Individual habitat transitions of Atlantic herring *Clupea harengus* in a human-modified coastal system

Florian Eggers[1,2,*], Esben Moland Olsen[3,4,5], Even Moland[3,4], Aril Slotte[1]

[1]Institute of Marine Research, Postbox 1870 Nordnes, 5817 Bergen, Norway
[2]University of Bergen, Department of Biology, Postbox 7803, 5020 Bergen, Norway
[3]Institute of Marine Research, Nye Flødevigveien 20, 4817 His, Norway
[4]Department of Natural Sciences, Faculty of Science and Engineering, University of Agder, 4604 Kristiansand, Norway
[5]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

ABSTRACT: Pelagic marine fish often display highly dynamic migration patterns. However, such movement behaviour is usually studied at the population or school level, while less is known about individual movement characteristics and habitat transitions. During March 2012 to June 2013, we used acoustic tags and moored receivers to monitor the behaviour of Atlantic herring *Clupea harengus* L. (N = 47) throughout a range of habitats on the Skagerrak coast in southern Norway. Five of the tagged herring entered a former lake transformed into an artificial estuary by a human-made canal linking the former lake to the open ocean. Herring resided in this system for up to 36 d. All tagged herring left the fjord where they were tagged by early August 2012. This habitat transition was detected by the receivers as 3 main pulses of tagged individuals, which were assumed to be formed by putative populations mixing in the area. Most transitions occurred during nighttime regardless of tidal cycle, and it is suggested that spawning is the primary driver for entering the fjord and artificial estuary. Later detections at a separate receiver system 17 km to the northeast suggest that some herring may overwinter in coastal areas. In the spring of 2013, 3 of the tagged herring returned to their original fjord tagging location. Our study reveals new aspects of herring migration dynamics linked to anthropogenic modifications of connectivity, and suggests that capacity for individual behaviours in schooling fish may be underestimated.

KEY WORDS: Schooling fish · Acoustic telemetry · Movement behaviour · Migration · Skagerrak

INTRODUCTION

Human activities shape the environments of wild populations around the world, and habitat loss represents a major threat to biodiversity (Fahrig 2003, Cushman 2006, Wiens 2009). In other cases, human-induced habitat changes may also present animals with new opportunities for expanding their range of movements, for instance when new canals connect aquatic ecosystems that have previously been isolated from each other (Silva et al. 2013, Eggers et al. 2014). Such human-induced alterations of connec-

tivity may influence population dynamics as well as interspecific competition and predator–prey relationships. Understanding behavioural responses to human-induced alterations of connectivity in aquatic systems is therefore potentially important from a management and conservation perspective.

The Atlantic herring *Clupea harengus* L. is widely distributed in the North Atlantic and adjacent seas. It has a complex population structure (Iles & Sinclair 1982, Sinclair & Iles 1988) and some populations, such as the Norwegian spring spawning herring, have supported important fisheries for centuries

(Toresen & Østvedt 2000). This clupeid is an iteroparous total spawner, it matures at 2 or 3 yr of age, aggregates at high densities at spawning time and deposits its sticky eggs on shells, gravel, coarse sand and small stones at depths down to 250 m (Runnstrøm 1941). Herring are thus susceptible to anthropogenic activities affecting the sea bed, e.g. gravel extraction and eutrophication causing oxygen depletion. Herring may also colonize artificial habitats and utilise these for spawning, e.g. the Kiel Canal (Paulsen et al. 2014). Larvae hatch after 2 to 4 wk, depending on temperature (Meyer 1878, Soleim 1942). Early stage larvae drift with the currents until metamorphosis (Russell 1976, Dragesund et al. 1980, Corten 1986), with vertical migration increasing throughout ontogeny, likely affecting the dispersal trajectories of larvae (Woodhead & Woodhead 1955, Blaxter & Parrish 1965).

Mature herring typically conduct annual migrations between wintering, feeding and spawning areas (Varpe et al. 2005). The timing and extent of these migrations are influenced by abiotic environmental factors such as temperature and salinity, as well as biotic factors such as prey distribution (Olsen et al. 2007, Broms et al. 2012). Also, learning and genetic factors may play a role (Fernö et al. 1998). Herring show fidelity, especially to overwintering (Dragesund et al. 1997) and feeding areas (Fernö et al. 1998), while the spawning area depends more on the individual state of the spawners (Slotte & Fiksen 2000). Also, the level of fidelity may change when schools are populated with newly recruited (more naïve) fish (Huse et al. 2010).

Monitoring the movements of individual fish in their natal marine habitat can be challenging, but is enabled by technological developments within the field of acoustic telemetry (Hightower et al. 2001, Pine et al. 2003). Networks of deployed acoustic receivers may be used to continuously log and store data from acoustic transmitter tags implanted in marine animals. This method of acoustic monitoring has been used successfully for species such as blacktip sharks *Carcharhinus limbatus* (Heupel & Simpfendorfer 2002), Atlantic cod *Gadus morhua* (Olsen & Moland 2011), pigeye sharks *C. amboinensis* (Knip et al. 2011) as well as Atlantic herring (Langård et al. 2012).

