Temperature and depth preferences of adult sea trout *Salmo trutta* during the marine migration phase

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ABSTRACT: We tagged 125 sea trout kelts (length: 460–925 mm) in Danish rivers with positively buoyant, depth- and temperature-sensing data storage tags. Eight tags were recovered from fish that had completed a full marine cycle (exit and return to natal river). Mean duration of the post-estuary marine cycle was 96.1 d (range: 47–142 d). The trout resided at depths of 0–3 m for 63.8% of the time and exhibited a characteristic diurnal behavioural pattern with repetitive dives deeper than 5.0 m during daytime and residency at the surface during night-time. The number of dives increased with day length, but dive duration was unaffected. Mean dive duration increased with water temperatures from 9.79 min at 5–7°C to 79.8 min at 17–19°C, and mean residence depth increased with water temperatures from 1.95 m at 5–7°C to 10.1 m at 17–19°C. The fish showed a marked response to temperatures above 17°C by residing at greater depths and by discontinuing the characteristic dive/surface residency pattern for prolonged periods of time during warm periods. Temperature data indicated that the fish were generally close to land in the beginning of the marine period and had migrated into open sea during summer. Our results suggest that Danish sea trout kelts aim to optimize their growth at sea by exhibiting a characteristic foraging pattern similar to that of Atlantic salmon and by seeking temperatures within the range reported as optimal for growth in the species.

KEY WORDS: Sea trout · Kelts · Telemetry · Data storage tag · DST · Temperature · Depth

INTRODUCTION

The lifecycle of anadromous brown trout *Salmo trutta* L. begins in freshwater streams and rivers where juvenile fish hatch and grow for a period of 1–8 yr before smoltifying and migrating to sea (Christensen et al. 1993, Elliott 1994). Brown trout migrants feed and grow at sea for a period of 0.5–4 yr before returning to the river to spawn (Crisp 2000, Thorstad et al. 2016). Increased food abundance at sea allows individuals to increase weight and length substantially. In consequence, most of the lifetime growth takes place in the marine phase of the sea trout lifecycle (Gross et al. 1988, Klemetsen et al.

2003), but although the marine stage of the sea trout lifecycle is fundamentally important for all individuals, detailed studies on behaviour at sea are still very scarce (Drenner et al. 2012, Thorstad et al. 2016).

There is substantial variation between individuals and populations in the time spent at sea for kelts (adult trout that have spawned at least once). In general, kelts spend 2–6 mo in the marine environment, which is substantially shorter than the reported marine period for first-time migrants (Bendall et al. 2005, Aarestrup et al. 2015). Most studies of sea trout behaviour suggest that a large proportion of individuals stay in littoral zones while large individuals may migrate into open sea (Klemetsen et al. 2003, del Vil-

lar-Guerra et al. 2013). Sea trout are generally oppor-
tunistic feeders, and studies have found a diet con-
sisting mainly of fish for long-distance migrants in
pelagic zones, while fish in the littoral zones feed on
polychaetes, insects, crustaceans and fish (Knutsen
et al. 2001, Klemetsen et al. 2003, Rikardsen &
Amundsen 2005).

Whilst at sea, trout experience a significantly dif-
ferent environment to that in freshwater, with
greater spatial freedom to choose their habitat. The
utilization of depth and thermal habitats at sea in
migratory fish is likely to reflect metabolic and eco-
logical factors at both broad and fine scales (Hansen
& Quinn 1998, Friedland et al. 2003, Reddin et al.
2004). Trout are metabolic conformers, and increas-
ing temperatures will therefore increase, to a certain
extent, their metabolic scope and alter the swimming
speed, foraging efficiency and digestive capability in
the fish (Spigarelli et al. 1982, Norin & Malte 2011,
Watz & Piccolo 2011). Migratory sea trout individuals
are expected to exhibit a preference for temperatures
that optimizes the scope for growth, reported to be
between 12 and 17°C depending on factors such as
fish size, food abundance and food quality (Elliott &
Hurley 2000a,b, Larsson 2005).

Despite the widespread presence of sea trout across
Europe (MacCrimmon et al. 1970), the depth and
temperature preferences of sea trout remain largely
unknown. Studies north of the Arctic Circle in Alta,
Norway, close to the northern boundary of the spe-
cies' distribution, have shown that sea trout reside
close to the surface and seek higher temperatures
than Arctic charr *Salvelinus alpinus* L. in the marine
environment (Rikardsen et al. 2007, Jensen et al.
2014). While these findings suggest active habitat se-
lection when temperatures are in the low end of the
range reported as optimal for growth, the response of
sea trout (and other salmonids) to sea temperatures
warmer than the range reported as optimal for
growth remain unknown. Their responses may, how-
ever, have important and far-reaching consequences
in the context of climate change. This could, for in-
stance, be geographical displacement (Walther et al.
2002, Hijmans & Graham 2006, Rijnsdorp et al. 2009),
or a combination of geographical displacement and
movement into deeper waters as observed for demer-
sal fish in the North Sea by Dulvy et al. (2008).

The aims of the present study were to investigate
the temperature and depth preferences of sea trout
kelts from Danish rivers by using surgically im-
planted data storage tags (DSTs) that log the temper-
ature and depth of individual trout every 5 min in an
area that provided the fish with a wide range of tem-

peratures during their marine period. The observed
behavioural patterns in this environment were ex-
pected to reflect attempts from each individual to
optimize growth and reduce the risk of predation.
High-resolution data of 769 days of marine behaviour
from a total of 8 tags is presented, enabling the most
comprehensive analysis of marine behaviour in sea
trout reported in the literature to date.

MATERIALS AND METHODS

Experimental area

Tagging took place in rivers on the Jutland penin-
sula, Denmark, with outlets geographically dispersed
from the southern part of the North Sea to the central
part of the Kattegat (Fig. 1).

The seas surrounding Denmark are generally shal-
low, with depths rarely exceeding 50 m, except in the
Skagerrak region north of Denmark. There is a strong
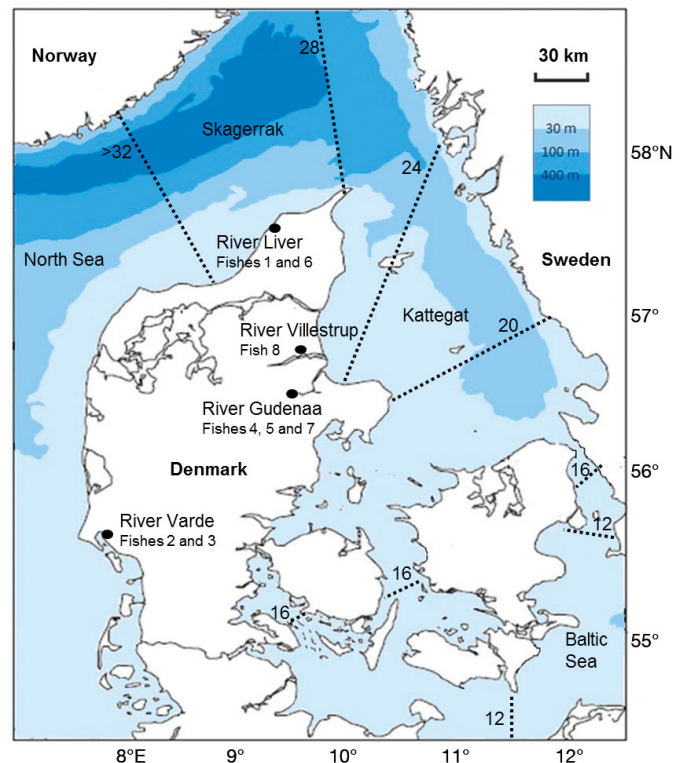halocline in the area at depths of 10–15 m between

Fig. 1. Denmark and surrounding waters. Dotted lines are
isoclines of the approximate surface salinities in the area,
which increase gradually from <12 in the Baltic to >32 in
the North Sea. Outlets of rivers where the study fish (see
Table 1 for fish numbers) came from are marked with black
circles where the rivers run into either fjords (Villestrup and
Gudenaa), estuaries (Varde) or the sea (Liver)

the high-salinity North Sea and the brackish Baltic Sea, reducing mixing of the water column throughout the year in this region (Pedersen 1992, Rasmussen 1995, Jakobsen 1997). As a result of this constant stratification, bottom waters of the Kattegat are warmer than surface waters during winter and colder during summer, but nutrient-rich throughout the year (Rasmussen 1995).

