

The marine temperature and depth preferences of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags

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ABSTRACT

Eleven Arctic charr (*Salvelinus alpinus*) (370–512 mm) and eight sea trout (*Salmo trutta*) (370–585 mm in length) were tagged externally or internally with depth- and temperature-measuring data-storage tags (DST) before they were released into the sea in the Alta Fjord in north Norway in June 2002. All sea trout were recaptured after they spent 1–40 days at sea, while all Arctic charr were recaptured after 0.5–33 days at sea. On average, trout preferred water about 0.6 m deeper and 1.3°C warmer than Arctic charr. Arctic charr spent >50% of their time between 0 and 1 m depth, while trout spent >50% of their time between 1 and 2 m depth. Both species spent >90% of their time in water no deeper than 3 m from the water surface. However, sea trout dove more frequently and to greater depths (max. 28 m) than Arctic charr (max. 16 m), and these deep dives were most frequently performed at the end of the sea migration. Arctic charr demonstrated a diel diving pattern, staying on average about 0.5 m deeper between 08:00 hours and about 15:00 hours than dur-

ing the rest of the 24 h, even though there was continuous daylight during the experiments. When comparing data obtained from the DSTs with temperature measurements within the fjord system, the two species were observed to select different feeding areas during their sea migration, the sea trout choosing the inner and warmer parts of the fjord, in contrast to the Arctic charr that preferred the outer, colder parts of the fjord. The observed differences in migration behaviour between the two species are discussed in relation to species preferences for prey and habitat selection, and their optimal temperatures for growth.

Key words: anadromy, archival tag, behaviour, brown trout, data-storage tag, life history, migration, optimal temperature

INTRODUCTION

Anadromous Arctic charr [*Salvelinus alpinus* (L.)] and brown trout [(*Salmo trutta* L.) hereafter referred to as sea trout] achieve most of their growth at sea during one to two summer months each year in northern Norway (Berg and Berg, 1989; Berg and Jonsson, 1990; Rikardsen *et al.*, 2000, 2003, 2004a). Both species reproduce and usually overwinter in fresh water, and normally make the annual seaward migration one to three times before they mature at an age of 6–9 years (Jonsson, 1985; Elliott, 1994; Rikardsen *et al.*, 1997, 2004a). Only 10–50% of post-smolts and 50–80% of fish that have been to sea one or more times before (veterans) survive the sea residency each year (Jensen and Berg, 1977; Berg and Jonsson, 1990; Finstad and Heggberget, 1993; Rikardsen, 2000; Rikardsen and Elliott, 2000).

The marine phase is therefore important for the life history and production of Arctic charr and sea trout. Despite this, knowledge of the marine ecology of both species is limited (Rikardsen *et al.*, 2000, 2006; Knutsen *et al.*, 2001), especially when they occur in sympatry in the northern part of Norway (Rikardsen and Amundsen, 2005; Rikardsen *et al.*, 2007). The sparse knowledge of the marine ecology of these two species is due in large part to methodological and

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technological problems related to data collection in the marine environment, as it is more costly and difficult to capture anadromous fish at sea than in fresh water (Knutzen *et al.*, 2001; Rikardsen *et al.*, 2004b).

Data storage tags (DST) for recording migratory behaviour in relation to preferences for salinity, temperature, depth and horizontal distribution now provide a cost-effective way to study migratory behaviour over long periods (Metcalf and Arnold, 1997; Moore and Russell, 2000; Moore *et al.*, 2000; Reddin *et al.*, 2004). For example, Sturlaugsson and Johannsson (1996) studied the marine migratory pattern of Icelandic sea trout using a DST and found that they spent most of their time in the uppermost 5 m of the water column, with occasional dives down to 26 m. No published information exists on the vertical distribution of Arctic charr and sea trout in other areas.

In contrast, the horizontal distribution of both Arctic charr and sea trout in northern Norway has been investigated over several years through conventional tag-recapture studies in the Vardnes River on the island of Senja (Jensen and Berg, 1977; Berg and Berg, 1987; Berg and Jonsson, 1989) and for Arctic charr in the Hals watercourse in the Alta Fjord (Heggberget, 1991). These studies showed that both species fed mainly in an area situated within 30 km from the river mouth, as 70–80% of the recaptures were within this area. Results from the Vardnes system also showed a different migratory pattern for each of the two species with regard to the timing of migration, size at smolt migration, straying and growth pattern (Berg and Berg, 1987, 1989). It was suggested that differences were partly due to different adaptations to water temperature in relation to activity, growth and salinity. However, to our knowledge, no studies have investigated the actual temperature preferences of Arctic charr and sea trout in the marine habitat in Norway.

To describe possible differences in the vertical distribution and temperature preferences of Arctic charr and sea trout, DSTs were used to measure both parameters at 10-min intervals during the whole period from tagging to recapture. The fish were from sympatric populations of these two species from the Hals watercourse in the Alta Fjord in northern Norway. The null hypothesis in the analysis was no difference in depth and temperature preferences of the two species while at sea.