Individual tracking of fish enables the investigation of different behaviours linked to biological and environmental factors. The monitoring of real-time movements of individual fish results in a determination of the exact abiotic environment. It has been shown that several fish species behave differently according to the influence of environmental factors, like oceanic tides (Lacroix et al. 2004, 2005), season or diel phases (Tolimieri et al. 2009), salinity, temperature and turbidity as characteristics of estuarine tides as well as the tidal phase (Childs et al. 2008). Likewise, biological factors such as size can influence the migration behaviour of fish (Lee et al. 2011). However, none of the above-mentioned studies evaluated the behaviour of typically schooling species such as Atlantic herring.

In schooling fish, the collective output of behavioural decisions forms the results of schooling dynamics, and individuals have to balance stimuli from their neighbouring conspecifics as well as from their environment (Pitcher & Parrish 1993, Parrish & Edelstein-Keshet 1999). To date, the complex nature of schooling has typically been studied by either recording multiple schools over large areas (Nøttestad et al. 1996, Gerlotto et al. 1999) or monitoring single schools over a limited time period (Axelsen et al. 2000).

We investigated individual habitat transitions of Atlantic herring by means of acoustic telemetry. We focused on a coastal system wherein a former lake (Landvikvannet) has been connected to the ocean to form an artificial estuary. Over time, the human-made canal between the former lake and the ocean has changed the freshwater environment into a brackish system, and the connection to a fully marine system allows movement of marine species into this brackish environment, thus making a new habitat available. The very different environment inside and outside Landvikvannet, as well as the tidal effects on currents in the human-made canal, make the area interesting for studying potential environmental drivers of herring behaviour. It is also an interesting area with regard to potential population differences in behaviour and internal drivers, such as maturation status of individual fish. Here, 3 putative herring populations were observed to co-occur at maturing, spawning and spent stages from March to June, where 1 population, 'Landvik herring', showed high fidelity to the artificial estuary (Eggers et al. 2014). In addition to 'Landvik herring', coastal Skagerrak spring spawning herring (CSS) exist in neighbouring fjords, without conducting large annual migrations like those of Norwegian spring spawning herring (NSS), which are also found here. NSS occur in this area mostly in March before starting their annual migration (Eggers et al. 2014). Using individual acoustic tagging and monitoring, herring habitat transitions in this complex artificial estuary-canal-fjord-ocean system were quantified and their pur-

pose evaluated. Our main study goals were (1) to quantify the among-individual synchrony or heterogeneity in movements; (2) to evaluate local environmental conditions as well as the internal status of individual herring as drivers resulting in habitat transitions; and (3) to identify potential behavioural differences supporting biological evidence of putative herring populations in the area.