In contrast, the southern part of the North Sea is generally well mixed throughout the year due to shallow waters and wind and tidally driven mixing, while the deeper northern part of the North Sea is stratified during summer (Bozec et al. 2005).

DSTs

A total of 125 sea trout kelts were tagged with G5 long-life archival tags (CEFAS Technology, www.cefastechnology.co.uk) fitted with a string of 11 mm diameter floats (the same diameter as the tag) to facilitate retrieval after shedding or death. The total length with plus floats was approximately 140 mm, weight in air was 9.8 g and the net buoyancy was 0.009 N, corresponding to a negative weight in water of 0.9 g. The floats were covered in silicon rubber (Dow Corning, 734) that is biologically inactive and harmless to the fish (Thorstad et al. 2013). The tag type has not been used in salmonids before, but studies of tagged European eel *Anguilla anguilla* found only very few incidents of initiation of tag expulsion (12%) after 6 mo of implantation (Thorstad et al. 2013).

The tags were programmed to record temperatures and pressure at 5 min intervals, all of which were date- and time-stamped. Internal tag memory was sufficient to record data for 2 yr. Temperature measuring range for the tags was −5 to 35°C, with an accuracy of at least 0.1°C and resolution of 0.03°C. Pressure, a proxy for depth, was measured in dbar (1 dbar [100 hPa] is equivalent to approximately 1 m in depth) to a maximum of 200 dbar (20 000 hPa), with an accuracy of ±1% and resolution of 8 cm. Tags were fitted with a reward notice and address asking people to return the tag upon recovery. Data were downloaded locally from the tags on their return.

Fish capture and tagging

The kelts were electro-fished or captured in traps during downstream migration in the rivers Liver, Gudenaa, Villestrup and Varde during winter or spring (see Table 1). Fish were anaesthetized (benzo-

caine, 300 ppm); sedation was considered to be complete when the opercular beat rate became slow and irregular (2–4 min). Once sedated, total body length and body mass was measured. The fish were then placed in a V-shaped surgical table and the DST was inserted by an experienced fish surgeon in accordance with the guidelines described in permission 2012-DY-2934-00007 from the Danish Experimental Animal Committee. The DST was inserted into the body cavity through a mid-ventral (8–10 mm) incision anterior to the pelvic girdle. The incision was then closed with 2–3 separate sutures. The operation lasted between 1 and 2 min. Recovery time was 2–5 min. After surgery and recovery (approximately 11 min), all fish were returned to the river.

The tag recovery strategy was entirely passive, relying on citizens to find the tag on the beach or river bank or to catch the fish and discover the tag. This made the study less labour-intensive, but also resulted in some limitations because the fish were not weighed and measured after recapture. Some tags were returned immediately after fish capture, while others spent several months on the beach or river bank before they were returned.

Data analysis

Most of the recovered tags were from fish that had died shortly after entering the sea or before entering it. To avoid bias associated with including incomplete records, only the 8 tags that recorded a full marine cycle were retained for the analysis of diving behaviour and environmental preference. The identification numbers 1–8 assigned to these fish in Table 1 are used throughout the paper.

Internal temperature and depth measurements recorded by the returned DSTs were summarized and compared to each other. The data treatment, analysis and plotting took place in R Studio Version 1.0.136 (www.rstudio.com, www.r-project.org) using standard R functions and the packages ggplot2 (Wickham 2009) and mgcv (Wood 2017).

Duration of the marine period

Due to heterogeneity of the rivers and some very shallow fjords and estuaries, it was not possible to distinguish fjord/estuary from rivers to a satisfactory level by depth or temperature in the dataset. We therefore set up a conservative criterion of first and last visit to a depth that could only be achieved in

the sea to ensure that the reported data was only from the marine period. Since all fjords and estuaries in the study are <10 m deep, a fish would only certainly have entered the sea after visiting a depth of >10 m. This is true for all the fjords and estuaries except for the 30 m deep Mariager Fjord, fed by the River Villestrup. Mariager Fjord is, however, almost permanently anoxic below 15 m, so a threshold of residency below 15 m for more than 5 min was used as a segregator for marine behaviour in fish from River Villestrup (Fallesen et al. 2000). The period between the day of the first and last registration between the thresholds of 10 or 15 m was therefore considered the marine period in the data analysis. Close inspection of the temperature profiles (see Fig. S2 in the Supplement at www.int-res. com/articles/suppl/m599p209_supp.pdf) revealed that the 6 fish that did not enter the sea directly (as fishes 1 and 6 from River Liver did) may have left the fjord/estuary 0–4 d earlier (suggested by a drop in the surface temperatures recorded) than when using the depth criteria alone, while the temperature upon return to the fjord/estuary appeared to be the same except in fish 8 (from River Villestrup) that may have returned 4 d later than when using the depth criteria alone. We chose to maintain the entirely quantitative assessment of the depth threshold in spite of these observations, and the marine periods in the present dataset are therefore defined solely on the 10 or 15 m threshold, and only data within this period is included in the following.

Diving behaviour

The data revealed a characteristic pattern of residency close to the surface (usually at depths of 0–3 m) interrupted by a repetitive series of dives to greater depths. A dive was defined as an entry below a depth of 5 m as in Reddin et al. (2011) in the analysis of this behaviour. Each dive was logged at the time of the first measurement below 5 m.

The diving activity and residence temperatures were investigated graphically for diurnal differences by dividing each day into 3 groups (daytime, crepuscular periods and night-time). The daytime group represented the period from 1 h after sunrise to 1 h before sunset, the crepuscular group represented the time from 1 h before and after sunset and sunrise respectively, and the night-time group represented the time from 1 h after sunset to 1 h before sunrise.

Temperature preferences

Temperatures measured by the DST were compared to satellite measurements of sea surface temperatures in the area within 53–59° N, 7–13.5° E as deviations between the 2 may indicate whether the fish are close to land or have migrated out to sea. The satellite measurements were downloaded from www. marine.copernicus.eu, and consisted of mean temperatures at 0–2 m in a 1 × 1 km grid from 21:00 to 07:00 h each day. Temperatures measured by the DSTs were calculated for the same depth and time span and compared to the satellite-measured temperatures. Due to the considerable delay in internal temperature change as documented by Reddin et al. (2011) and displayed in an example on Fig. S1 in the Supplement, temperature measurements from the DSTs for this analysis were only used when the fish had resided at depths of 0–2 m for a minimum of 20 consecutive minutes.

The effect of surface temperature on nightly residence depth was investigated with a generalized additive model (GAM) with a gamma distribution in the mgcv package in R (Wood 2016, 2017). Nightly residence depth in the fish was entered as a response variable, and nightly mean temperature recorded by the DST (when the fish were at depths of 0–2 m for a minimum of 20 consecutive minutes) was entered as the dependent variable. The GAM included fish ID to account for repeated measures on the 8 individuals. Model diagnostics showed no signs of violation of assumptions for the GAM, e.g. the residuals showed no patterns when plotted against covariates.

