Rejected	Male	Mature	378	-	
	-	17.10.2006	Internal	16.09.2007	Fieldwork	Rejected	Male	Spent	415	764	
	-	11.10.2006	Internal	15.09.2007	Fieldwork	Rejected	Male	Spent	397	579	
	-	11.10.2006	Internal	25.09.2007	Fieldwork	Rejected	Female	Spent	425	697	
	Trout	1	30.09.2005	Externa	25.06.2007	Rod	Recovered	Female	Spent	540	1636
		9	08.10.2005	Externa	15.05.2006	Rod	Recovered	Female	Spent	727	-
		19	25.09.2005	Externa	06.05.2006	Rod	Recovered	Male	Mature	438	899
27		25.09.2005	Externa	08.10.2006	Fieldwork	Recovered	Female	Mature	464	1123	
28		30.09.2005	Externa	01.08.2006	Net	Recovered	Female	Spawning	680	3436	
29		26.09.2005	Externa	03.05.2006	Rod	Recovered	Male	Immature	538	1640	
31		25.09.2005	Externa	08.10.2006	Fieldwork	Recovered	Female	Mature	554	1919	
32		30.09.2005	Externa	15.08.2006	Rod	Recovered	Female	Spawning	590	2074	
34		30.09.2005	Externa	19.06.2006	Rod	Recovered	Male	Mature	645	3300	
41		30.09.2005	Externa	27.06.2006	Net	Recovered	Male	Mature	515	1600	
42		26.09.2005	Externa	09.07.2006	Predation	Recovered	Male	Mature	775	c. 5500	
46		30.09.2005	Externa	11.09.2007	Fieldwork	Recovered	Female	Mature	730	3530	
48		30.09.2005	Externa	29.08.2006	Fieldwork	Recovered	Female	Mature	644	3500	
20		11.10.2006	Externa	19.06.2007	Net	Recovered	Male	Mature	497	1323	
68		17.09.2006	Internal	27.05.2007	Rod	Recovered	Female	Mature	628	2940	
89		17.09.2006	Internal	14.04.2007	Net	Recovered	-	Immature	810	6780	
244		11.10.2006	Internal	15.09.2007	Fieldwork	Recovered	Female	Mature	823	c.4500	
2284		08.10.2005	Externa	04.02.2006	Net	Recovered	Male	Mature	554	1850	
6411		30.09.2005	Externa	08.10.2006	Fieldwork	Recovered	Female	Mature	812	c.7500	
6336		30.09.2005	Externa	11.04.2006	Rod	Recovered	Female	Mature	570	2435	
6527		30.09.2005	Externa	18.05.2007	Rod	Recovered	Female	Mature	742	4120	
7628		08.10.2005	Externa	17.09.2006	Fieldwork	Recovered	Male	Mature	755	-	
-		26.09.2005	Externa	08.10.2006	Fieldwork	Malfunction	-	Immature	483	1255	
-		26.09.2005	Externa	23.09.2007	Fieldwork	Malfunction	-	Immature	431	790	
-		30.09.2005	Externa	08.10.2006	Fieldwork	Malfunction	Female	Spent	735	390	
-		17.09.2006	Internal	04.02.2006	Net	Malfunction	Male	Mature	638	2937	
-		17.09.2006	Internal	01.12.2007	Rod	Malfunction	Female	Mature	693	4035	
-		17.09.2006	Internal	06.06.2007	Rod	Malfunction	Female	Mature	670	3740	
-		17.09.2006	Internal	02.08.2007	Net	Malfunction	Female	Mature	628	2940	
-		17.09.2006	Internal	24.09.2007	Fieldwork	Malfunction	Female	Mature	685	4100	
-		11.10.2006	Internal	12.04.2008	Rod	Rejected	Male	Mature	535	1517	
-		11.10.2006	Internal	09.08.2007	Rod	Rejected	-	Immature	501	1490	

3.5 Data analyzes and statistical methods

The temperature profiles recorded by the DSTs on the recaptured fish were graphically related to the temperature recorded in the main river and sea in order to estimate their habitat use over time (appendices II & III). From the graphs, fish could easily be defined to be in either river or sea as long as they remained in a habitat for minimum a day (six temperature recordings). However, during the summer months (July and August) the temperature was less diversified between fresh and salt water than during winter and spring (November to June). The fluctuation in temperature on daily basis were larger in the river than in the sea during the summer months, and this difference in magnitude of fluctuations were used to determine which habitat the fish had been utilizing during the summer. In addition, the salinity data from the CTDs were graphically checked against the temperature recordings, to make sure the difference in temperature actually reflected shifts in habitat.

In order to determine when the fish was localized in the estuary, the variance in the six measurements recorded per day were used. A variance four times bigger than the variance recorded in the river and sea at a given day was found to correlate to the salinity data from the CTD-tags and was therefore used as definition of estuary use. This was mainly done to avoid defining fish as being in the estuary when they found different temperatures in the river and especially in the sea. To further verify the use of estuarine waters, the temperature recordings from fish were checked and found to correspond to the high and low tides recorded in the estuary. Average time spent in estuarine and marine waters during winter, date of first entry into the estuary and sea, and number of shifts in habitat during winter was analyzed to detect differences between the two species, and also between sexes within species. Fish were also divided into large (> 60 cm for sea trout, > 45 cm for arctic charr) and small individuals (< 60 cm for sea trout, < 45 cm for arctic charr), to detect if size could be a possible explanatory variable for differences within a species. Statistical analyzes were performed in Excel, using a single factor ANOVA.

4. RESULTS

4.1 Movements within the river

Of the recorded acoustically tagged fish, all sea trout except one (Trout no. 15) were registered on the ALS in the estuary between 22 September and 19 February (Fig. 4). Trout no.15 had not left the river during the last manual tracking day in late April. Twelve of the 14 sea trout were recorded in the estuary before 22 December, whereof minimum seven individuals (47 %, Trout no. 1, 4, 5, 6, 9, 10 and 13) returned to fresh water for periods after their first entry to the estuary. The longest return migration recorded was about 6.5 km upstream from the estuary (Fig. 4).

When comparing sea trout tagged above and below the power plant, it seems like the sexually mature sea trout tagged upstream from the power plant descend to the estuary later than the sea trout tagged below the power plant (Fig. 4). However, due to the low number of fish, this correlation turns out merely anecdotal. The three immature sea trout tagged (Trout no. 1, 2 and 3) seem to resemble the mature fish in migratory behaviour (Fig. 4).

All of the nine recorded Arctic charr were registered in the estuary between 10 October and 15 December (Fig. 5). Minimum two Arctic charr (22 %, Charr no. 20 and 21) returned to the river after their first recording in the estuary. The two immature Arctic charrs tagged (Charr no. 15 & 16) seem to resemble the mature fish in migratory behaviour (Fig. 5).

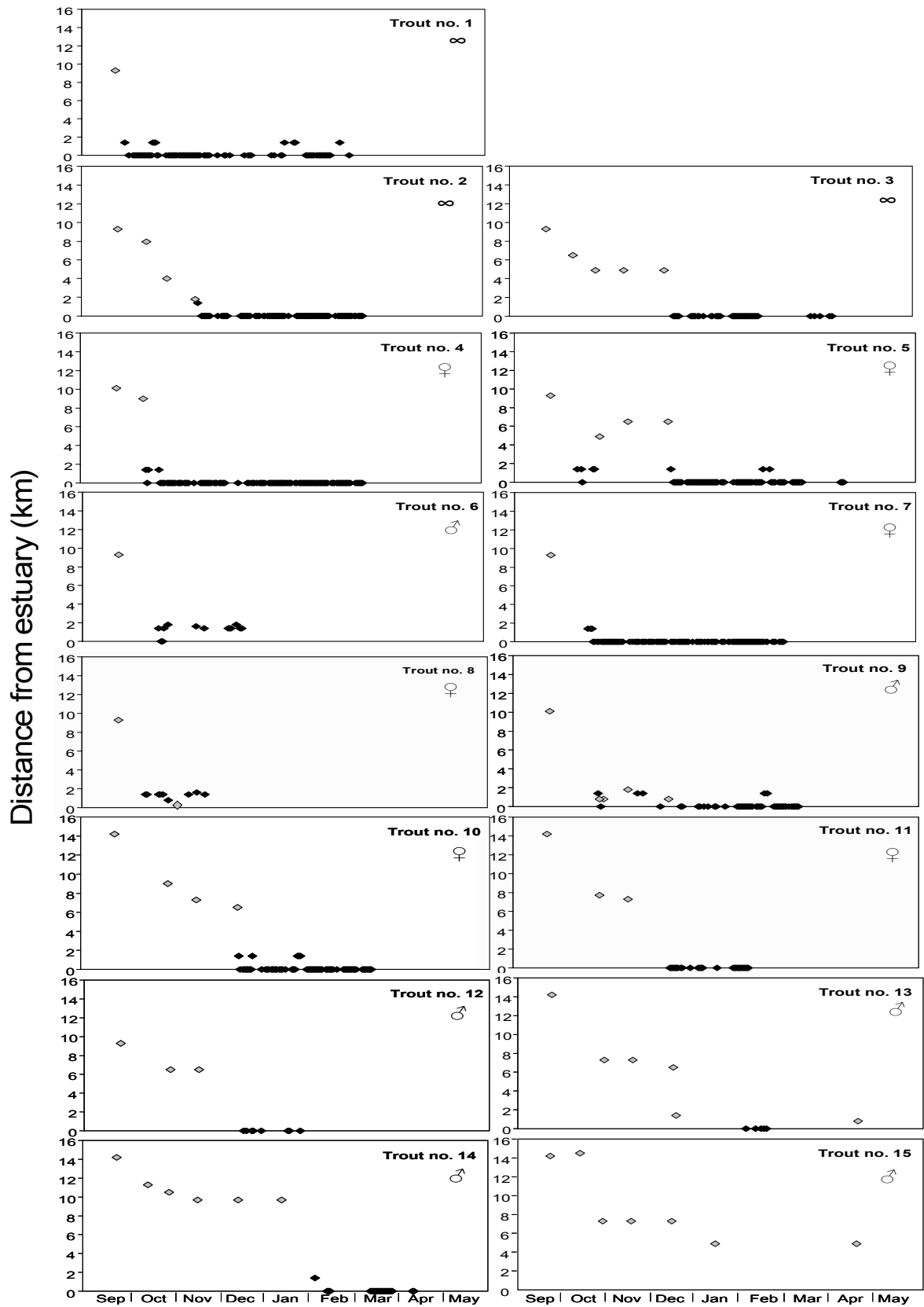


FIG. 4. Distance from the outer boundary of the estuary (0 km) upwards the river of individual sea trout, including sexually mature (♀ and ♂) and immature fish (∞), tagging location (first registration in figure) and registrations during manual (◇) and automatic tracking (◆).