MATERIALS AND METHODS

Study system

This study was conducted on the Norwegian Skagerrak coast, near the town of Grimstad (Fig. 1). The study area included the brackish former lake Landvikvannet (1.85 km^2, hereafter Landvikvannet) and the neighbouring fjords Strandfjorden and Bufjorden. Landvikvannet is connected to Strandfjorden by a 3 km long and, currently, 1 to 4 m deep canal. In 1877, the depth of the canal was artificially increased to drain water from Landvikvannet and thereby increase the surrounding agricultural areas. This construction allowed salt water and marine organisms to enter Landvikvannet from Strandfjorden, thus transforming the lake into an artificial estuary. Typically, Landvikvannet now has a highly stratified water column with a transition depth at 4 m. In May the upper layer has low salinity (<20 PSU) and higher temperature (>8°C), and is oxygen rich (>1 ml l^{-1}). In contrast, the lower layer has a constant temperature (7 to 8°C) and high salinity (>20 PSU), and no oxygen but toxic hydrogensulphide (for details, see
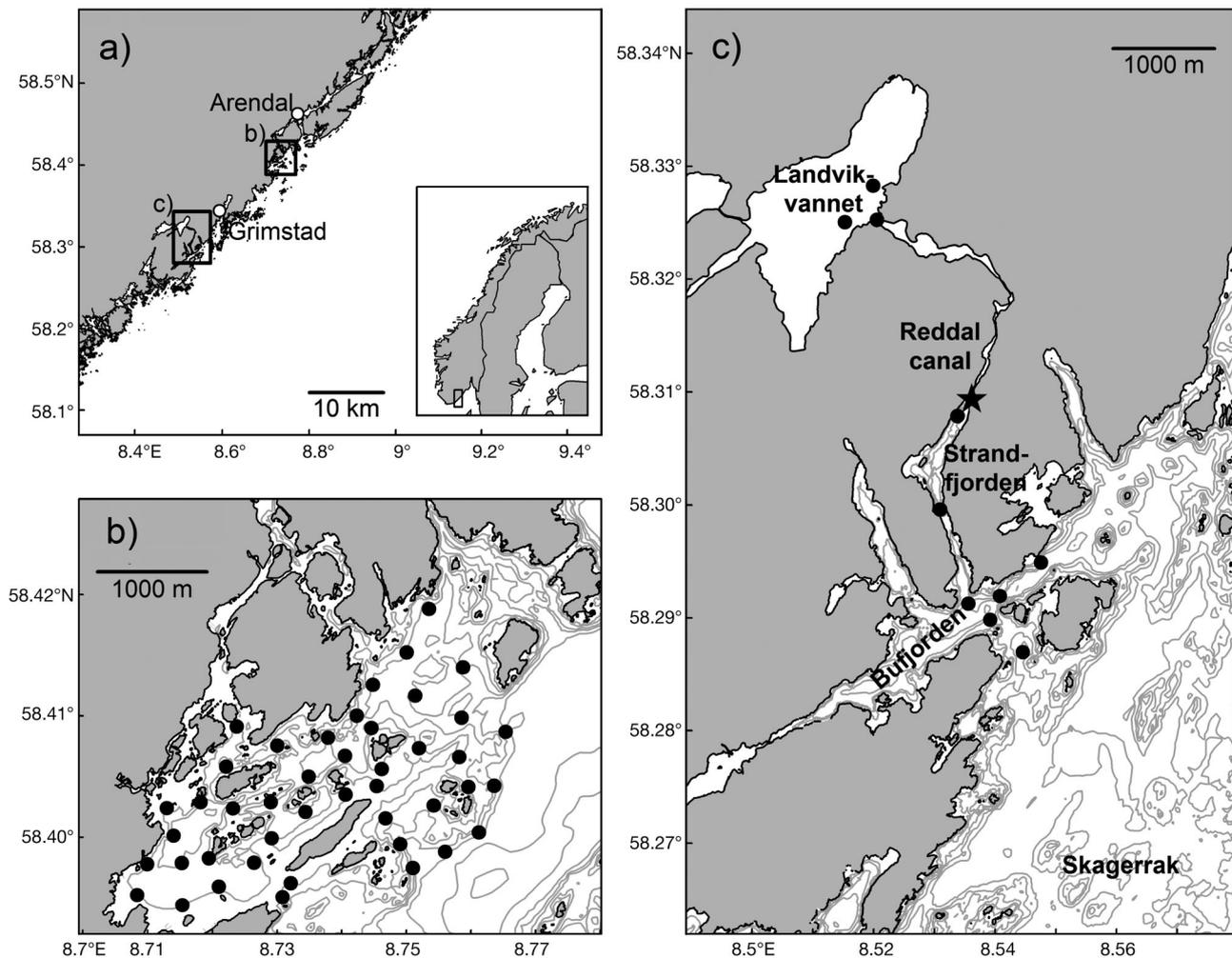

Fig. 1. (a) Study area along the Norwegian Skagerrak coast. (b) Location of the acoustic receiver array in Sømskilen near the town of Arendal. (c) Lake Landvikvannet and the connected fjords Strandfjorden and Bufjorden, showing the point of capture, acoustic tagging and release of Atlantic herring *Clupea harengus* (★), and positions of deployed acoustic receivers (●)

Eggers et al. 2014). Strandfjorden is about 2 km long and sheltered from the outer coast. The inner part has a relatively deep basin (10 to 13 m depth) while the outer part is narrower, and has a shallow sill of only 1 m which fish must cross when moving between inner and outer areas (Fig. 1). Both Strandfjorden and Bufjorden have fully marine conditions (salinity >30, oxygen >0.8 ml l^{-1}) and mainly rocky shorelines with sand and mud in deeper areas. Compared to Strandfjorden, Bufjorden is wider (5 km^2) and deeper (54 m). The fjord has 2 main outlets to the Skagerrak, with sill depths of 30 m (south) and 14 m (east).

Data collection

We captured wild Atlantic herring with hook and line in the inner Strandfjorden during March to June 2012 (Fig. 1). Tagging was conducted in the field. For this purpose, herring were kept in a tank (80 × 50 × 40 cm) in which 10 l of water were exchanged approximately every 10 min. Transmitters were surgically implanted in the abdominal cavity. A small incision was made posterior to the pelvic fins through which the transmitter was inserted. A tissue adhesive (Histoacryl®) was used to close the wound. Total length was measured to the nearest cm, and a few scales were removed for age determination. Tagged herring were left to recover in a separate tank for 30 min and thereafter released close to the site where they had been caught. In total, 11 herring were tagged with 7 mm acoustic transmitters (7.3 × 18 mm, weight in seawater 1.2 g, Thelma Biotel), while 50 herring were tagged with 9 mm acoustic transmitters (9 × 23 mm, weight in seawater 2.5 g, Thelma Biotel). Transmitters were programmed to transmit an identity code every 80 to 180 s, with random intervals to reduce code collision (i.e. 2 or more tags transmitting to the same receiver at the same time). Estimated battery life was 290 and 918 d for the 7 and 9 mm tags, respectively. Langård et al. (2012) used this technique for the first time on herring and concluded that it was suitable for behavioural investigations. Therefore no further analyses or experiments for the survival rate of hooked but untagged herring were conducted to show the effect of surgery on behaviour. The herring sampling and tagging procedure (this study) was reviewed and approved by the Norwegian Animal Research Authority (FDU).