METHODS

Study site

The study was conducted during June and July 2002 with Arctic charr and sea trout specimens from the

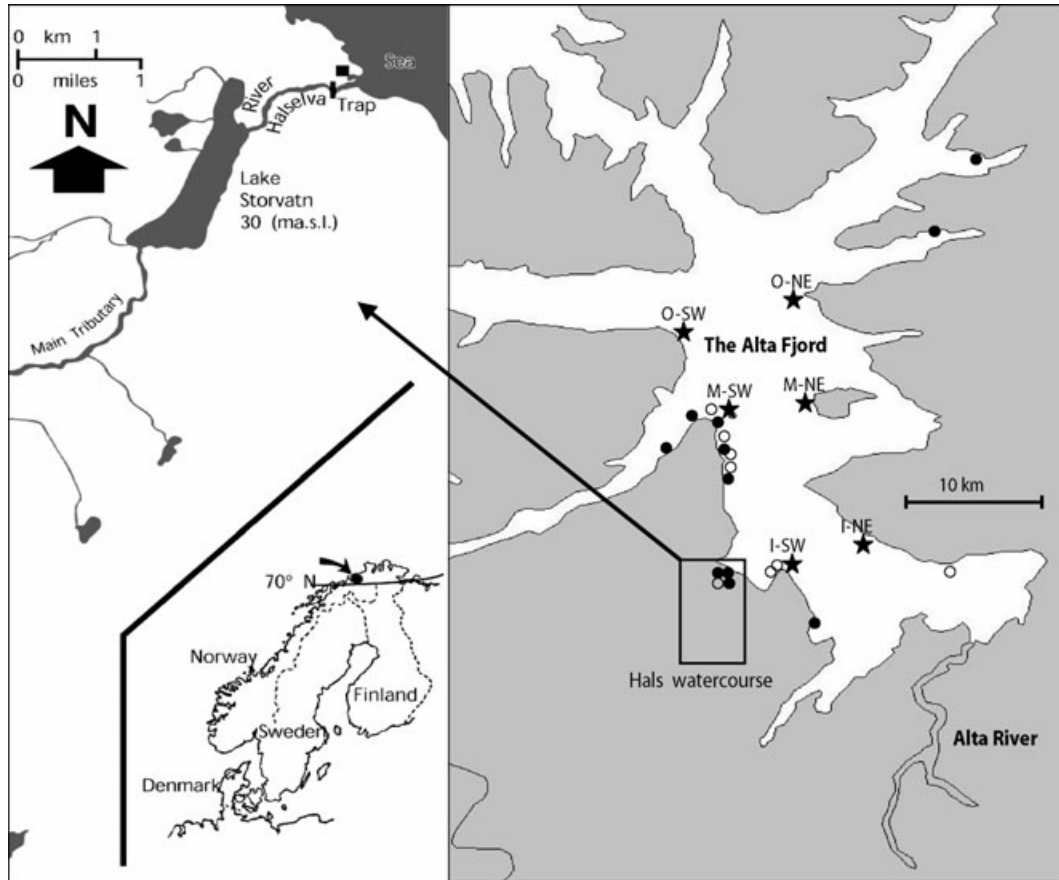
Hals watercourse (70°N; 23°E) which drains into the Alta Fjord, northern Norway (Fig. 1). The watercourse has a catchment area of 143 km² and a total length available for anadromous salmonids of about 20 km. This includes a lake 2.0 km from the sea (Lake Storvatn, 1.2 km²). A fish trap that has been in operation since 1987 is located 200 m upstream of the river mouth. All ascending and descending anadromous fish have been systematically recorded and fish larger than 18 cm (>14 cm from 1987 to 1993) marked individually with Carlin tags since 1987. Smaller fish have been group-tagged by cutting jawbones. In total, between 1000 and 3600 Arctic charr smolts, 300 and 1300 sea trout smolts, and 400 and 2300 Atlantic salmon smolts (*Salmo salar* L.) have been recorded while migrating to sea each year. The Alta Fjord is also supplied by several other watercourses, including the large Alta River.

Tagging

Eleven Arctic charr [mean fork length = 442 mm (370–512 mm), mean mass = 766 g (464–1079 g)] and eight sea trout [mean fork length = 493 mm (370–585 mm), mean mass = 1112 g (474–1621 g)] were trapped while descending the Hals River in 2002, and tagged with a DSTmilli (13 × 39 mm, 9 g in air; Star Oddi, Reykjavik Iceland) (Table 1). The tag stores data on temperature and pressure (depth) in relation to time. The sensor accuracy for the DSTmilli is ±20 cm for depth measurements and ±0.1°C for temperature measurements. While the depth response time is immediate, the temperature response time is 20 s to reach 63% (time constant), 3 min to reach 95%, and 6.37 min to reach 100% full value. When a fish is recaptured, data are retrieved by connecting the tag to an upload box linked to a computer. The tag can then be reused as long as the battery lasts (2–3 years according to the manufacturer). The tag weight in air was on average 1.0% (range 0.5–1.9%) of the body mass of the fish. Similar tag/fish mass relationships did not affect the swimming ability or food consumption of Atlantic salmon (Thorstad *et al.*, 2000; Robertson *et al.*, 2003). Each tag was set to record temperature and pressure (depth) at 10-min intervals. One tag was attached to each fish, either internally or externally. All tags were calibrated by placing them simultaneously at known depths and temperatures for 12 h.

The fish were anaesthetized by the use of clove oil (Iversen *et al.*, 2003). For internal tagging, the fish was placed with the ventral side up on a partly submerged V-shaped surgical table. An incision, approximately 2 cm long, was made on the ventral surface posterior to

Figure 1. Map of the study area showing the recaptures of tagged sea trout (○) and Arctic charr (●), and the inner (I), middle (M) and outer (O) temperature recording sites (★) on the southwest (SW) and northeast (NE) side of the fjord.



the pelvic girdle, using a scalpel. The DST was inserted through the incision and pushed into the body cavity above the pelvic girdle. The internal tag was equipped with an identification tube that was pushed through the body wall using a hollow needle. A knot was made outside on the tube to prevent it from sliding back into the body cavity. The incision was closed using two or three independent absorbable silk sutures (3/0 Ethicon, Dilbeek, Belgium). The external tags were attached to the fish below the dorsal fin. Two hollow needles were pushed through the dorsum of the fish 1.5–2 cm below the dorsal fin. The spacing between the needles matched the length of the tag. A plastic back plate was used on the opposite side to prevent erosion of the flesh by the attachment wire. Handling time was 3–5 min and recovery time (when the fish had returned to seemingly normal behaviour) was approximately 10 min for both methods. Prior to each incision, surgical equipment was rinsed in 96% ethanol.