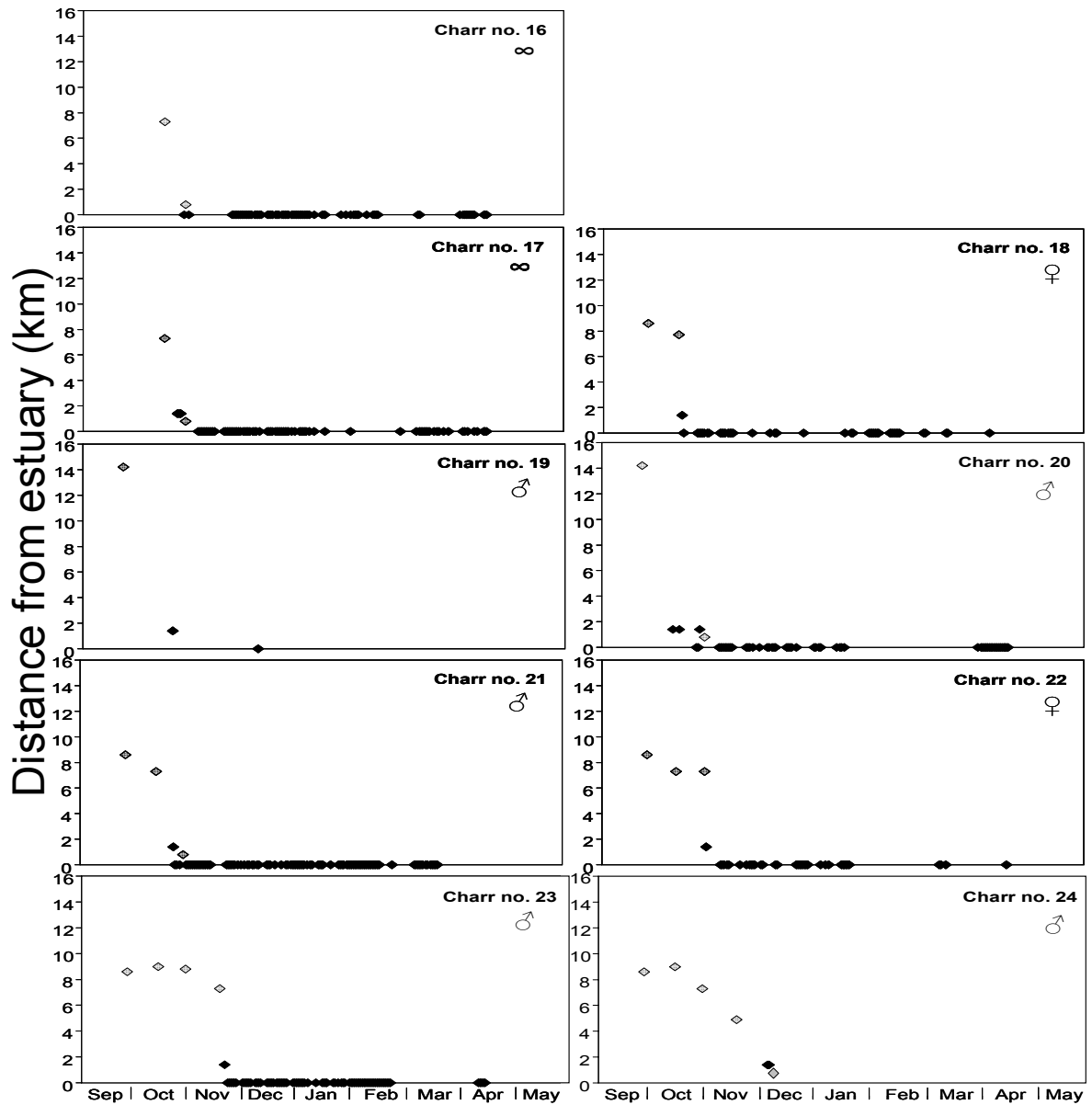


FIG. 5. Distance from the outer boundary of the estuary (0 km) upwards the river of individual Arctic charr, including sexually mature (♀ and ♂) and immature fish (∞), tagging location (first registration in figure) and registrations during manual (◇) and automatic tracking (◆).

4.2 Movements between river, estuary and sea

Although large individual variation, the temperature recordings from the DSTs showed that both Arctic charr and sea trout moved frequently between the different habitats throughout the winter and spring (Fig 7 & 8). The majority of the DST (91%) and acoustic tagged (93%) sea trout migrated from the river to estuarine and/or marine waters during autumn and winter (October to April) (Fig. 4 & 7). The DST and acoustic tagged Arctic charr showed a similar trend (80% and 100%, respectively, Fig. 5 & 8) although data from the DSTs indicated that there were no Arctic charr in pure marine waters before the beginning of December (Fig. 8).

Based on the DST-data, the duration of the continuous estuary or sea residency ranged from a few hours to 55 days during winter (Fig. 7 & 8) for the 91% of sea trout and 80% of Arctic charr residing in these habitats during winter. Three sea trout with very short residency in these habitats were recaptured or had other factors disrupting the temperature recordings (e.g. predation by European otter). The longest continuous time spent in estuarine water during winter was 22 days for sea trout (Trout no. 6336) and 49 days for Arctic charr (Charr no. 3073), while the longest continuous time spent in salt water during winter was 39 days for sea trout (Trout no. 29) and 55 days for Arctic charr (Charr no. 23).

There was also large individual variation in frequency of shifts between habitats during winter, with most numerous shifts during mid winter (January and February) in both species (ANOVA, $p > 0.05$) (Fig. 7 & 8). Fish of both species residing mainly in the river during the winter months seemed to have none or few shifts in habitat compared to the fishes residing mainly in the estuary or sea. Most of the shifts were between river/estuary and estuary/sea, but direct shifts between river and sea also occurred (i.e. Trout no. 7628, Fig. 7 and Charr no. 2388, Fig. 8). Although the behaviour of the acoustically tagged fish could not be constantly measured, minimum 47% of the sea trout and 20% of the Arctic charr had shifts between river and estuary, and the lack of continuous recordings in the estuary also during good weather conditions might indicate that acoustically tagged fish migrated away from the estuary, possibly to marine waters.

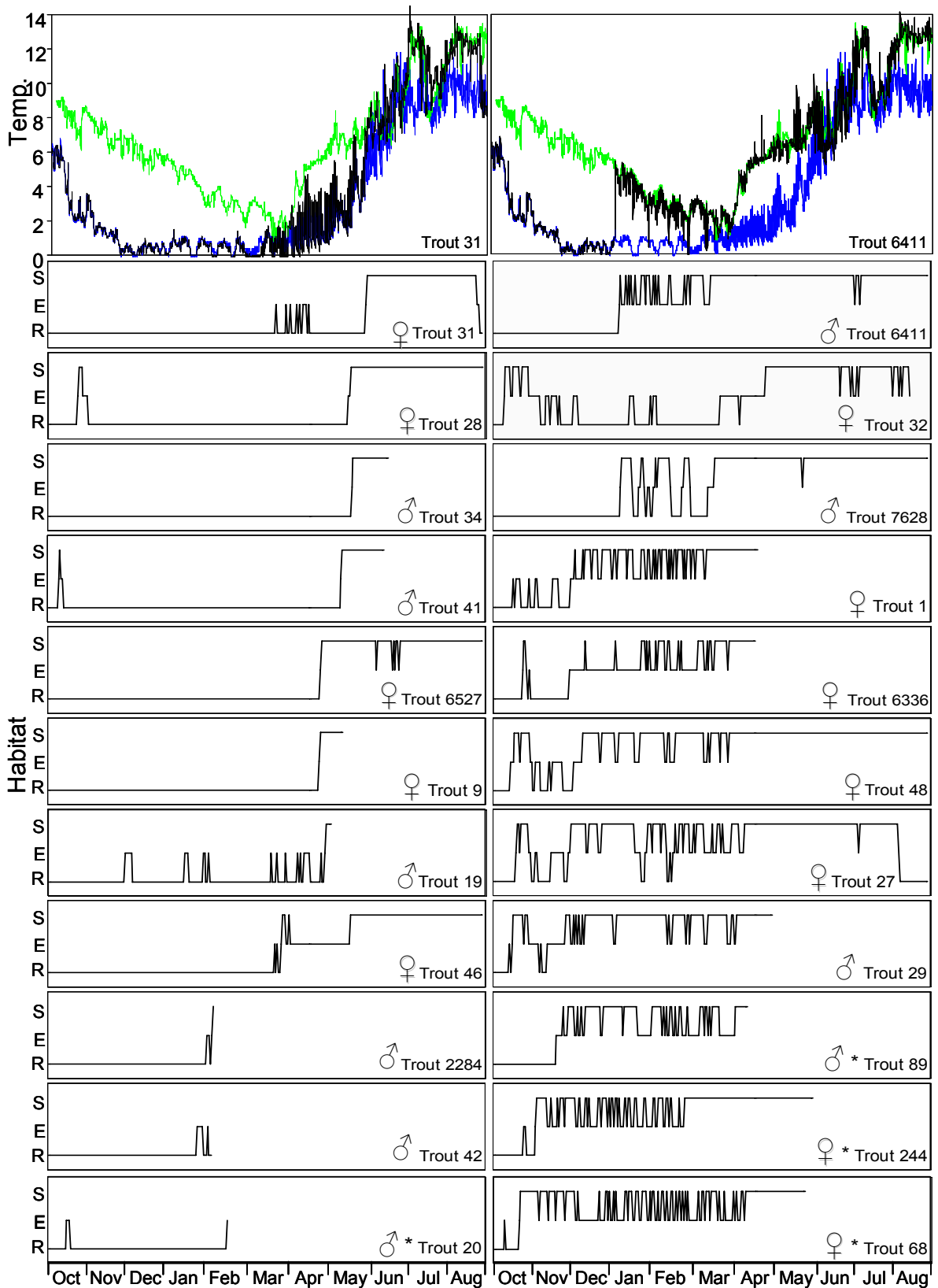


FIG. 7. Habitat choice of individual sea trout throughout the year, including residency in the river (R), estuary (E) and sea (S), sex ($\text{\textcircled{M}}$ & $\text{\textcircled{F}}$), and tagging year (fish tagged in 2006 are marked(*), remaining fish tagged in 2005). For illustration, the top two graphs show temperature as recorded by the fish ($\text{\textcircled{—}}$), in the main river ($\text{\textcircled{—}}$) and in the sea ($\text{\textcircled{—}}$).