RESULTS

Recaptures and duration of marine period

A total of 42% (53/125) of the tags deployed were retrieved. Eight of the retrieved tags contained data on a full marine cycle (fish leaving and returning to the natal river) and were used in further analysis. Six of these 8 tags were found in live fish caught by anglers, 1 tag was from a fish that was electro-fished, while 1 tag was found in the river separated from the fish with tooth marks on the floats.

The remaining 45 recovered tags were either corrupted (5 tags) or from fish that had died before reaching the sea (15 tags) or while they were at sea (25 tags). A total of 6 of these 45 tags were from anglers who had caught the fish, while the remaining 39 tags were returned by people who had found the

Table 1. Data on the 8 seatrout *Salmo trutta* whose data storage tag recorded a full marine cycle, sorted by estimated date of sea entry. River/fjord period: the time between tagging and sea entry dates. Dates are d-mo-yr

Fish no.	Tag ID	River of origin	Weight (g)	Length (cm)	Fulton's condition	Gender	Date of tagging	Date of sea entry	River/fjord time (d)	Marine period (d)
1	A08546	Liver	7150	91.5	0.93	Female	16-3-2012	27-4-2012	42	47
2	A08609	Varde	1650	54	1.05	Female	8-4-2013	10-4-2013	2	94
3	A08634	Varde	1650	57	0.89	Female	8-4-2013	14-4-2013	6	87
4	A08578	Gudenaa	1850	56.5	1.03	Male	27-3-2013	24-4-2013	28	105
5	A08543	Gudenaa	2400	58	1.22	Female	27-3-2013	2-5-2013	36	89
6	A08577	Liver	1736	55	1.03	Male	12-12-2012	6-5-2013	145	142
7	A08549	Gudenaa	2480	58	1.27	Female	27-3-2013	9-5-2013	43	87
8	A08640	Villestrup	1860	60.5	0.84	Female	13-4-2015	28-4-2015	15	118
Mean	–	–	2597	61.4	1.03	–	–	–	39.6	96.1

tag without the fish. Without flotation, the high proportion of tags returned from the shoreline would otherwise have remained unrecovered on the river- or sea-bed, which highlights the benefits of our approach.

The fish that died of natural reasons at sea did so shortly after entering it, and had a mean survival time of 14.3 d at sea. Data from these individuals are not included in further analysis.

The mean marine period of the 8 returning fish was 96.1 d (range: 47–142 d), and all 8 fish entered the sea between 10 April and 9 May (Table 1) and returned to the river between 12 June (fish 1) and 21 September (fish 6).

The 96.1 d is a minimum duration of the marine period that does not include the time spent in fjords and estuaries, as it was not possible to segregate fjord/estuary residency from rivers in the present dataset. For comparative reasons with other studies and as an alternative to the applied 10 or 15 m dive threshold, we used movement rate data collected from sea trout kelts from the Gudenaa (1.6 km d^{-1} outmigration and 7.2 km d^{-1} return migration; Aarestrup et al. 2015) to approximate the additional time spent in fjords or estuaries; the mean marine period was increased from 96.1 to 109.3 d (range of individuals: 47–142 d) assuming that similar travel speeds were maintained in the present study through the 15 km long estuary (fishes 2 and 3 from River Varde), the 28.7 km long Randers Fjord (fishes 4, 5 and 7 from River Gudenaa) and the 21 km long Mariager Fjord (fish 8 from River Villestrup). The range of individuals is unchanged at 47–142 d in spite of this addition, as the fish with the shortest (fish 1) and longest (fish 6) marine periods entered the sea directly from River Liver.

Diving behaviour

The kelts generally resided close to the surface during the marine cycle, with 63.8% of measurements occurring in depths shallower than 3 m (Fig. 2). The fish, however, left the surface regularly to a maximum recorded depth of 88 m (fish 1), but
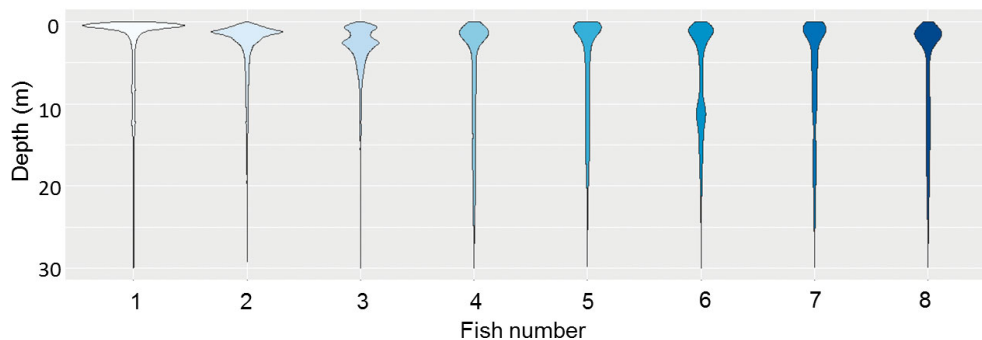

Fig. 2. Residence depths of the 8 sea trout *Salmo trutta* (see Table 1 for fish numbers). Width of the shapes represents the amount of measurements at a given depth. Fish generally spent most of their time in shallow depths. Fish 6 disrupted its normal behaviour for a long period during summer where it resided at depths of 8–14 m, which is shown here by an increased amount of observations at 10–15 m for fish 6
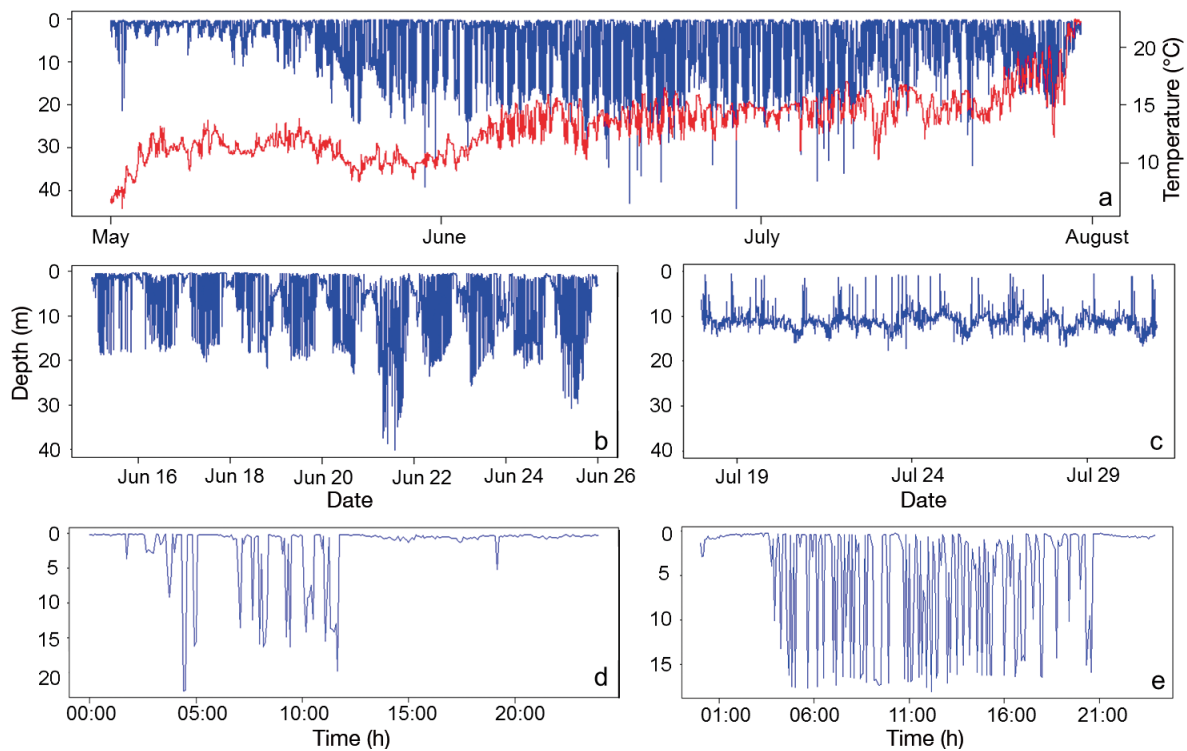
Fig. 3. Examples of marine behaviour with depth (blue) and temperature (red) records from individual sea trout *Salmo trutta* (see Table 1 for fish numbers), measured by data storage tags. (a) The entire marine period in fish 4. Dive depths increase for the first couple of months at sea, and recorded internal temperatures remain fairly stable between 13 and 16°C for a long period until the last week before re-entering the river. (b) A closer look at an example of the frequently observed diurnal pattern with a nightly pause and a repetitive series of dives during daytime from fish 5. The nightly pause in diving activity is evident on almost all days. (c) An example of the behaviour in fish 6 at the end of July during a period with warm waters. The fish resides at depths of 8–14 m and only pays a few short (<10 min) visits to the surface each day. (d) Depth recordings from fish 7 in a single day after 3 d at sea (10 May); diving activity is still quite scarce at this time. (e) Depth recordings from fish 7 in a single day after 31 d at sea (10 June); diving activity has now increased