Seventeen fish (10 Arctic charr and seven sea trout) were tagged on 4 June 2002 and kept in a tank

for observation over 24 h before being released below the trap (Table 1). In addition, one fish of each species was tagged and released on 15 June 2002 (using tags that were reused from recaptured tagged fish from the first period), making a total of 19 tagged fish altogether. The Arctic charr and sea trout were released at the same time for comparisons between the species.

Fish recaptures and temperature recordings in the fjord

Returning Atlantic salmon are fished using bag nets in the Alta Fjord, and larger Arctic charr and sea trout are frequently captured in these nets. Because of the external tag on the dorsal fin, large, tagged fish seem to be more easily entangled in these nets than untagged fish (Rikardsen and Thorstad, 2006). We therefore expected that several fish would be recaptured by local fishers, and return of the tags was rewarded with 500 NOK per tag. All tagged fish that returned to their home river were captured in the fish trap.

The DST-tagged fish were measured (fork length, L_f) to the nearest millimetre and weighed to the

Table 1. Different characteristics of the DST-tagged fish.

Species	No. days	L_f (mm)	W (mg)	Tagging method	No. migr.	Release	Recapture	Recapt. method	Mean depth	Mean temp.	
Charr	0.5	423	690	External	4	5 June	5 June	Net	1.4 ± 0.56	12.3 ± 1.09	
	0.7	493	937	External	15	5 June	5 June	Net	1.2 ± 0.52	10.2 ± 2.31	
	1	437	774	External	7	5 June	6 June	Net	1.0 ± 0.39	12.1 ± 0.93	
	5	430	727	External	6	5 June	10 June	Rod	1.4 ± 0.48	11.4 ± 0.82	
	8	402	578	External	6	5 June	13 June	Net	1.2 ± 0.71	11.1 ± 1.71	
	11	370	464	External	4	15 June	26 June	Net	1.5 ± 0.68	10.2 ± 1.22	
	17	455	898	Internal	12	5 June	5 July	Trap*	1.3 ± 0.67	11.0 ± 1.05	
	18	512	1079	Internal	8	5 June	23 June	Rod	1.1 ± 0.61	10.2 ± 1.82	
	20	439	688	External	5	5 June	25 June	Net	1.0 ± 0.50	10.4 ± 1.90	
	26	475	855	Internal	8	5 June	3 July	Trap*	1.1 ± 1.37	11.8 ± 1.08	
	33	451	755	Internal	8	5 June	8 July	Trap*	0.9 ± 0.59	10.0 ± 1.23	
	Trout	1	471	871	External	5	5 June	6 June	Net	0.8 ± 0.37	12.9 ± 1.19
		2	565	1544	External	7	5 June	7 June	Net	0.9 ± 0.48	12.7 ± 1.08
15		486	1112	External	4	5 June	20 June	Net	2.0 ± 0.79	12.6 ± 1.45	
22		485	1143	External	7	5 June	27 June	Net	1.8 ± 1.58	12.2 ± 1.49	
23		487	1022	External	4	5 June	28 June	Net	1.9 ± 0.98	12.7 ± 1.16	
28		583	1569	External	7	5 June	3 July	Net	1.5 ± 1.78	11.5 ± 1.76	
29		370	474	External	9	15 June	14 July	Net	1.9 ± 2.08	11.7 ± 1.74	
40		585	1621	Internal	8	5 June	15 July	Trap*	1.6 ± 1.20	11.7 ± 1.64	

*Some of these fish stayed in fresh water for some time before they were recaptured and the days at sea therefore do not necessarily correspond with time of recapture.

No. days = days at sea before recapture; fork length (L_f) and weight (W) at tagging; No. migr. = total number of recorded annual sea migrations during their lifespan.

Arithmetic mean depth and temperature are given for each fish with \pm SD.

nearest 0.1 g. Sex, degree of maturation and age (estimated from otoliths) were recorded whenever possible. All DST-tagged fish had also been previously tagged with individually numbered Carlin tags indicating their migration history based on movement into and out of the fish trap on the Hals system (Table 1).

Vertical temperature ($^{\circ}$ C) profiles (0–24 m depth; Table 2) were measured at different locations within the fjord on both the north-east and south-west side (Fig. 1) at four different time periods (6 June to 17 July) by using a hand-held YSI 85CE thermometer (YSI Inc., Yellow Springs, OH, USA).

Statistical analysis

All individuals with less than 2 days at sea before recapture were removed from the subsequent analysis, as the fish seemed to behave differently during this early period than in the later period (see Results). Average depth and temperature values were calculated for each individual, and the species mean depth and temperatures were estimated from the individual averages within the species. When comparing the two species with respect to the different parameters (mean depth, temperature, etc.), standard two-sample *t*-tests were used to determine if the observed difference

between sample mean values was significant ($P < 0.05$). The assumption regarding normally distributed variables was checked and accepted by the Shapiro–Wilk normality test (Zar, 1999). All statistical analyses were performed with the free statistical software R (<http://www.r-project.org>).