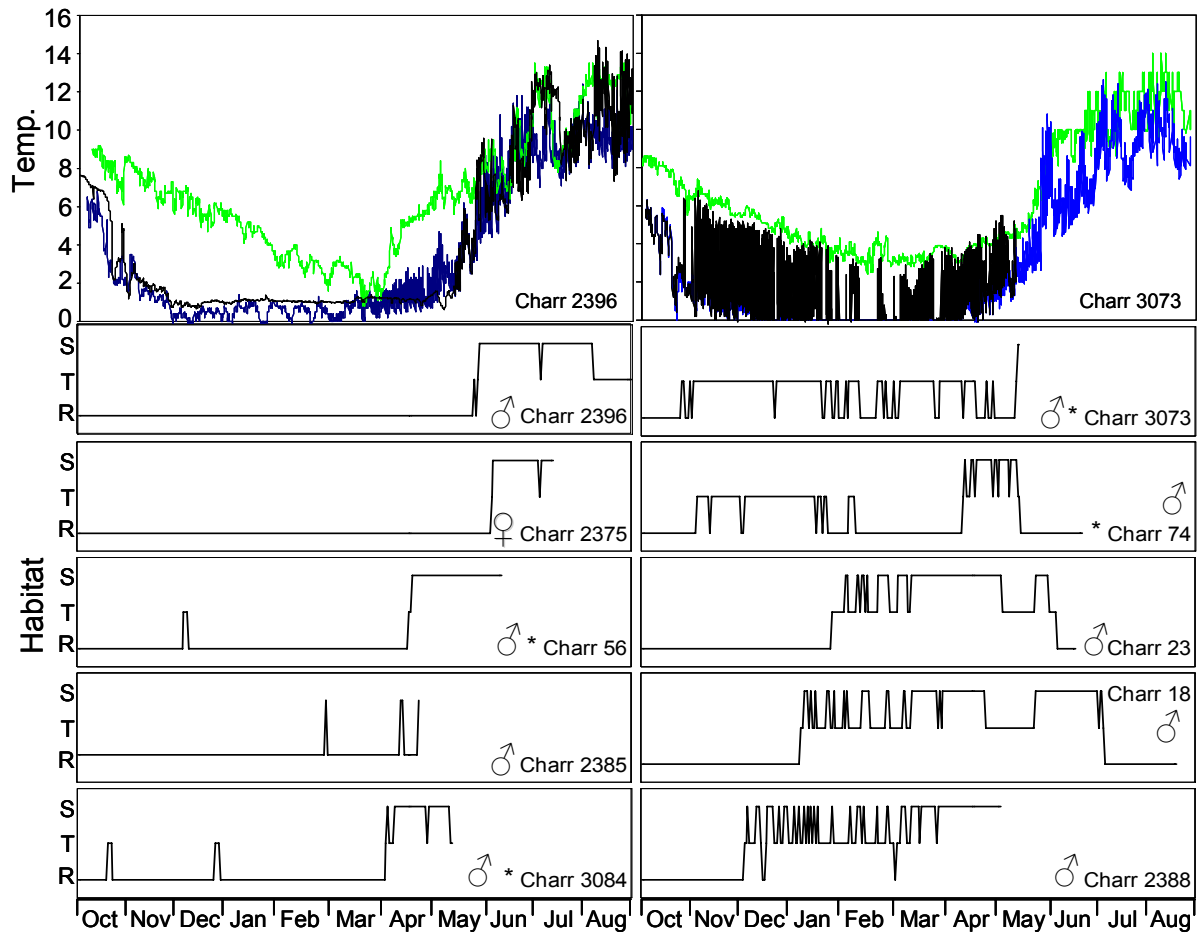


FIG. 8. Habitat choice of individual Arctic charr throughout the year, including residency in the river (R), estuary (E) and sea (S), sex (♂ & ♀), and tagging year (fish tagged in 2006 are marked(*), remaining fish tagged in 2005). For illustration, the top two graphs show temperature as recorded by the fish (—), in the main river (—) and in the sea (—).

4.3 Seasonal distribution

Based on the data obtained from the DSTs, it seems like a larger proportion of the sea trout than the Arctic charr utilize the marine habitat during the winter months (Fig. 9). Whereas individuals of sea trout were found continuously in the marine habitat from October with increasing numbers throughout the winter, Arctic charrs were found frequently in the estuarine habitat from November to February with increasing numbers of fish in the marine habitat from March and onwards (Fig. 9). It also seems like some sea trout migrates to estuarine and and marine waters immediately after spawning in October and then mirates back to the river for a shorter period in November, whereafter they again return to the estuarine and/or marine habitat (Fig 7 & 9).

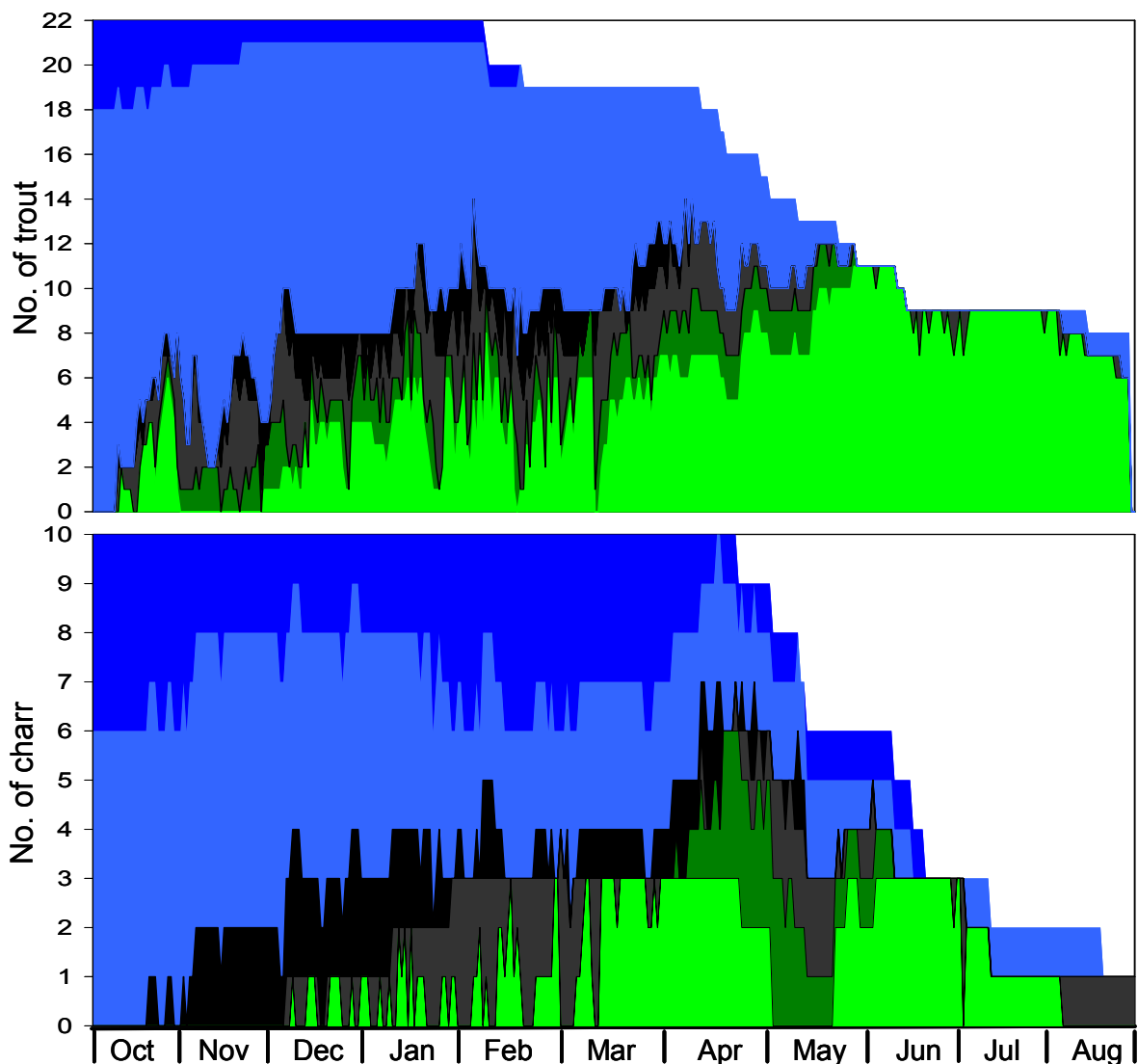


FIG. 9. Number of of sea trout (upper) and Arctic charr (lower) registered in the river (blue), the estuary (black) and the sea (green) from October to August. Lighter colours indicate fish tagged in 2005, darker colours fish tagged in 2006. Total number of fish decreases from february due to recaptures.

4.4 Differences between and within species

In general, there were no statistically significant differences (ANOVA, $p > 0.05$) between or within species of fish tagged with DSTs (Table 4). Average day of migration to marine waters were, however, 83 days later for Arctic charr than sea trout (ANOVA, $p = 0.02$) and there also seemed to be a tendency that average day of first recording in the estuary were 29 days earlier for sea trout than for Arctic charr (ANOVA, $p = 0.35$) (Table 4). Although not significant (ANOVA, $p > 0.05$), Arctic charr spent on average more time in estuarine waters than did the sea trout during winter, whereas sea trout on average spent more time in the marine habitat than did the Arctic charr. Female sea trout also migrated to estuarine and marine waters earlier than the males and spent more time in these habitats, while the opposite occurred in Arctic charr (Table 4). Smaller individuals of both species migrated to the estuary and sea earlier and spent more time in these habitats during winter than did larger individuals (ANOVA, $p > 0.05$) (Table 4).