In total, we deployed 10 acoustic receivers (VR2W-69kHz Acoustic Monitoring Receiver, Vemco Division, Amirix Systems) in the Landvik system in March 2012 to record transmitter signals. Receivers were deployed at 3 m depth and kept in position by a trawl float at 2.5 m depth and a 40 kg concrete anchor. Receivers were placed in Landvikvannet, Strandfjorden and Bufjorden (Fig. 1). This allowed us to quantify movements of tagged herring among these habitats, as well as out of the study area and into coastal waters. Stored data were downloaded from the acoustic receivers every 3 to 6 mo until June 2013, when the study ended and the receivers were removed.

In addition to the receiver array described above, we also included data from another receiver array near the town of Arendal, 17 km northeast of our study area, consisting of 44 receivers (Wiig et al. 2013). The reason for this was that some of the tagged herring eventually moved to the Arendal system (see 'Results'). Protocols for deployment of receivers and downloading of data were similar for both telemetry systems.

Data analyses

Presence and movement of fish within the study area were determined from detections at multiple receivers over time. In cases where detections eventually ceased at the edge of the study area (outermost receivers), this was defined as movement out of the study area. For the tag sizes used in our study, detection ranges of receivers in this coastal habitat are typically no less than 200 to 400 m (Olsen & Moland 2011). We were therefore able to detect movements of tagged herring from Strandfjorden to Landvikvannet or Bufjorden.

Probability of entering Landvikvannet

We used generalized linear models (McCullagh & Nelder 1989) to quantify how herring moved among the different habitats in our study system. First, we used logistic regression to estimate the probability of tagged herring entering Landvikvannet from the tagging location in inner Strandfjorden. Herring age (A) and total length (L) were included as continuous explanatory variables in the model; a working hypothesis was that exploratory movement would depend on these individual life-history characteristics:

$$\text{logit (e)} = \beta_0 + \beta_1 L + \beta_2 A \qquad (1)$$

where β_1 and β_2 describe the estimated effect of length and age, respectively, on the probability (e) of entering Landvikvannet.

Diel and tidal patterns in the habitat transition

Second, we analysed the movement of herring from the inner Strandfjorden to Bufjorden, closer to the open ocean. Since all fish eventually left Strandfjorden (except those that died), this analysis focused on understanding diel patterns in the habitat transition. Specifically, we estimated the probability of moving between Strandfjorden and Bufjorden during daytime (d) versus the night as a function of fish length (L), age (A) and direction (D). D was modelled as a factor with 2 levels (moving outwards to or inwards from Bufjorden). Because some fish moved back and forth between these 2 habitats several times, we included herring individual (i) as a random effect. Daytime was defined as the time interval between 06:00 and 18:00 h, while night was defined as the time interval between 18:00 and 06:00 h. Hence, the probability of moving during daytime was modelled as a dichotomous response variable in a logistic regression model:

$$\text{logit}(d) = \beta_0 + \beta_1 L + \beta_2 A + \beta_3 D \quad (2)$$

We did not account for any seasonal changes in daylight hours during the study period, since all habitat transitions out of Strandfjorden took place within 18 d (see 'Results'). A similar approach was conducted to analyse the influence of currents generated by tides. We used the same logistic regression model, but instead of d we used the tides (T). The tides were defined as high and low tides at the start of the migration. While low tides were the time between the highest and lowest water level (decreasing water level), high tides were during increasing water level. The water level and different tides are recorded by Kartverket og Meteorologisk Institutt (Norwegian Hydrographic Service, www.sehavniva.no). This model (without the direction variable) was also used for the departure time of herring.

Migration speed for transitions

Third, we analysed the speed of movement between inner Strandfjorden and Bufjorden. We used a linear mixed effects model including i as a random effect, accounting for repeated observations of individual fish movement. The model included fixed effects of L and A on migration speed (s, in hours). We also explored whether movement speed depended on the direction (D) of movement:

$$s = \beta_0 + \beta_1 L + \beta_2 A + \beta_3 D \quad (3)$$

The significance of β_1, β_2 or β_3 would indicate an effect of length, age or direction on the migration speed of herring.

Duration within the monitoring array

Fourth, we modelled the duration (T) of herring presence within the monitoring array, where they were tagged, south of Grimstad. A linear model was used including total length (L), age (A) and date of the tagging experiment (E) as predictor variables:

$$T = \beta_0 + \beta_1 L + \beta_2 A + \beta_3 E \quad (4)$$

The dependence of these life-history characteristics on duration would be indicated by significant β_1 or β_2 values.

Departure time of herring

Lastly, a K-means clustering (Hartigan & Wong 1979) was conducted to analyse similarities of herring according to their time of departure against total length or age. Day of the year was used as a variable for the departure time. Based on the observed results, we used $K = 3$ clusters for this analysis. The centres of the 3 clusters (C) were compared for each variable — day of the year (Y), total length (L) and age (A) — with a linear model:

$$C = \beta_0 + \beta_1(Y, L \text{ or } A) \quad (5)$$

A significant β_1 term would demonstrate that the 3 clustered groups differed depending on the tested variable.