usually to depths between 10 and 40 m (Fig. 3). Maximum recorded depth for the other 7 individuals was 66 m for fish 2, while fishes 3–8 all had maximum recorded depths of 44–46 m (Fig. S2 in the Supplement). Dive depth showed an increasing trend during the first 1–2 mo at sea for all fish.

The mean depth through the entire marine period of all fish was 5.98 m (range of mean for individuals: 3.29–7.44 m), while the median depth was 2.69 m (range of median for individuals: 0.7–5.0 m). However, these overall values mask the differences in diving activity between different times of day. Hence the mean depth at daytime was 7.33 m, while mean depth during crepuscular hours was 3.89 m and mean depth during night-time was 2.73 m. The depth preferences of the fish appeared to be linked with surface water temperatures (see Fig. 6b) and therefore changed during the season (Figs. 3a & S2).

Diving activity generally ceased during night-time, when the kelts remained close to the surface with lit-

tle or no depth change (Fig. 3d,e). The lack of diving activity during night was a common phenomenon observed in all fish, and the activity at night remained low throughout the marine period (Fig. 4a). This was in contrast to daytime and crepuscular periods, where diving activity generally increased with day length (Fig. 4a).

The general behaviour with repeated dives during daytime and surface residency during evening and night-time was representative for most of the dataset, but did appear to be disrupted when surface water temperatures increased above 17°C.

Depth change was not evenly distributed during the dives. Most dives were initiated and completed with a steeper phase, with mean depth changes of 0.028 m s^{-1} during the first 5 min of descent and 0.033 m s^{-1} during the last 5 min of ascent, and a lower rate of change whilst at depth. Excepting continuous movements, these velocities are likely under-estimates of depth change, because the 5 min logging interval of
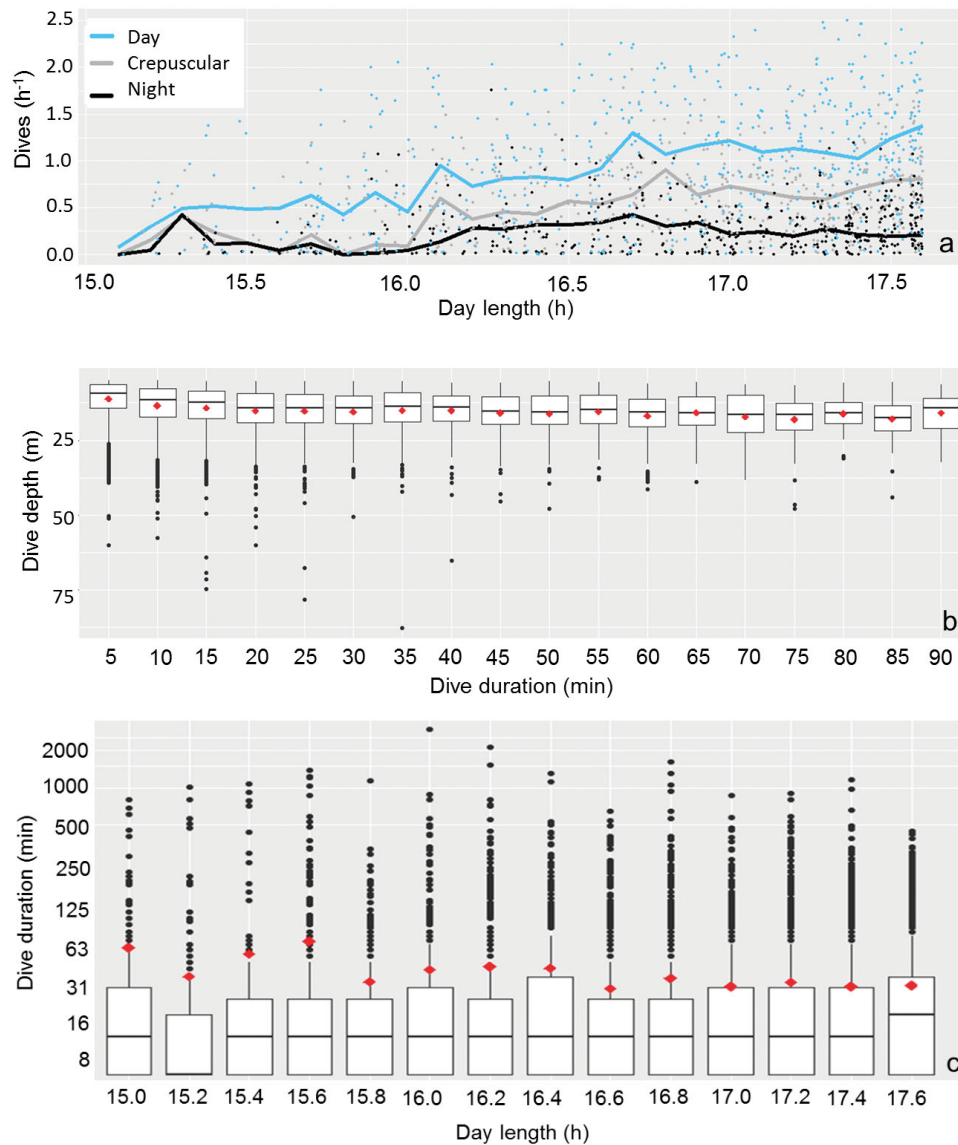
Fig. 4. *Salmo trutta*. (a) Mean diving activity at day, night and crepuscular (±1 h from sunset and sunrise) periods plotted against day length during the period when a minimum of 3 fish are in the sea (24 April–1 August). Individual daily measurements are included as points. Diving activity during daytime is consistently higher than during crepuscular periods and nighttime. (b) Dive depth versus dive duration. Note the lack of correlation between dive depth and duration for dives >20 min. (c) Duration of dives performed at different day lengths (in both panels b and c: red diamond = mean; thick horizontal line = median; box limits = 1st and 3rd quartiles; whiskers = 1.5 times the interquartile range; dots = outliers). Note the $\log_{10}$ scale of the *y*-axis. Dive duration does not appear to be correlated with day length

the DST is coarse relative to the potential of the kelts to move freely in the water column.