RESULTS

Recaptures

All 11 Arctic charr were recaptured after 0.5–33 days at sea, while all eight sea trout were recaptured after they spent 1–40 days at sea (Table 1). Two Arctic charr were recaptured by sports fishermen in the sea, 13 fish of both species were recaptured in salmon bag nets mostly on the south-west side of the fjord, while three Arctic charr and one sea trout were recaptured in the fish trap when returning to fresh water (Table 1). All fish were recaptured within the Alta Fjord (Fig. 1).

Temperature profiles within the fjord

At 0–4 m depth on the south-west side of the fjord system (where most of the fish were recaptured), there

Table 2. Temperatures (°C) taken at different depths (m) in the inner, middle and outer part of both the north-east (NE) and south-west (SW) side of the Alta fjord.

Side of fjord	Depth	6 June			14 June			2 July			17 July		
		Inner	Middle	Outer	Inner	Middle	Outer	Inner	Middle	Outer	Inner	Middle	Outer
SW	0	14.2	12.2	13.8	13.6	12.1	13.1	13.3	13.1	11.8	16.5	14.0	12.5
	1	12.8	11.1	11.6	13.6	12.0	11.7	12.9	12.9	10.4	16.3	13.8	12.2
	2	12.3	9.4	8.4	13.6	10.2	8.6	11.5	12.8	9.6	15.3	14.0	12.2
	4	9.6	8.3	8.0	10.1	8.4	7.5	9.8	12.0	8.6	13.9	12.7	12.1
	8	7.4	7.4	7.8	7.4	7.0	7.1	8.1	8.0	7.3	11.2	11.7	12.0
	12	7.0	7.5	7.5	6.4	6.1	6.2	7.5	7.0	6.7	9.7	10.5	11.8
	24	5.8	6.8	7.1	5.2	4.9	4.8	5.4	5.6	5.5	6.9	7.4	9.5
	0–4	12.2	10.3	10.4	12.7	10.7	10.2	11.9	12.7	10.1	15.5	13.6	12.3
NE	0	13.2	10.7	13.2	9.3	12.3	14.2	14.0	14.5	14.5	14.7	15.3	14.7
	1	12.3	9.9	12.8	9.2	11.9	12.6	13.9	13.8	12.7	14.6	15.0	13.2
	2	9.9	9.3	11.0	8.6	11.6	12.4	13.6	12.5	12.4	13.6	14.4	13.0
	4	8.2	8.2	7.9	7.4	9.6	10.3	11.0	12.2	12.0	13.0	14.0	13.0
	8	7.4	7.7	7.1	6.7	8.0	8.4	8.8	9.2	8.4	11.8	12.4	12.6
	12	7.2	7.6	6.8	6.1	7.3	6.6	7.1	8.4	7.7	9.9	11.9	11.3
	24	5.7	6.5	5.8	5.1	5.1	5.6	5.3	5.9	6.5	6.7	6.4	7.0
	0–4	10.9	9.5	11.2	8.6	11.4	12.4	13.1	13.3	12.9	14.0	14.7	13.5

See Fig. 1 for location of the measuring stations.

was a general trend of warmer water in the inner, compared with the middle and outer parts (Table 2). No such trend was found on the north-eastern side, which generally had lower surface temperatures (0–4 m depth) in the inner part during the first half of June because of mixing of colder freshwater runoff from the Alta River during this period. The Alta River has its runoff outward on the north-eastern side of the inner part of the fjord. In all locations and periods, the warmest water was found at the surface with temperature decreasing with depth. The thermocline was usually found between 2 and 8 m in June and 4 and 12 m in July.

Mean depth and ambient temperature experienced by the fish

Sea trout stayed significantly deeper (t -test, $P < 0.001$) and preferred significantly warmer water (t -test, $P < 0.001$) during their sea migration than Arctic charr (Fig. 2). Overall mean depth for Arctic charr and sea trout was 1.2 m (SD = 0.19) and 1.8 m (SD = 0.20), respectively, while overall mean temperature during the same period was 10.7°C (SD = 0.66) and 12.1°C (SD = 0.51), respectively (Table 1, Fig. 2). If all dives >5 m depth were considered outliers and not included in the calculations, the species difference in depth preference was still significant (t -test, $P = 0.013$), but the mean depth was reduced to 1.17 m for Arctic charr compared with 1.58 m for sea trout.

Time at depth and diving frequency

Arctic charr spent 53% of their time between 0 and 1 m depth, while trout spent the same amount of their time between 1 and 2 m depth (Fig. 3a). Arctic charr and sea trout spent 97% and 93% of their time, respectively, in water no deeper than 3 m.

Although there were individual differences in diving patterns within the species throughout the sea migration (Fig. 4), the mean depth showed that during the first 5 days after entering saltwater, the sea trout generally spent double the amount of time (46%) between 0 and 1 m than during the rest of their sea migration (19%) (Fig. 3c). Throughout the sea migration, sea trout also spent an increasing amount of time at water depths >5 m. In contrast, Arctic charr had a more uniform depth preference during the same period (Figs 3b and 4). This difference was largely due to the fact that the sea trout had a higher frequency of deep dives (t -test, $P = 0.035$) and to greater depths than the Arctic charr (max. depth = 28 and 16 m, respectively; Fig. 4), and that the deep dives of sea trout increased in frequency and maximum depth during the second half of their sea migration. For both species, >93% of the deep dives were of short duration, i.e. only one or two succeeding records >5 m depth for the 10-min recording intervals. Only the sea trout that had stayed at sea for >4 weeks (T-28, T-29 and T-40; Table 1 and Fig. 4) had deep dives that lasted for more than 1 h (one, two and one dive, respectively).