RESULTS

In total, we tagged 61 herring in the inner Strandfjorden during March to June 2012. The age of the tagged herring ranged from 2 to 15 yr, and the total length ranged from 19 to 34 cm (Table 1). Out of these, a total of 14 herring apparently died within the study area shortly after tagging (inferred from cessation of signals or movement during the first 3 d). These fish were censored from further analyses; thus, 47 individuals were used in our analyses, constituting the tagged population. As we had no reason to infer differences in behaviour of herring tagged with the 2 types of acoustic tags used, all

Table 1. Summary details of acoustically tagged Atlantic herring *Clupea harengus* from Strandfjorden, coastal Skagerrak, showing the tagging dates in 2012, the sample sizes (N), herring total lengths (TL mean and range) and herring ages (mean and range) estimated from scale readings

Tagging date	N	TL (cm)	Age (yr)
28–29 March	43	28.8 (24–34)	4.9 (2–15)
15–16 May	13	25.0 (20–30)	3.4 (2–7)
20–21 June	5	21.8 (19–23)	2.8 (2–3)

analyses were carried out with acoustic tag types merged.

Fidelity of herring to Landvikvannet

A total of 10.6% (N = 5) of the tagged population made the transition from Strandfjorden to Landvikvannet through the human-altered canal. These upstream movements took place during May to July 2012, and were not temporally synchronized (Fig. 2). Time spent swimming up the canal ranged from 10.0 to 27.3 h (mean = 22.3 h), while the duration of the Landvikvannet stay ranged from 2 to 36 d (mean = 17.0 d). When returning to the fjord, time spent swimming down the canal ranged from 12.7 to 107.5 h (mean = 41.9 h). There was no significant effect of total length and age on the probability of entering Landvikvannet ($\beta_1 = -0.18$, SE = 0.21, p = 0.41; $\beta_2 = 0.13$, SE = 0.2, p = 0.52).

Diel and tidal patterns in the habitat transition

Besides movements between Strandfjorden and Landvikvannet, we observed movements between Strandfjorden and Bufjorden. All transitions were made within 18 d after tagging, except for two which took place more than 1 mo after tagging. Most movements were made during the night in both directions (77.3% into Strandfjorden, 97.6% out of Strandfjorden). The probability of moving during the

day was not influenced by fish length or age ($\beta_1 = -0.17$, SE = 0.24, p = 0.94; $\beta_2 = -0.09$, SE = 0.22, p = 0.69), but the effect of direction was marginally significant ($\beta_3 = -2.48$, SE = 1.24, p = 0.05). The movement out of Strandfjorden was less likely to happen during the day. Even though all transitions occurred within a limited time interval, none of the herring migrated at the same hour. Herring tended to migrate during low tides, for both directions (In: 61.4%; Out: 63.4%), but the habitat transitions of tagged herring were not significantly influenced by currents generated by tides. Fish length, age and migration direction had no influence on the probability of migration during low or high tide ($\beta_1 = 0.02$, SE = 0.15, p = 0.90; $\beta_2 = -0.04$, SE = 0.12, p = 0.74; $\beta_3 = -0.09$, SE = 0.46, p = 0.85). Even though 63.6% left the system during low tides, the probability of departure during high or low tide was not significantly influenced by fish size or age ($\beta_1 = 0.03$, SE = 0.16, p = 0.84; $\beta_2 = -0.08$, SE = 0.17, p = 0.61).
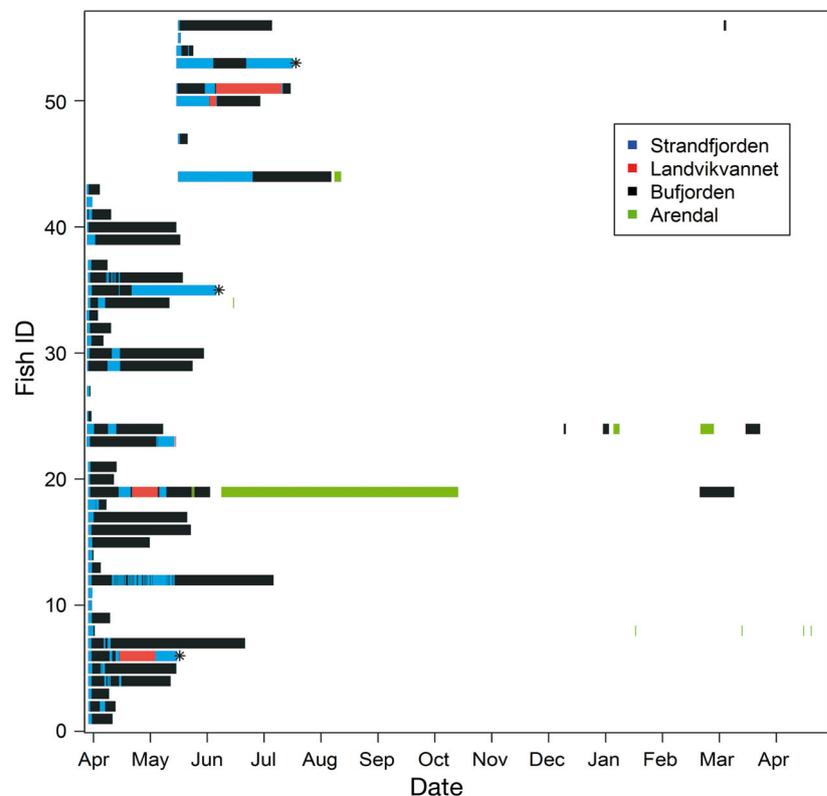