The highest dive velocities recorded were 0.22 m s^{-1} descending and 0.23 m s^{-1} ascending, which corresponds to a depth change of 66.5 and 68 m, respectively, within a single 5 min measuring interval.

Dive duration did not appear to restrict maximum dive depth, and 3 of 18 recorded dives deeper than 50 m took only 5 min (Fig. 4b). All recorded dives deeper than 50 m took <45 min and 15 of 18 recorded dives deeper than 50 m took <30 min.

The mean number of dives per day was 18.8 (range between individuals: 11.2–23.7 dives d^{-1}). The mean dive duration was 28.6 min (range between individuals: 16.9–34.3 min), while the median dive duration was 10 min for all fish. Dive duration did not appear to change with day length (Fig. 4c) but was affected by temperature (Table 2).

Table 2. Amount of recorded fish days, mean and median depth, mean dives per day, total recorded dives, and mean and median dive duration versus observed internal temperatures in all 8 sea trout *Salmo trutta* when at 0–2 m during 19:00–03:00 h each night

Night temp. at 0–2 m (°C)	Recorded fish days in temp. interval	Contributing individuals (n)	Depth		Mean dives d^{-1}	Recorded dives	Dive duration	
			Mean (m)	Median (m)			Mean (min)	Median (min)
5–7	31	6	1.95	1.20	2.26	70	9.79	5
7–9	46	8	2.54	1.30	9.11	328	18.7	5
9–11	137	8	3.77	1.64	16.5	2254	18.7	10
11–13	139	8	4.85	1.89	19.4	2693	22.0	10
13–15	144	8	5.92	2.51	24.9	3583	22.3	10
15–17	180	7	7.90	5.50	19.7	3546	33.8	15
17–19	73	6	10.1	9.00	16.6	1214	79.8	15

Temperature preferences

The mean temperature recorded by the DST through the marine period of all 8 individuals was 12.6°C. Fish 1 returned to the river on 12 June and had the lowest mean temperature of 10.4°C, while fish 6 returned to the river on 20 September and had the highest mean temperature of 13.0°C. The other fish had mean temperatures of 11.3°C (fish 2), 11.1°C (fish 3), 12.8°C (fish 4), 13.6°C (fish 5), 13.3°C (fish 7)

and 12.4°C (fish 8), which generally reflected the length of the period at sea.

The DSTs documented variation in temperature during the day and season (Fig. 5a). After a period of general increase from the initial 5–8°C, temperatures stabilized between 13 and 16°C from early June (day of the year [DOY] = 160). Temperatures during daytime were consistently lower than during night-time and crepuscular periods from this date.
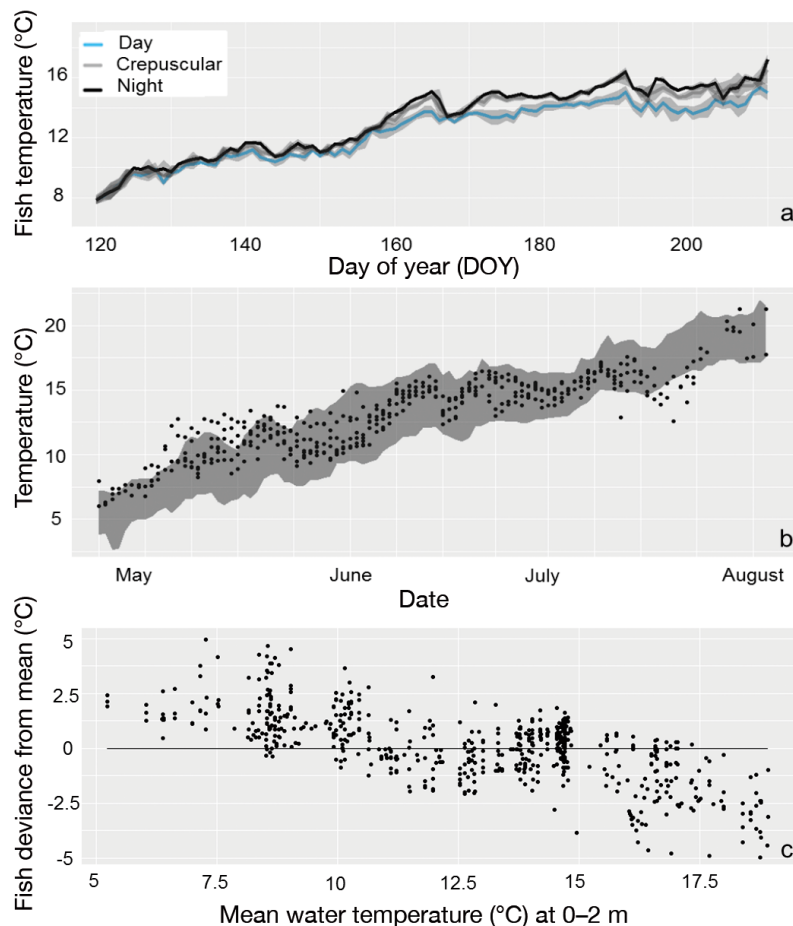

Fig. 5. *Salmo trutta.* (a) Observed mean temperatures recorded by data storage tags during the season at daytime, night-time and crepuscular hours (shaded areas: 1 SD of all measurements in each period). Temperatures are fairly similar across the day until June (day of the year [DOY] = 150), when elevated diving activity during daytime into the now colder deeper waters causes temperatures to be lower during the day. (b) Mean observed temperatures in fishes 2–7 (the fish that were at sea in 2013) (see Table 1 for fish numbers) when residing at 0–2 m for a minimum of 20 min versus satellite measurements of sea temperatures at 0–2 m in the 53–59° N, 7–13.5° E area. All fish and satellite observations are from 21:00 to 07:00 h. Grey shaded area: 95% of the satellite measurements of sea surface temperatures within the area. (c) Fish temperature deviance (when residing at 0–2 m for a minimum of 20 min) from mean sea surface temperatures at 0–2 m in the 53–59° N, 7–13.5° E area. All fish and satellite measurements are from 21:00–07:00 h

The comparison of satellite-measured temperatures and temperatures measured by the DSTs showed that the fish generally resided in warmer temperatures than the mean during spring and colder than the mean during summer (Fig. 5b), i.e. deviance between DSTs and satellite measurements were generally positive during April and May when sea surface temperatures were generally below 10°C and negative during July and August when sea surface temperatures were generally above 15°C (Fig. 5c).

Effect of temperature on behaviour

The general behaviour with repetitive dives during daytime and a prolonged period of surface residency during night-time appeared to shift when water temperatures increased above a certain threshold. This resulted in a changed behaviour where the fish resided at depths of 5–20 m for days (fishes 4, 5 and 7 from River Gudenaa and fish 8 from River Villestrup) or weeks (fish 6 from River Liver) with reduced vertical movement (Fig. 3c, Fig. S3 in the Supplement). This change in behaviour appeared to occur when internal temperatures measured by the DSTs rose above 17°C, and the behaviour was not observed in fish 1 (from River Liver) and fishes 2 and 3 (from River Varde), which did not experience surface temperatures above 17°C. The behaviour was predominant during a very warm period in late July and August 2013, when temperatures at 0–2 m were above 17°C in 97–98% of the area according to satellite measurements (Fig. 5b). During this period, 95% of all measurements from fishes 4, 5, 6 and 7 that were still at sea were from depths deeper than 2.0 m (Fig. 6a). All visits to depths shallower than 2.0 m that lasted >5 min in the end of July 2013 are from fishes 4 and 5 (from River Gudenaa) which re-entered rivers or estuaries on 31 July and 3 August, respectively. The measurements therefore occur in the last days of return migration for these fish. Fish 7 (from River Gudenaa) entered depths of 0–2 m and experienced internal temperatures between 17 and 20°C a few days later before re-entering the river on 6 August. Fish 6 (from

River Liver) continued to avoid the surface in August, except for a period of a few days' duration where the recorded fish temperature decreased to 8–10°C and the fish returned temporarily to the surface. The fish gradually returned to the normal combination of dives and surface residency in September before re-entering its natal river on 21 September.