TABLE 4. Differences between (S.T. = sea trout, A.C. = Arctic charr) and within species in average day of first registration in estuary and sea \pm s.d. (calculated from 1 October), average number of days spent in estuary and sea \pm s.d, and average number of switches in habitat during winter

	Average day since 1 October				Average no. days during winter				Average no. of habitat shifts	
	<i>n</i>	1st reg. in est.	<i>n</i>	1st reg. in sea	<i>n</i>	Estuary	<i>n</i>	Sea	<i>n</i>	Winter
S.T.	22	76 \pm 77	20	97 \pm 88	18	34 \pm 29	18	50 \pm 53	18	23 \pm 20
A.C.	10	105 \pm 84	9	180 \pm 70	10	40 \pm 46	10	25 \pm 32	10	15 \pm 15
<i>p</i>		0.35		0.02		0.67		0.19		0.28
S.T. ♀	13	66 \pm 73	12	84 \pm 84	12	40 \pm 29	12	54 \pm 49	12	25 \pm 20
S.T. ♂	9	91 \pm 84	8	115 \pm 96	6	21 \pm 24	6	44 \pm 49	6	17 \pm 20
<i>p</i>		0.46		0.45		0.18		0.71		0.39
A.C. ♀	1	250	1	252	1	9	1	0	1	0
A.C. ♂	9	89 \pm 84	8	172 \pm 69	9	43 \pm 48	9	28 \pm 32	9	17 \pm 15
<i>p</i>		0.06		0.31		0.52		0.43		0.33
S.T. < 60 cm	10	48 \pm 56	10	81 \pm 89	8	41 \pm 29	8	52 \pm 58	8	26 \pm 15
S.T. > 60 cm	12	100 \pm 86	10	113 \pm 88	10	28 \pm 29	10	49 \pm 53	10	21 \pm 23
<i>p</i>		0.12		0.43		0.35		0.9		0.63
A.C. < 45 cm	4	98 \pm 50	3	139 \pm 51	4	41 \pm 36	4	36 \pm 35	4	16 \pm 9
A.C. > 45 cm	6	110 \pm 106	6	201 \pm 72	6	39 \pm 56	6	18 \pm 30	6	14 \pm 19
<i>p</i>		0.84		0.23		0.93		0.41		0.86

5. DISCUSSION

5.1 Winter migrations

The present study for the first time shows that both riverine sea trout and Arctic charr can be found in estuarine and marine waters during winter at high northern latitudes, thus contradicting earlier studies of lake-dwelling populations of these species that have found both species to solely overwinter in fresh water at the same latitudes (e.g. Berg & Berg 1988; 1989; Finstad & Heggberget 1993; Klemetsen *et al.* 2003; Kristoffersen *et al.* 1994; Rikardsen *et al.* 1997; 2003; 2004). Including both recaptured DST-tagged fish and acoustically tagged fish, 92 % of the sea trout and surprisingly also 91 % of the Arctic charr in the River Skibotn migrated to estuarine and/or marine waters during winter (November - April). The length of their continuous residency in either estuary or sea during winter ranged from a few hours to a maximum of 55 days in the present study, and some fish left the river as early as mid October directly after spawning. Thus the first null hypothesis, stating that both riverine anadromous Arctic charr and sea trout overwinter in the river and migrate to the sea during summer, must be rejected.

Earlier migration studies conducted on these species at high northern latitudes have exclusively been of lake-dwelling populations (e.g. Berg & Berg 1989; 1993; Finstad & Heggberget 1993; Kristoffersen *et al.* 1994; Rikardsen & Elliott 2000; Rikardsen *et al.* 1997; 2000; 2003; 2007a; b), despite the existence of several riverine populations in the area, including large rivers as the River Alta, Tana, Reisa, Repparfjord and Lakselva in addition to the River Skibotn (A. H. Rikardsen, pers. com.). However, North Norwegian sea trout have been found in estuarine and marine waters during winter in three fjords (Ranafjord, Balsfjord and Repparfjord) (Rikardsen 2004; Rikardsen *et al.* 2002; 2006). Rikardsen (2004) found that some sea trout captured in the sea in early spring were infected with pre-adult or adult sea lice *Lepeophtheirus salmonis* Krøyer, indicating that they must have been at sea for up to several months. Following this, Rikardsen *et al.* (2006) showed that the same fish fed actively during winter and had a constant or increasing condition factor during winter, indicating that feeding of spent fish in saltwater during late autumn and winter may be beneficial compared to overwintering in freshwater, where prey abundance is much lower (Rikardsen *et al.* 2000; 2003). In contrast, no internationally published information has, to my knowledge, ever documented any migrations of Arctic charr to estuarine or marine waters during winter. Anadromous Arctic charr is generally assumed to feed in marine waters during summer and

return to their nursing river by the end of August (Berg & Berg 1993; Finstad & Heggberget 1993; Klemetsen *et al.* 2003; Rikardsen *et al.* 2000; 2004; Svenning *et al.* 2001). However, in a field survey in the estuary of the River Repparfjord (riverine populations) in Finnmark County, Rikardsen *et al.* (2002) found both immature Arctic charr and sea trout in the estuary area during late September (autumn), but only sea trout were captured in a similar survey in November (winter) at the same location.

In the earlier marine studies of northern winter migrating sea trout (Rikardsen 2004; Rikardsen *et al.* 2002; 2004), the origin of and reason for the migrations, duration of residency, geographical distribution, and what proportion of the population migrated could not be documented. It was hypothesised in these studies that the fish found in the estuary and at sea might have originated from riverine populations, where the advantages of residing in freshwater during the winter months might be reduced due to the harsh conditions (i.e. low water levels and difficult ice conditions) in the riverine habitat. The present study support this hypothesis, and also document that Arctic charr can be found in estuarine and marine waters during winter. The present study also provides information of which proportion of mature individuals can be found at sea or in the estuary during different parts of the winter. By use of electronic tracking technology, the present study was also able to track the individual fish long-term migration behaviour and habitat use, which to my knowledge have never been done before in these species during winter and only once during summer in the area (Rikardsen *et al.* 2007b).

The migratory behaviour of both sea trout and anadromous Arctic charr observed in the present study seem to resemble the behaviour of some more southern Norwegian and British populations of sea trout, which migrates to marine waters during winter (Elliott 1994; Heuch *et al.* 2002; Jonsson & Jonsson 2002; Pemberton 1976; Sømme 1941). In studies where the origin of sea trout at sea during winter is known, they are often found to originate from smaller streams where they return to saltwater directly after spawning (Elliot 1994; Jonsson *et al.* 2001). Sea trout are also frequently found feeding in coastal Skagerrak during winter, a behaviour that is most likely explained by sea trout from small local streams with poor overwintering conditions where the fish is forced to marine waters during winter (Knutsen *et al.* 2004; Olsen *et al.* 2006). Although the River Skibotn is much larger than the previously described rivers where migrations to marine waters during winter are documented, it seems reasonable to assume that the behaviour is at least partially related to the riverine habitat. If

this is correct, it might also explain the never previously documented winter migrations of Arctic charr, since no previous studies of winter migrations have been of riverine populations of this species. Sea trout is documented to be an opportunistic species capable of adjusting to a wide variety of habitats, but Arctic charr is also polymorphic and diverse in its habitat use (Klemetsen *et al.* 2003). If the migrations to marine waters during winter are in fact related to the riverine habitat, it seems reasonable that it should occur also in riverine populations of the polymorphic Arctic charr. However, the findings of sea trout feeding in marine waters both in southern and northern Norway (Knutsen *et al.* 2004; Olsen *et al.* 2006; Rikardsen *et al.* 2006), may indicate that feeding might also be an additional reason for marine migrations during winter.

What also becomes evident from the results obtained in the present study is that the estuarine environment can hold large amounts of fish during the winter months. Sea trout were found to reside continuously in the estuary for up to 22 days and Arctic charr for up to 49 days during winter in the River Skibotn. In general, the estuary is regarded as having three primary advantages; i) productive foraging, ii) relative refuge from predators, and iii) offering a physiologically intermediate environment for transition from fresh to salt water (Thorpe 1994). However, little is known on the estuary use of adult European salmonids (Thorpe 1994). Sea trout and Arctic charr are believed to stay close to their nursing river and normally feed within a range of three km from the river mouth during summer, even though migrations up to 940 km have been documented (Berg & Berg 1987; Berg & Jonsson 1989). The previous studies in the area have, however, not investigated estuary use. Unfortunately, no studies on diet were conducted in the present study and it is therefore not possible to conclude if the fish are on a feeding migration or starves during winter in this habitat.

The second potential advantage of estuarine residency, the possible relative refuge from predators, may apply to the present study when relating the estuarine habitat to the marine. However, one harbour seal *Phoca vitulina* L. was observed just outside the estuary during fieldwork, and two tags were found in the upper parts of the estuary with bite marks indicating predation by otter. The numbers of predators were not estimated during the study, and there might have been more predators residing in the area during winter. The number of encounters with seals and other predators are, however, most likely more numerous in the sea than in the estuary. If this statement of relative refuge from predators applies to the present study, it might explain why Arctic charr are found to inhabit the estuary to a greater extent

during winter than the sea trout. Since body size has major effects on predator-prey interactions (Cohen *et al.* 1993; Mittelbach 1981; Werner *et al.* 1983), one can assume that the Arctic charr in the present study experience a higher risk than sea trout of being predated due to their generally smaller body size.