Fig. 2. Acoustic telemetry observations on the duration of presence or absence of individual Atlantic herring *Clupea harengus* (listed by their fish ID number, N = 47) in the sheltered Strandfjorden, through the human-made Reddal canal and the connected Landvikvannet, the more exposed Bufjorden and the Arendal receiver system 17 km farther north-east. See also Fig. 1. Asterisks (∗) denote day of presumed expiry for herring that died within the monitoring area. The period shown spans April 2012 to April 2013

Migration speed for transitions

Movement from Bufjorden to Strandfjorden (mean duration: 2.3 h; range: 0.2 to 8.3 h) was significantly longer in duration than the reciprocal one (mean duration: 1.3 h; range: 0.3 to 6.7 h; $\beta_3 = -0.95$, SE = 0.38, p = 0.01). The duration of transitions between the 2 fjords was also significantly influenced by the age of herring ($\beta_2 = 0.25$, SE = 0.1, p = 0.03), whereby younger herring were faster than older ones, but this was not corroborated by total length ($\beta_1 = -0.23$, SE = 0.23, p = 0.06).

Behavioural differences within herring populations

Herring spent between 1 and 99 d after tagging within the Landvik system, with a mean duration of 27.6 d. There was no effect of length, age or date of the tagging experiment on the staying time within the system ($\beta_1 = -0.14$, SE = 3.04, p = 0.96; $\beta_2 = 1.73$, SE = 3.75, p = 0.65; $\beta_3 = 8.61$, SE = 16.46, p = 0.61).

Clustering of individuals according to time of departure

The clustering analyses with $K = 3$ clusters clearly grouped the individual herring according to their time of departure from the study system (Fig. 3). Both analyses showed high accordance comparing the within-clusters sum of squares by cluster, with 93.8% for total length and 94.2% for age. The groups differed significantly in their time of departure within the year ($\beta_1 = -0.02$, SE < 0.01, p < 0.01), but not in their total length ($\beta_1 = 0.05$, SE = 0.04, p = 0.19) or age ($\beta_1 = 0.01$, SE = 0.51, p = 0.87). The departure time of the different clusters was compared to the moon phase, but no significant correlation was found. The range of each cluster covered both, new and full moon, at least for some individuals. The first group showed a tendency to depart at full moon, whereas the second group tended to depart at new moon.

Migratory or stationary population

After leaving the Landvik monitoring array, 3 of the tagged herring (Fig. 2) were detected in the Arendal system and showed different behavioural patterns. One individual even moved back and forth between the 2 monitoring arrays and stayed for a longer time in the Arendal system. The other 2 individuals were
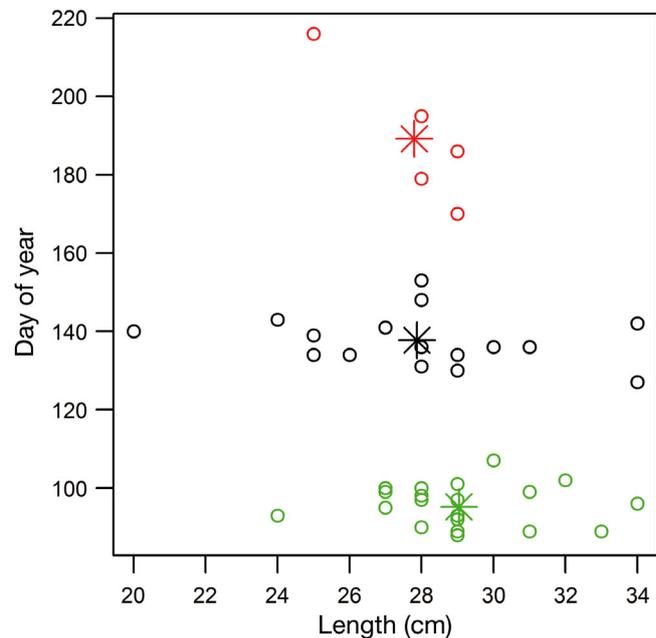

Fig. 3. Clustering analyses of the time of seaward departure by acoustically tagged Atlantic herring *Clupea harengus* (N = 47) from the Landvik system vs. body size (total length, cm) between 29 March and 30 August 2012. The 3 groups were in part assigned to disparate population components: Landvik herring (red symbols), coastal Skagerrak spring spawning herring (green symbols) and Norwegian spring spawning herring (black symbols). Asterisks denote mean departure date for each clustered group

only detected by the outermost receivers. Herring needed between 2.1 and 33.5 d to move between the 2 monitoring arrays with a mean travel time of 12.1 d. Excluding the travel time of 33.5 d of 1 herring, the mean travel time was 5 d, which is more precise because the travel duration for the other 3 migrations was at maximum 6.5 d. According to the straight line distance of 17 km between the 2 areas, herring exhibited an average swimming speed of 138 m h^{-1}. These estimates refer to net movement, but actual velocities of individual herring could have been greater as their movement was likely conducted in a back and forth or zigzag manner.