The change in behaviour during warm periods resulted in some very long dives as the fish stayed submerged at depths deeper than 5.0 m. These long dives were atypical, as they were generally characterized by limited vertical movement. A total of 60 long dives with durations of 500–2920 min were recorded during July and August, and while 1 of these dives went to 37 m, none of the remaining 59 long dives went deeper than 30 m, and most went to depths of 5–20 m.

This behaviour affected the mean dive duration, which increased from 9.79 min (range: 5–260 min) when internal temperatures at the surface (0–2 m) were 5–7°C, to between 18.7 and 22.3 min (range: 5–785 min) in the 9–15°C temperature intervals, to 33.8 min (range: 5–1595 min) at 15–17°C, and 79.8 min at 17–19°C (range: 5–2920 min) (Table 2). The median dive duration also increased from 5 min when temperatures were 5–9°C, to 10 min in the 9–
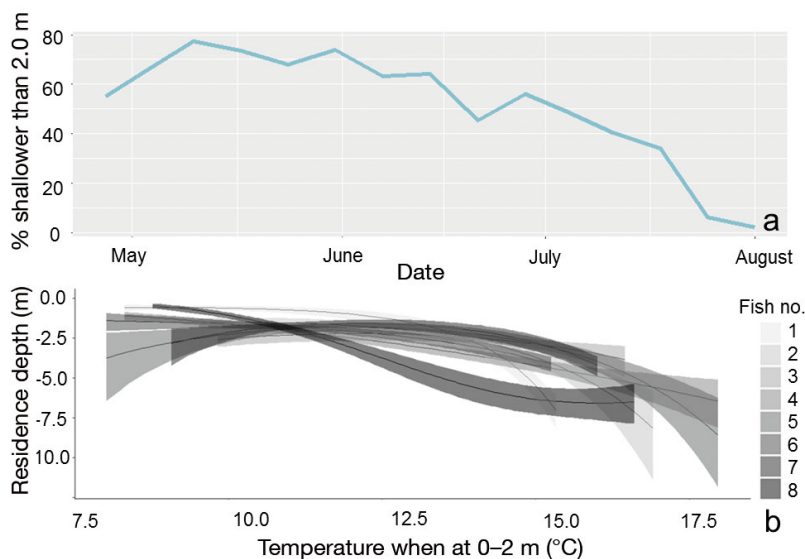

Fig. 6. *Salmo trutta*. (a) Percentage of nightly measurements that recorded a depth shallower than 2.0 m in fishes 2–7 (the fishes that were at sea in 2013) (see Table 1 for fish numbers). (b) Output of generalized additive model of mean nightly residence depth versus observed nightly mean temperatures in the fish when at 0–2 m for a minimum of 20 min. Each fish is only plotted in the temperature range they experienced while at sea. Shaded areas: 95% CI of the modelled curve for each fish. All fish reside at gradually greater depth as temperatures increase above 13°C. The rare visits to depths shallower than 2.0 m in warm waters results in the increased uncertainty in the model that is visible for the high-temperature area

15°C interval, and 15 min when temperatures were above 15°C.

Mean depths increased during the season from 1.95 m (range: 0–12.5 m) on days when mean internal temperatures were 5–7°C at the surface (0–2 m), to 10.1 m (range: 0–35.5 m) when mean internal temperatures were 17–19°C at the surface (Table 2). Median depths increased from 1.2 m on days when mean internal temperatures were 5–7°C at the surface, to 9.0 m when mean internal temperatures were 17–19°C at the surface. This development was accompanied by an increase in diving activity as the fish increased the diving frequency during the first 2 mo at sea (Fig. 4a). The residence depth of the fish at night-time versus the temperature they experienced when visiting depths of 0–2 m was modelled with a GAM (Fig. 6b). The p-values for the smoother of individual fish ranged from 0.001 in fish 3 (River Varde) to between 1.08×10^{-10} and $<2 \times 10^{-16}$ for the other fish. The R^2-value of the model was 0.59. All fish resided at gradually greater depths when temperatures recorded at the surface by the DST started to increase above 13°C.

DISCUSSION

Sea trout possibly adopt 2 strategies to optimize growth at sea

The present study generated one of the most detailed datasets on marine behaviour of sea trout presented in the scientific literature, and it is the only study in the literature to report sea trout behaviour outside fjords and estuaries. The dataset provides a unique possibility to investigate the marine behaviour in adult sea trout on a detailed level in an area characterized by shallow seas exposed to widespread warming during summer. The results suggest that sea trout adopt 2 strategies to optimize their growth at sea: first, through a diel behavioural pattern that enables efficient foraging activity, and second, by residing in water temperatures within the range reported as optimal for growth in the species.

Recaptures and duration of marine period

In total, 53 tags (42%) were returned, but only 8 tags were from fish that had completed a marine cycle and returned to the river. Eight tags (6.4% of all tagged fish) is a low rate of return for fish that have made it back to the river compared to Reddin et al.

(2011, return rate of 50% of 26 fish), Rikardsen et al. (2007, return rate of 100% of 8 fish) and Jensen & Rikardsen (2012, return rate of 33% of 96 fish), but these studies also applied active recapture methods (e.g. traps and nets) for the returning fish. A study setup with positively buoyant DSTs and entirely passive recovery is therefore not ideal if the aim is to recover a high number of tags from fish that made it back to the river.

The study setup also only provided scarce information on fish condition upon recapture, which would be useful in future studies with positively buoyant DSTs to determine possible tag effects on behaviour and survival. Some of the returned tags from angled fish did come with a short note regarding the condition of the fish, none of which suggested visual tagging effects or similar negative effects caused by participation in the study. The high early mortality that was observed in the returned tags could indicate post-tagging effects on the fish, but high early mortalities have also been observed in studies with 9.0 mm acoustic tags in downstream migrating Danish sea trout kelts, where mortalities ranging between 37% (the river Gudenaa; Aarestrup et al. 2015) and 62% (the River Karup; M. Kristensen unpubl. data) have occurred before the fish had made it to sea.

Although we cannot rule it out, we therefore see no indications that the DSTs altered the behaviour and survival of the tagged fish, and we encourage researchers to consider positively buoyant DSTs for future studies to utilize the new possibilities that these tags provide, and to gain further knowledge regarding the possible effects on the fish from using them.

The observed mean marine period of 96.1 d (109.3 d when estimated fjord/estuary time was included) is within the range of 2–6 mo reported in other studies (Bendall et al. 2005, Jensen & Rikardsen 2012, Aarestrup et al. 2015). The values are, however, not directly comparable because those studies were able to report the exact duration of the marine period including the fjord/estuary component, which had to be estimated in the present study.