The third assumption about residency in the estuarine environment, that the habitat offers a physiologically intermediate environment for transition from fresh to salt water, seems to apply poorly to the fish in the present study. Fish were found to reside in the area for long continuous periods, but when residing in the estuary during winter fish did not always migrate into water with intermediate salinity. They rather seemed to stay at the bottom of the estuary and experience large shifts in salinity four times a day according to the high and low tide (see appendices II & III). These shifts in salinity are physiologically stressful for salmonids. Energy is demanded to regulate plasma ions in the face of changing external salinity, which is an obvious necessity for fish that live in estuaries or that move between freshwater and seawater (McCormick 2001). Fish can, however, survive for a long time in seawater with high ionic concentrations in the body fluids even though the appetite is reduced and they normally stagnate in growth (Clarke 1982).

Studies on smolts of Arctic charr have shown that they can not survive salinity stress at low temperatures during winter (Arnesen 1994; Arnesen & Halvorsen 1990; Finstad & Heggberget 1993; Finstad *et al.* 1989), and this is also true for rainbow trout *Oncorhynchus mykiss* (Walbaum) (Finstad *et al.* 1988). However, it has been shown that larger immature individuals of Arctic charr (20 – 27 cm) can survive salinity stress during winter if the temperature is raised to 8 °C (Arnesen *et al.* 1993), and it has also been shown that larger individuals of salmonids can handle salinity stress better than smaller ones (Finstad & Ugedal 1998; Hoar 1976; Ugedal *et al.* 1998). This might possibly be due to the decreased surface/volume-relationship when fish grown larger, or that the mechanisms for osmoregulation evolves gradually with fish size (McCormick & Saunders 1987). This could possibly apply for all adult Arctic charr and sea trout, or the low salt water tolerance at low temperatures might vary between populations. Differences in osmoregulatory capacity have been shown under experimental conditions between land-locked and anadromous strains of Arctic charr (Eliassen *et al.* 1998). The anadromous Arctic charr and sea trout of the River Skibotn were in addition to the long estuarine residency found to reside continuously in marine waters for up to 25 and 50 days, respectively, and must thus be at least partially

adapted to the full strength salt water (salinity > 30) at low winter temperatures (down to about 2 °C) in the estuarine and marine environment.

5.2 Effects of the power plant and ice conditions

The River Skibotn is regulated for hydropower since 1980, and the area upstream from the power plant has a reduced discharge. Anadromous fish spawn in the area, but due to small pools and thick ice cover (up to 1.5 m some places, pers. obs.) the suitability of the area for overwintering fish is most likely reduced. This theory is also supported by the fact that none of the acoustically tagged fish were found to reside in the area upstream from the power plant during the manual tracking in the area in January. Some of the DST-tagged fish did, however, have temperature profiles that did not correspond to the temperature measured in the stretches beneath the power plant (e.g. Trout no. 28, appendix II, Charr no. 2396, appendix III). Some of these temperature profiles match the one measured above the power plant, but due to the low numbers of temperature recordings in the river, analyzes of the DST-tagged fish locations within river is difficult to obtain.

The increased temperature due to the power plant also makes the river downstream from the power plant remain at least partially free from surface ice during winter, and also causes frazile ice to form extensively in the river during the entire winter. Frazile ice (small disc-shaped ice crystals) is formed in rapid waters without ice cover and can float freely in the water or aggregate on the substratum (Devik 1944). Both phenomena were observed during the winter months in the River Skibotn, and the frazile ice was also observed to aggregate in the lower parts of the pools and cause hanging dams (ice clogs the lower part of the pool and dams it). Hanging dams have been shown to force brown trout and common carp *Cyprinus carpio* L. out of pools classed as good overwintering areas (Brown *et al.* 2000), and the ice aggregating on the substratum in pools further reduces the number of hiding places available to adult fish. In addition, it has been speculated that free floating frazile ice could directly affect the respiratory system of fish by clogging the gills, and at high densities cause suffocation (Brown *et al.* 1994). The reduced surface ice also gives homeothermic predators' access to overwintering fish residing in the river. For example, the European otter reside in the river, and a predation event on a large sea trout (3–4 kg) was observed during the fieldwork period. Two tags were also found on the river beach in the upper part of the estuary with bite marks, indicating predation by otter. The ice conditions due to the hydropower plant might thus additionally reduce the number of overwintering pools in the entire anadromous

stretch of river, and also increase the predation risk in the area downstream from the power plant.

The ice conditions related to the increased water temperature are normally not found to the same extent in rivers that are not regulated for hydropower, and could therefore possibly explain the migrations to estuarine and marine waters observed in the present study. However, the findings of Rikardsen (2004) and Rikardsen *et al.* (2002; 2006) of sea trout in marine waters during winter in three fjords without regulated watercourses close to the current study site strongly indicate that this type of behaviour can be typical for at least riverine populations of sea trout. Furthermore, unpublished results from a parallel project have shown that at least 2 out of 10 acoustic tagged Arctic charr from the nearby (30 km) unregulated River Signaldalen were recorded in marine waters during winter (A. Rikardsen *et al.* unpubl. data). Thus, the migratory behaviour of Arctic charr observed in the present study might also apply to other northern riverine populations of anadromous Arctic charr. In sum, the effect of the power plant could possibly amplify the profits of leaving the riverine habitat (reduced number of overwintering pools and predation), forcing larger proportions of the populations to sea than would occur in unregulated rivers.

5.3 Winter activity

Both the mature Arctic charr and sea trout in the River Skibotn had shifts in habitat during winter. Shifts in habitat were easiest to detect in fish tagged with DSTs, and many of the DST-tagged fish had numerous shifts in habitat during winter. The acoustic tagging showed that the returns to the freshwater habitat after registration in the estuary could include migrations up to 6.5 km. The fish have to move actively during these habitat shifts. This contradicts the second null hypothesis stated in this thesis: that the fish remains stationary during winter and have low activity. Also this null hypothesis must thus be rejected. Previous studies have shown that both species have no or little feeding after their return to freshwater and during overwintering in lakes (Boivin & Power 1990; Dutil 1986; Elliot 1997; Rikardsen *et al.* 2003; Sprudles 1952), and also that they most likely rest on the bottom during overwintering in lakes (A. Rikardsen *et al.* unpubl. data). As fish are heterothermic, their body temperature is essentially identical to that of their surrounding environment (Fletcher *et al.* 1988), reducing their metabolism. It has been suggested that the energy expenditure for adult resident charr and trout of finding and processing food may be greater than the energy acquired when feeding in freshwater during winter (Forseth *et al.* 1994; Jonsson & Jonsson

1993). Low activity during winter thus seems like a good strategy to save the sparse resources fish have left after spawning. However, as with the salinity tolerance, there might be differences between populations, or there might be differences between the habitats. The energy put into spawning or the energy expenditure of feeding could differ from the previous studies in the River Skibotn, where fish must have resources left or acquire them after spawning for active migrations during winter.

5.4 Do Arctic charr and sea trout behave differently during winter?

For both species, the results showed large individual variation within species, ranging from a few fish residing in freshwater through the entire winter, to fish migrating between river, estuary and sea during most of the winter, as well as fish migrating more or less directly to sea after spawning. The large individual variation combined with the relatively few recaptures of DST-tagged fish made the reliability of the statistical analyses low. In addition, the average time of first arrival in estuary by DST-tagged fish were found to be later for Arctic charr than sea trout, whereas acoustically tagged Arctic charr were found to migrate to the estuary about one month earlier than the majority of the sea trout. The results from the two methods used thus contradict each other. The third null hypothesis stated, that there is no difference in the seasonal migration behaviour between the two species, as well as between sex and size classes within the species, could thus not be rejected.

Although few significant differences, there seems to be some trends in the data material. For example, average day of first registration in marine waters by DST-tagged fish were statistically significant about three months later for Arctic charr than sea trout. Furthermore, although not statistically significant, Arctic charr were also found to spend on average more time in the estuary than the sea trout during winter. Within species, there seemed to be a trend that female sea trout migrated to estuarine and marine waters earlier than the males, and also that they spent more time in these habitats. This could not be estimated for Arctic charr, as there was only one female recaptured. It also seemed like smaller individuals of both species migrated to the estuary and sea earlier and spent more time in these habitats during winter than the larger individuals. The statistical reliability also in these results were low ($p > 0.90$ in some analyses), but it is worth noticing that exactly the same trends regarding timing and length of marine residency were found in a 10-year study in the close by Vardnes River during summer (Berg & Berg 1988; 1993). Due to the statistically low significance in the results, the relationship turns out merely anecdotal, but might indicate that the differences

between and within species previously documented during summer (Berg & Berg 1988; 1993) might also occur during winter.

5.5 Methodical experiences and challenges

The use of temperature as an indirect measurement of habitat utilization proved to be an excellent method in the present study. The iB-tags used here are inexpensive in telemetric context, and still provided good continuous data on individuals habitat use over time. This would require tremendous effort if it were to be done with other methods (Metcalf & Arnold 1997). DSTs also proved to be an excellent method for registration of fish in the estuary. The DSTs does, however, need to be recaptured, and if the recapture or survival rate differentiate between e.g. fish migrating to marine waters early and late the results of the population as a whole might possibly be biased. The acoustic telemetry gave additional detailed information on the migrations within the river. Positioning of fish in marine waters by use of DSTs were proved difficult, but has been done in oceanic water before (Friedland *et al.* 2001) and might be achieved with more frequent recordings. Acoustic data from the fjord (A. Rikardsen *et al.* unpubl. data) will hopefully provide a more detailed picture of the migrations in this habitat.

Whereas more detailed information on marine migrations might need acoustic methods, a more detailed description of the movements within the river could possibly have been achieved with the DSTs if temperature were recorded on more locations in this habitat. However, the temperature differences described here is strongly related to the alteration of the riverine habitat due to the hydropower plant, and the method of localizing fish by using temperature difference within the river is most likely limited to a very small number of freshwater habitats. The resolution of the results would also most likely never be as good as what can be achieved with acoustic or especially radio telemetry, but these methods are time-consuming and less cost efficient, and DSTs might therefore be a good alternative in the River Skibotn.