Homing of herring

After overwintering outside the study areas, 3 herring returned to the Landvik system (ID nos. 19, 24, 56) and 1 returned to the Arendal system (Fig. 2, Table 2; ID no. 8). Two herring (ID nos. 19 and 24), which had both been detected in the Landvik system in spring 2013, were also detected in the Arendal sys-

Table 2. Summary details of acoustically tagged Atlantic herring *Clupea harengus* detected during spring 2013. Fish ID as in Fig. 2, herring total lengths (TL) and ages were estimated from scale readings, and cluster affiliation is based on the departure time. The system with which they were affiliated in 2013 is also shown

ID	TL (cm)	Age (yr)	Cluster	System
19	28	4	2	Landvik
24	34	12	2	Arendal + Landvik
56	28	Unknown	2	Landvik
8	28	4	1	Arendal

tem previously. Those herring stayed for a longer time in both systems and were detected by receivers inside the system, but not in Strandfjorden. The other 2 herring individuals were only detected by the outermost receivers for a short time period, indicating that those herring only passed by the different systems, but did not enter them. The ages of these individuals were estimated to be 4, 4 and 12 yr (for 1 herring, age could not be determined from scales) and the lengths were 28, 28, 34 and 28 cm. Except for herring ID no. 8, which left the system directly within 3 d, all herring were grouped in the second cluster (see Fig. 3) for the first departure time from the Landvik system. The 2 herring which had been detected inside the system after returning already showed migratory behaviours during the 2012 season. Both migrated between Bufjorden and Strandfjorden, while ID no. 19 migrated farther into Landvikvannet. Even though ID no. 56 did not migrate between the different habitats, the data indicate a migration into the inner Bufjorden, which is a sheltered and closed fjord, before it finally left the monitoring system.

DISCUSSION

Using acoustic tagging and monitoring, the present study demonstrates how individual herring differ in their movements throughout a complex coastal system, including habitat transitions from an artificial estuary to a fjord through a human-made canal, and farther out into more exposed coastal habitat. In light of our main findings, we discuss to what extent (1) migration of herring could be based more on individual decisions rather than decisions made at the school level; (2) whether the observed movements in our study area could be motivated by environmental conditions and spawning behaviour; and (3) whether the 3 co-occurring putative populations can be sepa-

rated based on behavioural patterns. Further, we discuss how these individual-based observations can help to improve our understanding of the migration dynamics of pelagic schooling fishes in coastal habitats modified by humans.

Individual movements versus school dynamics

Herring are known for maintaining large schools and conducting synchronized annual migrations. However, our observations indicate that herring entered Landvikvannet more at the individual level, instead of the school level. In fact, we observed herring swimming upstream the canal in schools of less than 10 individuals. Likewise, the recorded movements between Bufjorden and Strandfjorden were not synchronized among individuals. Similar results were observed by Langård et al. (2015), who demonstrated an increase in individual day-to-day variability of spawning herring activity in both horizontal and vertical dimensions, indicating a shift from strong school coherence to high individual variability. Hoare et al. (2004) studied context-dependent grouping size choice in a shoaling fish experimentally, and suggested that fish may individually adjust grouping behaviour without requiring extensive information on the position and movement of all possible shoalmates. This suggests that a highly dynamic environment, such as the artificial estuary-fjord-coast continuum studied herein, may confer variability in spatial decisions. An alternative explanation for the individual habitat transitions could be an effect of disruption of the school structure. After capture, tagging and release, individual herring might have lost contact with their original shoalmates and could not associate with existing herring schools. To avoid such a disruption effect in future studies, tagged and untagged herring could be held together in a larger container from which they are all released simultaneously.

None of the investigated factors, either biological (size or age) or environmental (tides or tidal cycle), explained the observed individual variation in movement patterns. However, our results clearly demonstrated a diel effect on the migration of Atlantic herring. Herring tend to migrate during the night, regardless of tide and current direction. In other species, e.g. Atlantic salmon *Salmo salar*, the tides play an important role for the different migration patterns (Lacroix et al. 2004, 2005). The prevailing direction of the coastal current, known as the Norwegian coastal current, in the general study area was westward along the coast in the Skagerrak (Sætre 2007). The

fact that all herring left the Landvik system through the 2 possible southward or eastward corridors without any clear pattern does not support a strong influence of the Norwegian coastal current on the behaviour of tagged herring.