The small number of individuals that contributed to the dataset of the present study makes the results more susceptible to individual variations, and it is notable (Table 1) that fish 1 (River Liver) was much larger (7150 g versus 1650–2480 g for the other 7 individuals) and had the shortest marine period (47 d versus 87–142 d for the other 7 individuals). The mean duration of the marine period was increased from 96.1 to 103.1 d without fjords/estuaries and from

109.3 to 118.2 d with fjords/estuaries if fish 1 is excluded. By defining the marine period between the first and last 10 m registration (15 m for River Villestrup), the time spent at sea (outside fjords/estuaries) in the present study must be considered a minimum value. This is because some of the fish may have entered the sea but not yet visited depths below 10 or 15 m. The fish generally visited depths below 10 m at least once every 2–4 d during the first month at sea and almost every day from then on, while fish 8 (from River Villestrup) visited depths below 15 m once every 3–4 d during the first month at sea and every day from then on. This uncertainty aligns well with the qualitative inspection of temperature profiles that suggested the marine entry may have occurred 0–4 d earlier than established using the depth criterion alone.

Diving behaviour

A total of 63.8% of all measurements in the dataset were from depths shallower than 3.0 m (Fig. 2), and this residence at the surface aligns well with other findings of studies of sea trout behaviour in fjords (Rikardsen et al. 2007, Eldøy et al. 2017). This may therefore be a general behavioural characteristic for sea trout in marine environments, as it is for Pacific and Atlantic salmon (Walker et al. 2000, Friedland et al. 2001, Reddin et al. 2004, 2011, Tanaka et al. 2005).

The observed behavioural pattern with repeated dives during daytime and resting at the surface during the night (Fig. 3) also has a commonality with findings in DST studies of Atlantic salmon (Reddin et al. 2004, 2011) and Pacific salmon (Walker et al. 2000, Friedland et al. 2001, Tanaka et al. 2005), but the behaviour has so far not been documented to a similar detail in sea trout. Eldøy et al. (2017) found a slightly deeper mean depth during day (1.9 m) than during night (1.2 m) in the Snillfjord in central Norway, indicating the presence of some small-scale diel vertical movements there, while Rikardsen et al. (2007) found no difference in depths during daytime and night-time in the Altafjord in northern Norway during a period of continuous light.

Diving activity in the present study was highest during daytime, reduced during crepuscular hours, and low during night (Fig. 4a), and diving activity generally increased with day length. The nightly pause in diving activity is likely due to reduced feeding opportunity in deep waters in low-light conditions or because predator avoidance may not be necessary in such conditions. This aligns with the absence of diurnal patterns in continuous light during the studies of Rikardsen et al. (2007). Studies on other trout species support the feeding hypothesis by documenting a marked decrease in feeding efficiency in darkness (Mazur & Beauchamp 2003), which was also observed in Atlantic salmon by Fraser & Metcalfe (1997) and Pacific salmon by Flamarique (2005), and feeding is also the most common interpretation of the behaviour in other studies of salmon (Walker et al. 2000, Tanaka et al. 2005, Reddin et al. 2011). However, the nightly pause could also be a response to prey items following a diel pattern and entering shallower waters in the dark, thereby making deep dives unnecessary for the sea trout at this time of the day (Stich & Lampert 1981, Bollens & Frost 1989, Neilson & Perry 1990, Brierley 2014).

The surface visits between dives (Fig. 3) may provide increased digestive capability in the warmer surface waters and increase metabolism in the fish, thereby providing an advantage during dives over prey residing in deeper and colder waters, as discussed by Watz & Piccolo (2011), Norin & Malte (2011), Reddin et al. (2011) and Rikardsen et al. (2007). The fish in the present study did, however, also reside close to the surface and dive from there during spring when surface water temperatures were similar to deeper water temperatures in the stratified parts of the Danish waters (Rasmussen 1995, Jakobsen 1997). It can be seen on Fig. 5a that the temperatures experienced by the fish are similar throughout the day until June (DOY = 150), in spite of the increased diving activity during daytime, which should result in a different temperature during daytime if temperatures change as the fish descend through the water column. This suggests that the fish stay close to the surface and dive from there even though the temperature is similar at depth, and that the metabolism hypothesis alone does not explain the tendency towards surface residency.

Predator evasion is another factor that could affect the behaviour of the trout. Harbour seals *Phoca vitulina* have become quite abundant in the region over the past decades (Larsen et al. 2015), and although very limited data are available on this, seals are believed to be the main predator of adult sea trout. There is a substantial prey item overlap between seals and sea trout kelts, as seals are known to hunt along the sea bed for herring, gadoids and flatfish (Härkönen 1988, Tollit et al. 1998, Lunneryd 2001). Meetings between seals and kelts in the coastal areas may therefore be quite frequent and cause some of the rapid vertical movements in the dataset as the trout seeks to avoid predation.

The deepest recorded dive of 88 m in the present study is the deepest recorded dive for sea trout reported in the scientific literature; Eldøy et al. (2017) observed dives down to 24 m and Rikardsen et al. (2007) observed dives down to 28 m. All fish in the present study visited depths deeper than 44 m, and generally behaved like the Atlantic salmon studied by Reddin et al. (2011) where the fish visited depths down to 50 m.

The median dive duration of 10 min is also similar to that found by Reddin et al. (2011), and the fact that 3 of 18 dives deeper than 50 m lasted only 1 measurement (5 min), and maximum recorded depth changes between 2 measurements were 66.5 m descending and 68.0 m ascending (Fig. 4b), reveals that sea trout are capable of performing rapid vertical movements similar to that of Atlantic salmon. Future investigation with measurements on a finer scale may reveal even faster vertical movements in sea trout, while accelerometers with short logging intervals could provide valuable information on what the fish are doing during the dives. Diving activity has been observed in previous studies with accelerometers on salmonids (e.g. Tanaka et al. 2001, 2005, Wilson et al. 2014), but so far, no studies have uncovered the final explanation as to the reason for the dives.

The observed increase in dive amplitudes during the first 2 mo of the marine period may indicate that the fish were close to land in the beginning of the season and migrated further into open sea with deeper waters as the season progressed, as observed in other studies (Klemetsen et al. 2003, del Villar-Guerra et al. 2013, Jensen et al. 2014, Eldøy et al. 2015).

Horizontal movement was not directly detected by the DSTs of the present study, but with temperature and depth data indicating that the sea trout of the present study migrated into open sea, we suggest that they have a constant migratory pattern, as observed in Pacific salmon by Tanaka et al. (2005) and Atlantic salmon and brown trout post-smolts by Thorstad et al. (2004).

Temperature preferences

The relatively constant temperatures of 13–16°C recorded by the DSTs from June to the end of the marine period (Fig. 5a) is in the high end compared to other studies on salmonids, where temperatures during the marine period rarely exceeded 15°C (Walker et al. 2000, Friedland et al. 2001, 2003, Reddin et al. 2004, 2011, Tanaka et al. 2005, Holm et al. 2006, Rikardsen et al. 2007, Jensen & Rikardsen 2012, Jensen et al. 2014).

The experienced temperatures align well with the 12–17°C range reported as optimal for growth in brown trout (Elliott & Hurley 2000a,b, Larsson 2005), and the fish resided frequently in temperatures within that range in spite of a general increase in sea surface temperatures until August (Fig. 5b). This appeared to be a consequence of the fish actively avoiding warm waters on a fine scale (see next section) and because they resided in areas corresponding to the warmer parts of the 53–59° N, 7–13.5° E area during April and May and the colder parts of the area during July (Fig. 5b). Several of the DST measurements during May were 0–7°C warmer than the 2.5% warmest areas, and with a grid size of 1 × 1 km in the satellite data, we suggest these fish may have been very close to shore at night, as temperatures were presumably warmer here during this period.