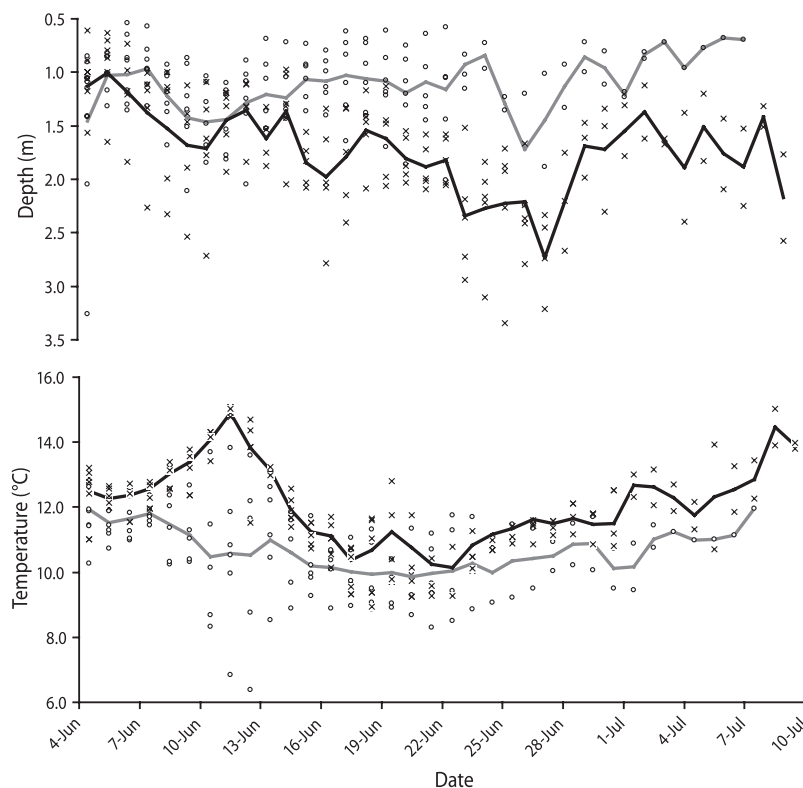


Figure 2. Mean temperature ($^{\circ}\text{C}$) (lower figure) and depth (m) (upper figure) of sea trout (black line) and Arctic charr (grey line) during the sea migration. To show the individual variation, the daily average for each fish is given for both Arctic charr (O) and sea trout (x).

Diel and tidal diving pattern

Arctic charr demonstrated a diel diving pattern, with an amplitude of approximately 0.5 m. Individuals stayed at greater depth ($\pm\text{SE}$) (1.4 ± 0.04 m) between 12:00 and 16:00 hours, and at shallowest depth (0.8 ± 0.02 m) around midnight (23:00–01:00 hours), even though there was continuous daylight over 24 h during the time of the experiments (Fig. 5a). A slightly similar pattern occurred in sea trout, but was less pronounced than that for Arctic charr. Both species stayed in slightly warmer water during the second half of the day (Fig. 5b).

The Arctic charr seemed to stay in deeper water at extreme low tide and in shallower water at extreme high tide (Fig. 5c). The sea trout showed the same pattern at extreme low tide but, in contrast to Arctic charr, they seemed to prefer deeper water also at extreme high tide. At extreme low tide, both species experienced higher water temperatures in contrast to extreme high tide where they stayed at lower water temperatures (Fig. 5d).

DISCUSSION

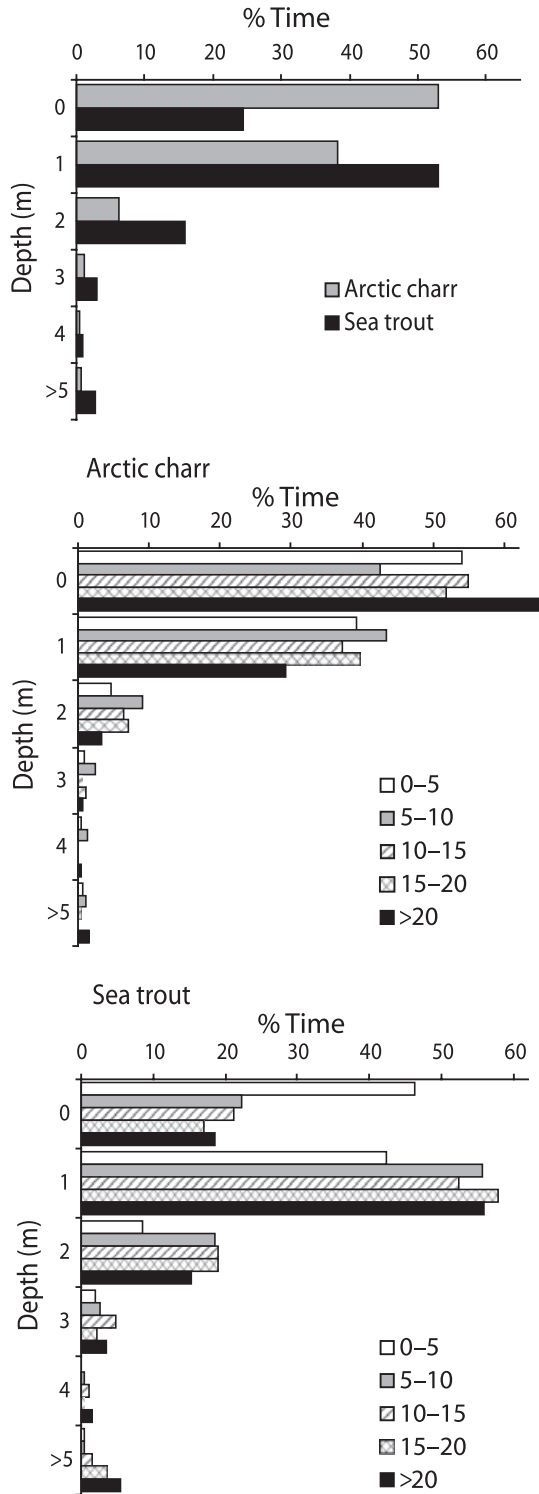
Temperature and depth preferences

There were significant differences in both mean depth and mean temperature preference between the two