The problem of tag expulsion (shedding of tags through the incision wound, an intact part of the body wall or through the intestine (Jepsen *et al.* 2002)) and malfunctioning tags were encountered in the present study. More Arctic charr than sea trout had rejected their tag upon recapture, and smaller individuals also seemed to be more prone to reject their tags (Table 3). Rates of tag expulsion depend on species, fish condition, tag weight and environmental conditions (Jepsen *et al.* 2002). It seems like there might be differences in tag retention between the two species. However, the weight of the tag in relation to the size of fish was on

average higher for the smaller Arctic charr, and might explain the differences observed between the two species. The material or shape of the tags could also possibly explain the difference in tag retention, since they are made of different materials and less of the cylindrical acoustic tags were rejected than the hexagonal DSTs. The problem with malfunctioning tags could probably be avoided with long-term testing of tags prior to tagging. In conclusion, the DSTs proved to be an excellent and cost efficient method to track individual movement between habitats with different temperature regimes over time, whereas the acoustic data provided more detailed information on migrations within the river.

6. CONCLUSIONS AND FUTURE RESEARCH NEEDS

The present study has shown that both riverine anadromous Arctic charr and sea trout at high northern latitudes can be found in estuarine and marine waters during winter, contradicting the general view that both species solely overwinter in freshwater in the area. The species thus seem to have a more complex and flexible life history pattern than previously believed. This knowledge is of management value, since all current management of northern anadromous Arctic charr and sea trout is based on the assumption that both species reside in freshwater during winter and migrates to sea to feed for one to three months during summer.

According to catch statistics, northern populations of anadromous Arctic charr, but not sea trout, have decreased significantly in abundance over the last years, without any good explanation of why this is happening (M. Johansen, fish manager, County of Finnmark, pers. com). One possible explanation can be that the species responds differently to change in climate, in addition to other factors like e.g. human influence. Therefore, further detailed studies of the anadromous forms of these species are needed, especially in relation to their responses to changes in environmental parameters. The present and future development of advanced telemetry techniques may be excellent in this regard, and may reveal new and unknown information that has not been possible to achieve before. The present study is an example of that, and has shown that the harsh environmental conditions in the riverine habitat may be a plausible explanation for why migrations to estuarine and marine waters occur among riverine populations of Arctic charr and sea trout, although some of this behaviour may also be influenced by hydropower production. Further studies, involving also undisturbed rivers, are thus needed to conclude if the winter migrations to marine and estuary waters are common in all northern riverine populations of the two species. Also, their seasonal geographical distribution at sea and in different freshwater habitats should be investigated in future studies, as well as why they are found in different habitats at different times.

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8. REFERENCES

- Arnesen, A. M. (1994). Seawater adaptation in Arctic charr, *Salvelinus alpinus* (L.). Dr. Scient. Thesis. University of Tromsø.
- Arnesen, A. M. & Halvorsen, M. (1990). Oppdrett av røye i sjøvann? Aspekter ved saltvannstoleranse og vekst. FTFI rapport **U55** (in Norwegian).
- Arnesen, A. M., Jørgensen, E. H. & Jobling, M. (1993). Feed intake, growth and osmoregulation in Arctic charr, *Salvelinus alpinus* (L.), transferred from freshwater to saltwater at 8°C during summer and winter. *Fish Physiology and Biochemistry* **12**, 281-292.
- Berg, M. (1964). *Nordnorske Lakseelver*. Oslo: Tanum. 300 pp (in Norwegian).
- Berg, O. K. & Berg, M. (1987). Migrations of sea trout (*Salmo trutta* L.) from the Vardnes River in northern Norway. *Journal of Fish Biology* **31**, 113-121.
- Berg, O. K. & Berg, M. (1988). Sea growth and time of migration of anadromous Arctic char (*Salvelinus alpinus*) from the Vardnes River, in northern Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 955-960.
- Berg, O. K. & Berg, M. (1989). The duration of sea and freshwater residence of the sea trout, *Salmo trutta*, from the Vardnes River in northern Norway. *Environmental Biology of Fishes* **24**, 23-32.
- Berg, O. K. & Berg, M. (1993). Duration of sea and freshwater residence of Arctic char (*Salvelinus alpinus*), from the Vardnes River in northern Norway. *Aquaculture* **110**, 129-140.
- Berg, O. K. & Jonsson, B. (1989). Migratory patterns of anadromous Atlantic salmon, brown trout and Arctic charr from the Vardnes River in northern Norway. In *Proceedings of the Salmonid Migration and Distribution Symposium* (Brannon, E & Jonsson, B., Ed.), 106-115.
- Berg, O. K. & L'Abée-Lund, J. H. (1991). Livshistorie og vandringer hos sjøørret. *Ottar* **91**, 26-30 (in Norwegian).
- Boivin, T. G. & Power, G. (1990). Winter condition and proximate composition of anadromous Arctic charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. *Canadian Journal of Zoology* **68**, 2284-2289.
- Brown, R. S., Stanislawski, S. S. & Mackay, W. C. (1994). Effects of frazile ice on fish. In *Proceedings of the Workshop on Environmental Aspects of River Ice* (Prowse, T. D.,

- ed.), 261-278. Saskatoon, Sask: NHRI Symposium No. 12, National Hydrology Research Institute, Environment Canada.
- Brown, R. S., Power, G., Beltaos, S. & Beddow, T. A. (2000). Effects of hanging ice dams on winter movements and swimming activity of fish. *Journal of Fish Biology* **57**, 1150-1159.
- Clarke, W. C. (1982). Evaluation of the seawater challenge test as an index of marine survival. *Aquaculture* **28**, 177-183.
- Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* **62**, 67-78.
- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. & Butler P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* **19**: 334-343.
- Dempson, J. B. & Kristoffersen, A. H. (1987). Spatial and temporal aspects of the ocean migration of anadromous Arctic charr. *American Fisheries Society Symposium* **1**, 345–357.
- Dempson, J. B., Shears, M. & Bloom, M. (2002). Spatial and temporal variability in the diet of anadromous Arctic charr, *Salvelinus alpinus*, in northern Labrador. *Environmental Biology of Fishes* **64**, 49– 62.
- Devik, O. (1944). Ice formation in lakes and rivers. *The Geographical Journal* **103**, 193-203.
- Dodson, J. J. (1997). Fish migration: an evolutionary perspective. In *Behavioural Ecology of Teleost Fishes* (Godin, J. G. J., ed.), 10-36. New York: Oxford University Press.
- Dutil, J. D. (1986). Energetic constraints and spawning interval in anadromous Arctic charr (*Salvelinus alpinus*). *Copeia* **1986**, 945-955.
- Eliassen, R. A., Johnsen, H. K., Mayer, I. & Jobling, M. (1998). Contrasts in osmoregulatory capacity of two Arctic charr, *Salvelinus alpinus* (L.), strains from northern Norway. *Aquaculture* **168**, 255-269.
- Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. New York: Oxford University Press.
- Elliot, J. M. (1997). Stomach content of adult sea trout caught in six English rivers. *Journal of Fish Biology* **50**, 1129-1132.

- Finstad, B. & Heggberget, T. G. (1993). Migration, growth and survival of wild and hatchery-reared anadromous Arctic charr (*Salvelinus alpinus*) in Finnmark, northern Norway. *Journal of Fish Biology* **43**, 303-312.
- Finstad, B. & Ugedal, O. (1998). Smolting of sea trout (*Salmo trutta* L.) in northern Norway. *Aquaculture* **168**, 341-349.
- Finstad, B., Staurnes, M. & Reite, O. B. (1988). Effect of low temperature on sea-water tolerance in rainbow trout, *Salmo gairdneri*. *Aquaculture* **72**, 319-328.
- Finstad, B., Nilssen, K. J. & Arnesen, A. M. (1989). Seasonal changes in sea-water tolerance of Arctic charr (*Salvelinus alpinus*). *Journal of Comparative Physiology B* **159**, 371-378.
- Fletcher, G. L., Kao, M. H. & Dempson, B. (1988). Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. *Aquaculture* **71**, 369-378.
- Forseth, T., Ugedal, O. & Jonsson, B. (1994). The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. *Journal of Animal Ecology* **63**, 116-126.
- Friedland, K. D., Walker, R. V., Davis, N. D., Myers K. W., Boehlert, G. W., Urawa, S. & Ueno, Y. (2001). Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Marine Ecology Progress Series* **216**, 235-252.
- Grønvik, S. & Klemetsen, A. (1987). Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* L. and Atlantic salmon *Salmo salar* L. off Senja, N. Norway. *Polar biology* **7**, 173-177.
- Gross, M. R. (1987). Evolution of diadromy in fishes. *American Fisheries Society Symposium* **1**, 14-25.
- Heuch, P. A., Knutsen, J. A., Knutsen, H. & Schram, T. A. (2002). Salinity and temperature effects on sea lice over-wintering on sea trout (*Salmo trutta*) in coastal areas of the Skagerakk. *Journal of the Marine Biological Association of the UK* **82**, 887-892.
- Hoar, W. S. (1976). Smolt transformation: evolution, behaviour, and physiology. *Journal of the Fisheries Research Board of Canada* **33**, 1233-1252.
- Huusko, A., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Koljonen, S., Louhi, P. & Alfredsen, K. (2007). Life in the ice lane: the winter ecology of stream salmonids. *Rivers Research and Applications* **23**, 469-491.
- Jepsen, N., Koed, A., Thorstad, E. B. & Baras, E. (2002). Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia* **483**, 239-248.

- Jepsen, N., Schreck, C., Clement, S. & Thorstad, E. (2004). A brief discussion on the 2% tag/body mass rule of thumb. In *Aquatic Telemetry: Advances and Applications, Proceedings of the Fifth Conference on Fish Telemetry* (Spedicato, M. T., Lembo, G. & Marmullaed, G. eds), 255-259. Rome: FAO/COISPA.
- Johnson, L. (1980). The Arctic charr, *Salvelinus alpinus*. In *Charrs, Salmonid fishes of the Genus Salvelinus* (Balon, E. K., Ed.), 15-98. The Hague: Junk.
- Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society* **114**, 182-194.
- Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348-365.
- Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology* **47**, 1391-1401.
- Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P. J. (2001). Life history traits of brown trout vary with the size of small streams. *Functional Ecology* **15**, 310-317.
- Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**, 1-59.
- Knutsen, J. A., Knutsen, H., Gjøseter, J. & Jonsson, B. (2001). Food of anadromous brown trout at sea. *Journal of Fish Biology* **59**, 533-543.
- Knutsen, J. A., Knutsen, H., Olsen, E. M. & Jonsson, B. (2004). Marine feeding of anadromous *Salmo trutta* during winter. *Journal of Fish Biology* **64**, 89-99.
- Kristoffersen, K., Halvorsen, M. & Jørgensen, L. (1994). Influence of parr growth, lake morphology, and freshwater parasites on the degree of anadromy in different populations of Arctic char (*Salvelinus alpinus*) in northern Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1220-1246.
- Kristoffersen, R., Rikardsen, A. H., Winger, A. C., Adolfsen, P. & Knudsen, R. (2005). Røye som landtidsvert og smittereservoar for *Gyrodactylus salaris* i Skibotnelva i Troms. *NINA rapport* **36** (in Norwegian).
- L'Abée-Lund, J. H., Jonsson, B., Jensen, A. J., Sættem, L. M., Heggberget, T. G., Johnsen, B. O. & Næsje, T. F. (1989). Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* **58**, 525-542.