Similarly, the apparent nightly residence in temperatures colder than the 2.5% coldest surface waters in the area during July 2013 indicates that the 4 fish still at sea at this stage had migrated into open sea by then. This image is corroborated by the temperature deviance plot on Fig. 5c, where DST-measured temperature deviations from the satellite-measured mean show a decreasing trend from positive in the early marine period to negative in the end.

A similar migration from shore areas to more open waters during the marine period has previously been observed in other studies of sea trout (Klemetsen et al. 2003, del Villar-Guerra et al. 2013, Jensen et al. 2014, Eldøy et al. 2015). It is unknown if this migration is driven by an adaptation to optimize the temperature range experienced during the season or if other factors such as prey or predator abundance are the main drivers. It is, for instance, known that seals mainly stay within 30 km from shore, and migration into open sea would therefore reduce the temporal extent of habitat overlap (Tollit et al. 1998, McConnell et al. 1999). Temperature as a driver in diadromous migrations has, however, been argued for by Jensen et al. (2014), where sea trout only started to visit the outer fjord when temperatures reached 14°C, while Arctic charr *Salvelinus alpinus* moved to the outer fjord at lower temperatures. Studies of other salmonids in rivers have revealed temperature-driven habitat selection on a finer scale, as Chinook salmon *Oncorhynchus tshawytscha* actively sought out colder waters than the mean to conserve energy, and brook trout *S. fontinalis* and rainbow trout *O. mykiss* sought out colder waters to avoid near-lethal temperatures around 25°C (Berman & Quinn 1991, Baird & Krueger 2003).

The seas surrounding Denmark do not provide a similar temperature gradient as that of the Altafjord in northern Norway (where Jensen et al. 2014 conducted their experiments) to facilitate relatively fast horizontal movements to colder water, and the area is exposed to much more pronounced heating of the surface during summer, where even the North Sea reaches temperatures above 17°C in warm summers like 2013. The fish therefore appeared to regulate their temperature by utilizing a combination of horizontal migration into open sea — possibly driven by factors other than temperature — and behavioural adjustment to find cooler water at depth on a finer scale.

Effects of temperature on behaviour

The behavioural adjustment to temperatures consisted of both a gradual increase in residence depth as temperatures increased and a more marked and sudden response where the normal dive/surface residency behaviour was disrupted if internally measured temperatures rose above 17°C. Fig. 6a shows quite clearly how the fish gradually avoided depths shallower than 2.0 m as temperatures started to increase, and the modelled nightly residence depths versus sea surface temperature (Fig. 6b) reveals an increase in residence depths with increasing temperatures for all fish.

The marked response to internal temperatures above 17°C where the fish changed behaviour and disrupted their characteristic dive/surface residency behaviour to stay submerged at depths of 5–20 m, usually only with a few short (<10 min) daily visits to the surface, is visible on Figs. 3c & S3. The behavioural response to surface temperatures drives the mean dive duration up from 18.7 to 22.3 min in the 9–15°C range and further up to 79.8 min when internal temperatures increased above 17°C (Table 2). This behavioural change appeared to be driven by temperature (Fig. 6b) and not by day length, as only diving activity (Fig. 4a) and not the duration of the dives (Fig. 4c) appeared to increase with day length.

Other temperature and depth studies of sea trout (Rikardsen et al. 2007, Jensen et al. 2014, Eldøy et al. 2017) or salmon (Walker et al. 2000, Reddin et al. 2004, 2011, Tanaka et al. 2005) have generally been carried out in areas with cooler water and less summer-heating of the surface, and these studies have not observed a similar behaviour.

For example, 90% of all observations on sea trout in the northern Norwegian Altafjord (Rikardsen et al. 2007) were from depths shallower than 2.0 m and the maximum recorded temperature there was 15°C. Eldøy et al. (2017) did not measure temperature in their study in the central Norwegian Snillfjord, but did record a change in the mean depth for sea trout during summer from 1.1 m in May to 4.0 m in August, indicating that there may have been a similarity with the behaviour observed in the present study. It is therefore possible that sea trout adjust their residence depth to regulate their temperature, while the marked behavioural change that was observed when internal temperatures rose above 17°C is so unique among sea trout and salmonids that it calls for further investigation of the driver behind the behaviour.

We hypothesize that the observed behaviour with residency at depths of 5–20 m during warm periods may be a result of the fish seeking towards the halocline, which is usually found at depths of 10–15 m in the Kattegat region and closer to the surface in the Skagerrak region (Pedersen 1992, Jakobsen 1997). By positioning themselves close to the halocline, the fish may be able to regulate their temperature and physiological scope with a minimum of vertical movement while they may also potentially be feeding on food items aggregating at the halocline.

The observed response to internal temperatures above 17°C also calls for further investigation in the context of climate change to establish whether the behavioural change occurs out of a physiological need or other factors such as adjustment to prey abundance. Much research on climatic effects on marine fishes has focused on changes in geographical distribution (Walther et al. 2002, Hijmans & Graham 2006, Rijnsdorp et al. 2009), while Dulvy et al. (2008) observed both geographical displacement and a movement to deeper waters for demersal species in the North Sea as temperatures increased. The results of the present study show that the vertical distribution is affected by temperature for sea trout (Fig. 6b) and adds that the behaviour on a finer scale may be altered by increasing temperatures. This could have potential consequences for the species in a warmer future climate, but we believe further investigation with a larger sample size and a comparison of behaviour during different years is preferable before any final conclusions on this topic are drawn for sea trout.

Summary

The main findings of the present study such as the characteristic dive/surface residency behaviour and the apparent avoidance of internal temperatures above 17°C generally appeared to be representative

for the 8 individuals included, but there is a natural uncertainty to this, given the low amount of individuals that were included in the study. Fish 1 (River Liver) is the largest sea trout (7150 g) included in published studies of marine behaviour in the species, and fish 1 had a shorter marine period (47 d) and also visited the greatest depth (88 m) of all 8 individuals, but still had a similar behaviour of surface residency at night and dives during daytime. Fish 1 also appeared to adjust its nightly depth preferences when temperatures increased (Fig. 6b) like the smaller individuals, although it left the sea before temperatures increased above 15°C. We therefore find it likely that the main behaviour traits observed in the present study are fairly representative of Danish sea trout, although differences in fish size, age or river of origin could result in behavioural differences that were not observed in the relatively small sample size of the present study. This is particularly true for individuals that were too small to tag with the positively buoyant DST, as these fish may stay closer to shore and feed on different prey items and therefore exhibit a different behaviour than that of the larger, tagged fish (Knutsen et al. 2001, Klemetsen et al. 2003, Rikardsen & Amundsen 2005).

In summary, we found marine behavioural patterns in sea trout comparable to those observed in both Pacific and Atlantic salmon, with a repetitive series of dives preferably to depths of 20–40 m divided by short periods of surface residency between the dives and a long period of surface residency during night. Diving activity generally increased with increasing day length, and dive amplitude peaked a couple of months into the marine period for 5 fish and only very few days before re-entry to the fjord/estuary in 3 fish. Dive duration did not appear to limit dive depth, and dive duration increased with internal temperatures above 15°C but did not appear to be correlated with day length. The observed temperatures and dive amplitudes suggest that the fish were close to shore during April and May and migrated into open sea later in the marine period. The fish appeared to avoid internal temperatures above 17°C, which is the upper range reported as optimal for growth in the species, by residing at greater depths at night and between dives and by discontinuing their characteristic dive/surface residency pattern for prolonged periods of time during warm periods.

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