species at sea. In addition, there seemed to be some differences in depth and temperature preferences in relation to time spent at sea, tides and time of day. Therefore, the null hypothesis of no difference between species was rejected. Although both species were previously assumed to co-occur and feed in shallow, near-shore areas (Pemberton, 1976; Grønvik and Klemetsen, 1987; Lyse *et al.*, 1998; Rikardsen *et al.*, 2000, 2006; Klemetsen *et al.*, 2003), the results of the present study show that there are subtle differences in how they behave at sea.

Almost all sea trout not only remained deeper, but also in warmer water, than Arctic charr. As the warmest water was found at the surface and water temperature decreases with depth in the Alta Fjord during summer, the species differences in temperature and depth preference strongly indicate that the two species must have selected different feeding areas during their ocean migration. This was also supported by the within-species similarities in temperature profiles of the individual fish during their sea migrations. For example, sea trout experienced a gradually increasing water temperature profile during the first 10 days at sea, while Arctic charr usually experienced a decreasing water temperature at the same time (Figs 2 and 4). The difference in migration behaviour between the two species may be related to differences

Figure 3. Percentage of time spent at different depths for sea trout (grey) and Arctic charr (black) during the total sea migration (a), and for different periods after the Arctic charr (b) and sea trout (c) first entered the sea, given as 5-day intervals.



in their preferences for prey and habitat selection and/or their optimal temperatures for growth.