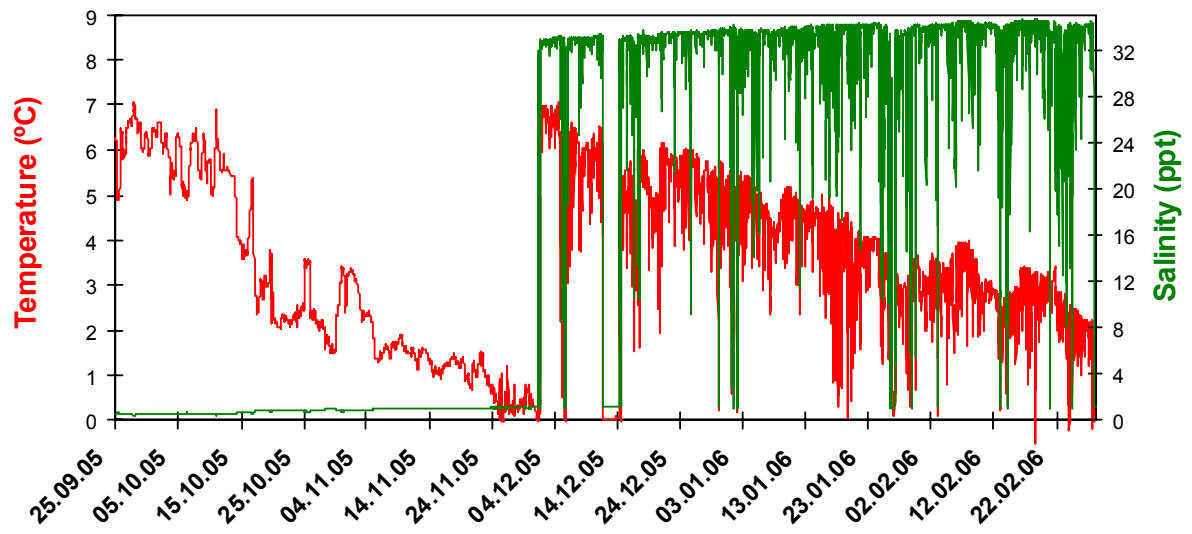
- Limburg, K. E., Landergren, P., Westin, L., Elfman, M. & Kristiansson, P. (2001). Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. *Journal of Fish Biology* **59**, 682-695.
- Lyse, A. A., Stefansson, S. O. & Fernö, A. (1998). Behaviour and diet of sea trout post-smolt in a Norwegian fjord system. *Journal of Fish Biology* **52**, 923-936.
- Mathisen, O. A. & Berg, M. (1986). Growth rates of the char *Salvelinus alpinus* (L.) in the Vardnes River, Troms, northern Norway. *Report of the Institute of Freshwater Research, Drottningholm* **48**, 117-186.
- McCormic, S. D. (2001). Endocrine control of osmoregulation in teleost fish. *American Zoologist* **4**, 781-794.
- McCormic, S. D. & Saunders, R. L. (1987). Preparatory physiological adaptations for marine life of salmonids: Osmoregulation, growth, and metabolism. *American Fisheries Society Symposium* **1**, 211-229.
- Metcalfe, J. D. & Arnold, G. P. (1997). Tracking fish with electronic tags. *Nature* **387**, 665-666.
- Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**, 1370-1386.
- Nilssen, K. J., Gulseth, O. A. , Iversen, M. & Kjøl, R. (1997). Summer osmoregulatory capacity of the world's northernmost living salmonid. *American Journal of Physiology* **272**, 743-749.
- Nordeng, H. 1983. Solution to the char problem, based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1372-1387.
- Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B. & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of Freshwater Fish* **15**, 446-452.
- Pemberton, R. (1976). Sea trout in North Argyll sea lochs, population, distribution and movements. *Journal of Fish Biology* **9**, 157-179.
- Rikardsen, A. H. (2004). Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. *Journal of Fish Biology* **65**, 711-722.
- Rikardsen, A. H. & Elliot, J. M. (2000). Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. *Journal of Fish Biology* **56**, 328-346.

- Rikardsen, A. H. & Thorstad, E. B. (2006). External attachment of data storage tags increases probability of being recaptured in nets compared to internal tagging. *Journal of Fish Biology* **68**, 963-968.
- Rikardsen, A. H., Svenning, M.-A. & Klemetsen, A. (1997). The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. *Journal of Fish Biology* **51**, 447-461.
- Rikardsen, A. H., Amundsen, P.-A., Bjørn, P. A. & Johansen, M. (2000). Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. *Journal of Fish Biology* **57**, 1172-1188.
- Rikardsen A. H., Sandring, S. & Knudsen, R. (2002). Marin vintervandring til sjøørret i Nord-Norge. *NINA Oppdragsmelding* **738** (in Norwegian).
- Rikardsen, A. H., Amundsen, P.-A. & Bodin, P. J. (2003). Growth and diet of anadromous Arctic charr after their return to freshwater. *Ecology of Freshwater Fish* **12**, 74-80.
- Rikardsen, A. H., Thorpe, J. E. & Dempson, J. B. (2004). Modelling the life-history variation of Arctic charr. *Ecology of Freshwater Fish* **13**, 305-311.
- Rikardsen, A. H., Amundsen, P.-A., Knudsen, R. & Sandring, S. (2006). Seasonal marine feeding and body condition of sea trout *Salmo trutta* at its northern distribution. *ICES Journal of Marine Science* **63**, 466-475.
- Rikardsen, A. H., Dempson, J. B., Amundsen, P. A., Bjørn, P. A., Finstad, B. & Jensen, A. J. (2007a). Temporal variability in marine feeding of sympatric Arctic charr and sea trout. *Journal of Fish Biology* **70**, 837-852.
- Rikardsen, A. H., Diserud, O. H., Elliott, J. M., Dempson, J. B., Sturlaugsson, J. & Jensen, A. J. (2007b). The marine temperature and depth preferences of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. *Fisheries oceanography* **16**, 436-447.
- Sømme, I. D. (1941). Ørretboka. Oslo: Jacob Dybwads Forlag. 591 pp. (in Norwegian).
- Sprudles, W. M. (1952). The Arctic charr of the west coast of Hudson Bay. *Journal of the Fisheries Research Board of Canada* **9**, 1-15.
- Stoklosowa, S. (1970). Further observations on the sexual dimorphism in the skin of *Salmo trutta trutta* in relation to sexual maturity. *Copeia* **2**, 332-339.
- Svenning, M., Johansen, M. & Rikardsen, A. H. (2001). Kartlegging av potensielle sjørøyevassdrag i Finnmark – del 3. *NINA Oppdragsmelding* **699** (in Norwegian).
- Thorpe, J. E. (1994). Salmonid fishes and the estuarine environment. *Estuaries* **17**, 76-93.

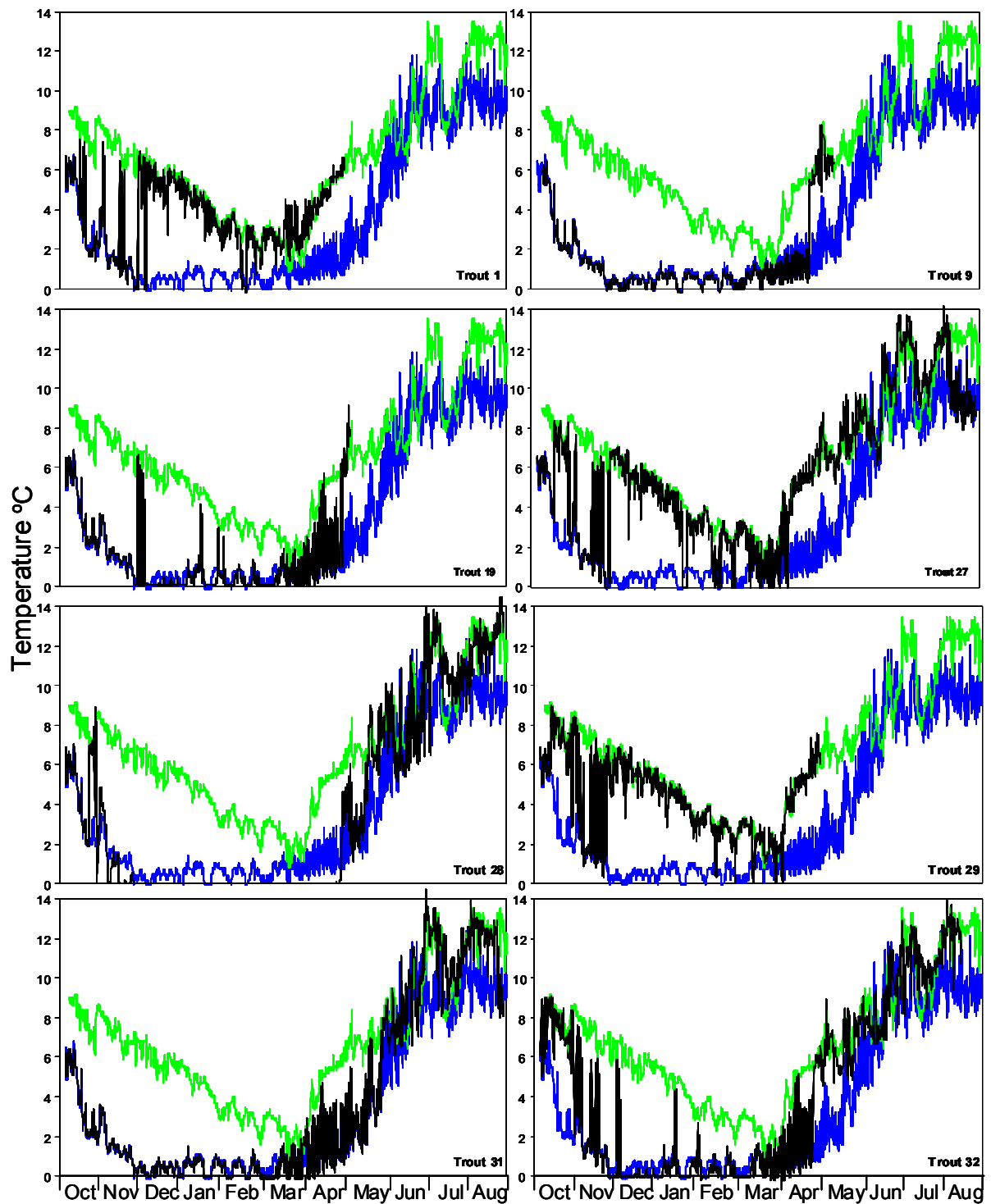
- Thorstad, E. B., Økland, F., Rowsell, D. & McKinley, R. S. (2000). A system for automatic recording of fish tagged with coded acoustic transmitters. *Fisheries Management and Ecology* **7**, 281-294.
- Ugedal, O., Finstad, B., Damsgård, B & Mortensen, A. (1998). Seawater tolerance and downstream migration in hatchery-reared and wild brown trout. *Aquaculture* **168**, 395-405.
- Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540-1548.
- Winger, A. C., Kanck, M., Kristoffersen, R. & Knudsen, R. (in press). Seasonal dynamics and persistence of *Gyrodactylus salaris* in two riverine anadromous Arctic charr populations. *Environmental Biology of Fishes*. DOI 10.1007/s10641-007-9274-x.