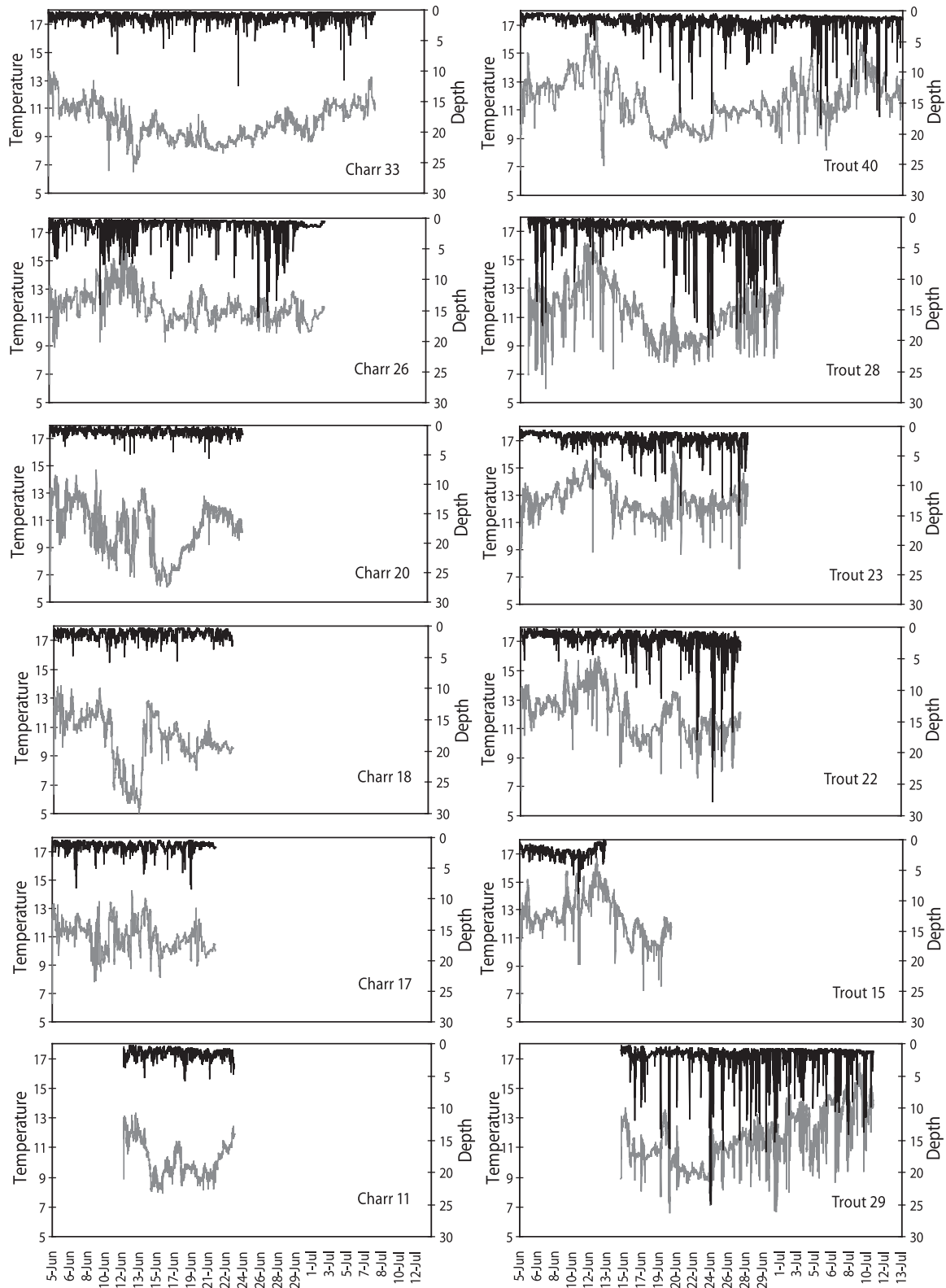
Prey selection

In general, sea trout feed proportionally more on marine fish than on crustaceans and surface insects compared with Arctic charr (Pemberton, 1976; Grønvik and Klemetsen, 1987; Rikardsen *et al.*, 2000, 2003, 2006; Knutsen *et al.*, 2001; Rikardsen and Amundsen, 2005). Therefore, Arctic charr may be better adapted to feed near the surface on insect and surface-oriented planktonic crustaceans than sea trout. However, Rikardsen *et al.* (2007) found that while sea trout >250 mm in the Alta Fjord fed almost exclusively on herring (*Clupea harengus*), nearly all the Arctic charr became piscivorous at a length >400 mm, feeding significantly also on gadoids and sand eels (*Ammodytes* spp.) together with herring. As most Arctic charr in the present study were >400 mm, they were probably piscivorous and, therefore, the different preferences of the two species for depth and temperature may also be related to factors other than food preferences, e.g. different optimal temperatures.

Optimal temperature

Temperature is a factor not only affecting the physiology and behaviour of a fish, but is also a characteristic of a fish's habitat, being one axis of its multidimensional niche (Magnuson *et al.*, 1979; Elliott, 1994; Larsson, 2005). The upper thermal limits for survival are about 3°C higher for brown trout than for Arctic charr in fresh water, otherwise, their thermal limits for growth and feeding may be similar (Baroudy and Elliott, 1994; Elliott and Baroudy, 1995; Lyytikäinen *et al.*, 1997; Thyrel *et al.*, 1999; Elliott and Klemetsen, 2002; Larsson *et al.*, 2005). No such data exist for the two species in salt water. It is possible that the preference for slightly warmer water shown by the trout in the present study reflected their higher temperature tolerance, even though temperatures in the Alta Fjord were well below the upper critical limits for the survival of both species. In general, the inner south-western parts of the fjord were found to have a higher water temperature than the outer part. Therefore, the observed preferences in temperature between the two species may be a consequence of sea trout generally preferring the inner and warmer parts of the fjord, in contrast to Arctic charr that may chiefly utilize the outer or other colder part of the fjord. The different temperature preferences of the two species could also be due to their optimum temperatures for efficiency of food conversion. In fact, Larsson (2005)

Figure 4. Depth (m) (black line) and temperature (°C) (grey line) preferences for individual sea trout (right figures) and Arctic charr (left figures) from tagging until recapture. Values are given every 10 min.



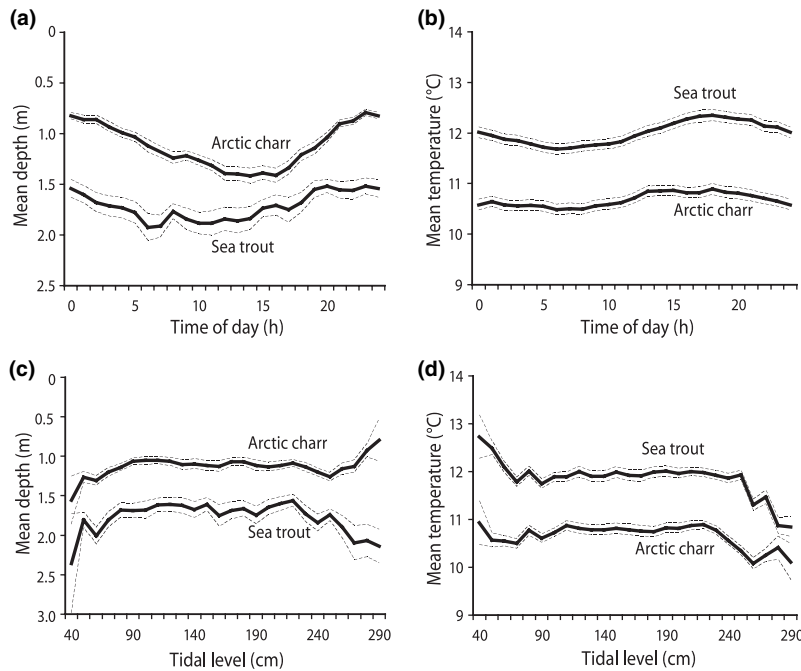


Figure 5. The diel preferences in (a) mean depth and (b) mean temperature and the tidal preferences in (c) mean depth and (d) mean temperature for all sea trout and Arctic charr. The start of a new day is indicated by 0 h, while the dotted line indicates 95% CL, where the CL was calculated by first estimating the average for each fish within each hour, and then the variation of all individual averages within the species and hours.

has recently shown in a laboratory experiment that brown trout preferred the reported optimal temperature for growth (approximately 16°C) while the Arctic charr selected a significantly lower temperature (approximately 11°C) that is closer to its optimal temperature for growth efficiency (approximately 9°C) than its optimal temperature for growth. He argued that charr were optimizing their growth efficiency instead of their growth rate. This corroborates the results in the present study, and such a bioenergetics hypothesis could explain some of the movements observed for both species in the Alta Fjord. For Arctic charr, which are found to inhabit the most arctic and hostile habitats of all freshwater fishes (Klemetsen *et al.*, 2003), a strategy of utilizing limited resources in an optimal way will possibly be favoured for this species both in salt water and freshwater habitats. However, it must be emphasized that all the information on the temperature preferences of the two species has been obtained in fresh water and chiefly on juvenile fish. There is a paucity of similar information for larger fish of both species in sea water, and clearly some studies are required to test if the relationships described above are generally applicable.

Deep dives

Diving patterns similar to those observed in our study have been noted for adult salmon at sea while migrating back to rivers in Sweden (Westerberg, 1982), Norway (Døving *et al.*, 1985) and Iceland

(Sturlaugsson and Thorisson, 1997) and for Atlantic salmon post-smolts in a fjord in Norway (Holm *et al.*, 1996). In all of these studies the fish periodically underwent a series of rapid dives below the thermocline, often down to 20–40 m or deeper before entering fresh water. In the present study, such dives were frequently followed by a marked drop in temperature for fish with externally attached tags, indicating that the fish dived below the thermocline, which was at a depth of 2–12 m in the Alta Fjord. These drops in temperature were not seen clearly in fish with internal tags, suggesting that dives were likely of too short a duration to result in a change in temperature within the belly of the fish.

As dives in the present study were usually of short duration and less frequent in the early season, which is usually the period of highest feeding intensity (Rikardsen *et al.*, 2000, 2006), the dives were probably not used to search for prey or for more efficient digestion at lower temperatures (see earlier discussion). The deep dives were also probably not related to predator avoidance as the fish in this experiment are generally too large to be taken by sea birds (Svenning *et al.*, 2005) and most marine fish (Hvidsten and Møkkelgjerd, 1987), and marine mammals (e.g. seals) are usually not abundant within the Alta Fjord (A. H. Rikardsen, pers. obs.).

The deep dives seen in the earlier studies of Atlantic salmon were most frequently found in highly stratified and/or turbulent water (Westerberg, 1982;

Holm *et al.*, 1996; Sturlaugsson and Thorisson, 1997). By comparing the vertical diving behaviour of Atlantic salmon with blocked olfactory organs with that of control fish, as well as the neural responses to water from different depths, Døving *et al.* (1985) concluded that vertical dives were related to olfactory orientation at different stratified water layers in near-shore regions. As the upper 30 m of the water column in the Alta Fjord was often highly stratified with regard to temperature, salinity and current (A. H. Rikardsen, pers. obs.), it is possible that the deep dives below the thermocline were also used by the fish for purposes of orientation in relation to homing. This may explain, in part, why dives were most frequently seen at the end of the sea migration, especially for sea trout. It is more difficult to explain why the same pattern was less clearly observed for Arctic charr, but this could be related either to species differences, or that charr utilize other areas and cues (e.g. less stratified waters) more, so that deep dives are less needed for orientation purposes. Note that the Arctic charr that dived most frequently (Charr 26, Fig. 4) had a temperature profile more similar to the sea trout than the rest of the Arctic charr, indicating that this charr may have been in the same area as the sea trout.

The length of deep dives could also be related to the depth for neutral buoyancy. For example, Harden Jones and Scholes (1985) showed that if a cod was neutrally buoyant at 2 m, it had to use energy at greater depths to maintain depth-compensating activity for their updraft. Therefore, the duration of the vertical dives shown by Arctic charr and sea trout in the present study might also be a trade-off between energy demand to remain at depth and prey encounter rate.

Diel and tidal pattern

The diel differences in depth, where the Arctic charr generally stayed about 0.5 m deeper during the day, were less clear for the sea trout. This difference between the species may be related to their differences in prey selection. Despite continuous daylight over 24 h during summer in these latitudes, fish prey such as planktonic crustaceans display diel vertical migrations and usually stay near the surface when the sun is at its lowest (Falkenhaug *et al.*, 1997). Rikardsen *et al.* (2007) found Arctic charr to feed proportionally more on planktonic crustaceans than the more piscivorous sea trout, which may explain the diel pattern observed with Arctic charr. However, as discussed earlier, the Arctic charr may also seek slightly deeper cooler water to avoid surface heating of the water between 08:00 and about 18:00 hours. This diel behaviour may therefore be more easily seen in the Arctic charr as

this species usually stays closer to the surface than the sea trout.

In general, there were no effects of ordinary tide level on the depth distribution of the two species. However, Arctic charr seemed to stay in deeper water at extreme low tide and in shallower water at extreme high tide, while the sea trout stayed in deeper water at both extreme low and high tide. Arctic charr may frequent shallower water at extreme high tides to feed on submerged prey, or feed more on drifting prey items flooded by the high tide. Reasons why sea trout prefer deeper water during periods of high tide, or why both species prefer deeper water during extreme low tide cycles are unclear but could be related to availability of shelter. During periods of low tide there may be less shelter or food available along the shoreline as most seaweed is drained, forcing fish to seek out deeper, more off-shore areas. Alternatively, both species may stay in deeper water at extreme low tides because of the seemingly higher temperature at the surface during this period.

CONCLUSION

Arctic charr and sea trout select different feeding areas during their sea migration: Arctic charr choose colder water and probably the outer parts of a fjord system, in contrast to sea trout that prefer the warmer inner parts. The two species also showed differences in depth preference and diving frequency, which may be related to the species preferences for prey and habitat selection, orientation and their optimal temperatures for growth. Therefore, there is probably little competition for food and habitat resources at sea between the two species. However, to further evaluate the observed differences, the horizontal distribution, in combination with depth and temperature measurements, needs to be studied. Studies like this will be important for predicting species-specific responses to climate change, as different species seemingly respond differently to possible long-term changes in the marine environment.

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