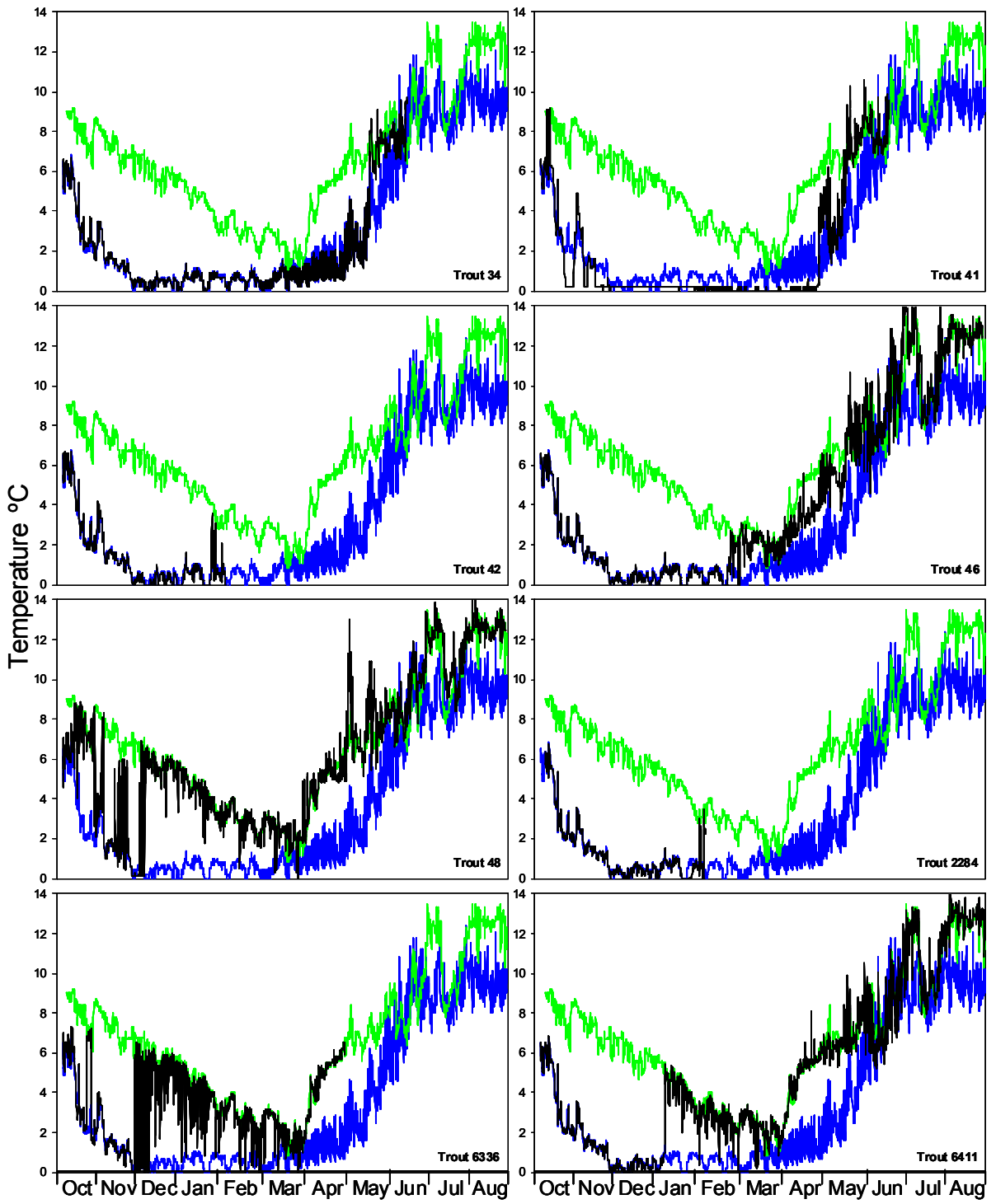
9. APPENDICES

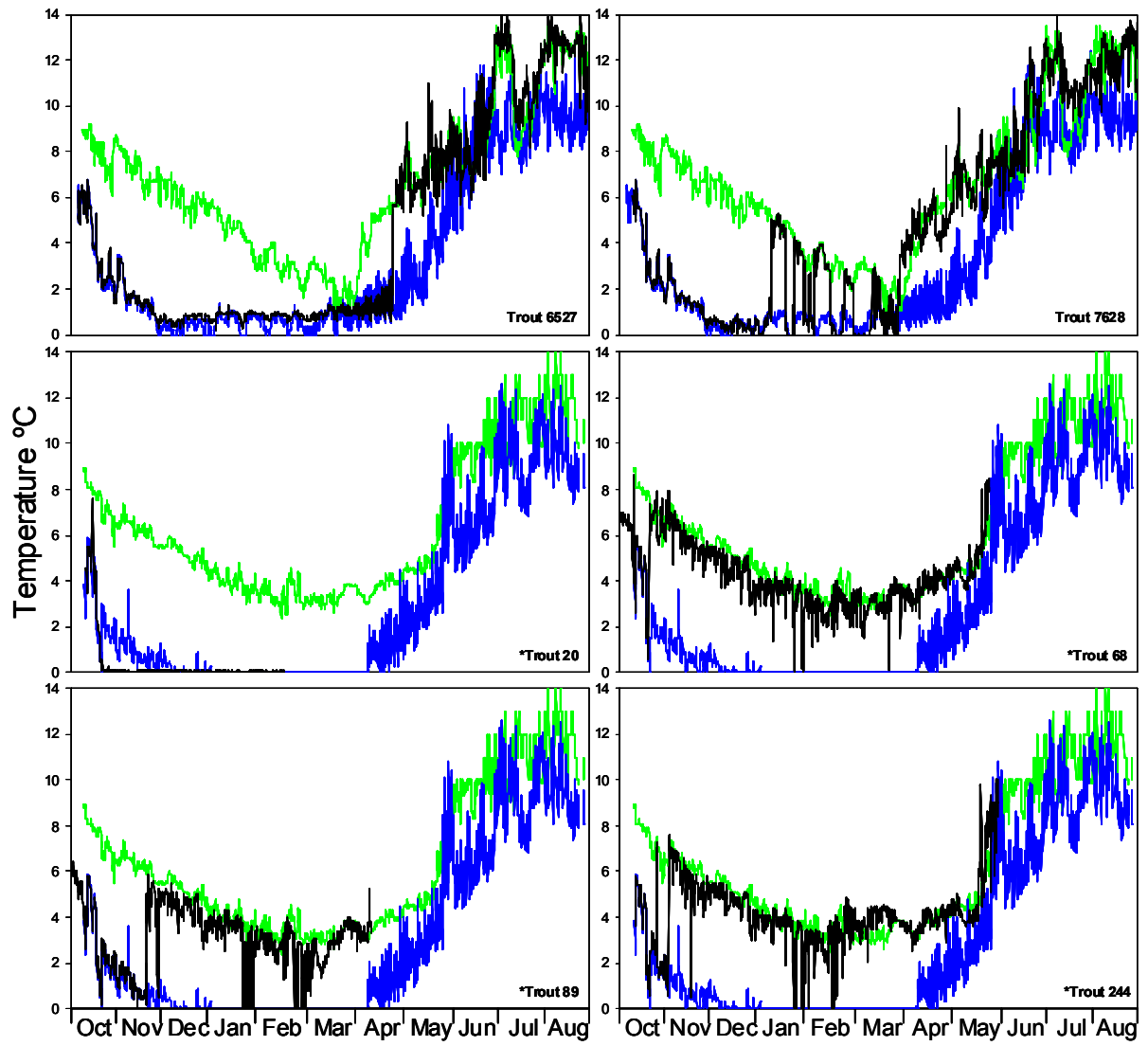
APPENDIX I. Temperature and salinity, as recorded by an Arctic charr (not calibrated).



APPENDIX II. Temperature recorded by individual sea trout (—) related to the temperature recorded in the main river (—) and in the sea (—). Fish tagged in 2006 are indicated (*), the remaining fish were tagged in 2005.







APPENDIX III. Temperature recorded by individual Arctic charr (—) related to the temperature recorded in the main river (—) and in the sea (—). Fish tagged in 2006 are indicated (*), the remaining fish were tagged in 2005.