Motivation for habitat transitions

Habitat transitions in this complex artificial estuary-canal-fjord-ocean system conferred a high predation risk for herring, especially when crossing shallow waters in the canal as well as over the sill between Strandfjorden and the open ocean (see 'Materials and methods'). Consequently, a high motivation must exist for undertaking these potentially hazardous movements. When viewing this trade-off in context with the observed movement patterns, for instance the transitions from Bufjorden to Strandfjorden, spawning can be assumed to be the most likely motivator. With a significantly longer transition (timewise) into Strandfjorden, herring would increase their predation risk even more. Also, older herring spent more time in the shallow part than their younger conspecifics. Older herring are more experienced, repeated spawners, balancing personal information based on past experiences with social information based on the behaviour of other individuals (see e.g. Miller et al. 2013). This trade-off, involving higher predation risk, can be explained by higher probability of successful recruitment due to spawning taking place in better conditions (Candolin 1998).

The only factor influencing the transitions between both areas was the diel cycle, where most migrations occurred during the night, also supporting spawning movements as motivation. However, those diel activity patterns may need to be controlled by several fixed-location control tags to avoid the influence of factors in the absence of animal behaviour (Payne et al. 2010). Typically spawning herring aggregate in schools during daytime in pelagic waters to avoid predation (Nøttestad et al. 1996, Axelsen et al. 2000), and also perform diel vertical migration where shallow habitats are only visited during dark hours (Woodhead & Woodhead 1955, Blaxter & Parrish 1965). In shallow waters, however, as found in our study area, spawning herring may stay in touch with the bottom at all hours and without dispersing closer to the surface during darkness (Slotte 1998). Also, small schools may split from the large aggregation for spawning and migrate to their spawning grounds (Johannessen et al. 1995, Skaret et al. 2003).

Besides Strandfjorden, potential spawning could occur in Landvikvannet as well as in the Reddal canal. Both areas hold suitable habitats for herring to spawn. Herring may colonize artificial habitats for spawning, as seen in the Kiel Canal (Weber 1971, Paulsen et al. 2014) or the Østerbøvatn (Aasen 1953). While the environmental conditions in the Kiel Canal are similar to the Baltic Sea and herring found inside the canal did not form an individual population, the herring in Østerbøvatn are classified as a single population, distinct from the neighbouring population in the full marine habitat. Also, the varying residence time of tagged herring in Landvikvannet of 2 to 36 d suggests that the lake may be suitable for long-term residence for herring populations adapted to the environmental conditions of this marginal habitat (Eggers et al. 2014), whereas populations not adapted may choose to leave quickly. Besides the artificial estuaries Landvikvannet and Østerbøvatn, herring have colonized habitats with similar environmental conditions and can be phenotypically distinct from other populations (Neb 1970, Hognestad 1994).

Population separation based on individual behaviour

Eggers et al. (2014) studied the population structure of herring both inside and outside the Landvikvannet habitat over the full spawning season in 2012, from February to June, by means of monthly gill net sampling and biological analyses. They found that 3 different herring populations seem to co-occur in the study area during spawning: Norwegian spring spawning (NSS), coastal Skagerrak spring spawners (CSS) and a third population termed 'Landvik herring'. This third population is a putative local population presumably spawning inside Landvikvannet, mainly recognised on the basis of consistent low mean vertebral counts in samples collected during 1984 to 2012 (Eggers 2013). The other 2 populations, NSS and CSS, have been suggested to visit the artificial estuary in minor proportions as an explorative behaviour (Eggers et al. 2014). Hence, tagged fish staying inside Landvikvannet for only 2 d would likely belong to the CSS or NSS population, whereas the ones staying for up to 36 d may belong to the locally adapted Landvik herring. The co-occurrence of tree putative populations was also evident when viewing departure dates. The clustering analyses of time of herring departure (see Fig. 3) corroborated this, at least in part, by showing 3 different groups leaving at disparate times of the year. In Eggers et al.

(2014), data on temporal and spatial changes in catch per unit effort combined with observed changes in biological parameters such as stage of maturation, vertebral count, otolith shape and length at age, indicated different peak occurrence and spawning of the 3 herring populations. They found that NSS and CSS herring arrived early in the season in February and March, and with NSS herring finishing spawning at an earlier time than the CSS herring. The Landvik population arrived and entered the artificial estuary in May, having a later spawning peak. The results from the present study support the conclusion from Eggers et al. (2014), where the first (and largest) group of tagged fish leaving early (end of March) were probably NSS herring. Tagged CSS herring were the next to leave in June, followed by individuals of the local Landvik herring which stayed until as late as August.

The potential spawning events demonstrated through migratory behaviour inside the monitoring system, in conjunction with the affinity of CSS, and especially of Landvik herring to this local area, may lead to expectations of a high returning rate of individuals in the tagged herring population. However, in this study only 3 tagged herring returned to the Landvik system and 2 to the Arendal system farther east. One of those fish returned to both systems. This may be an indication of returning herring, but as long as the herring stayed in Bufjorden and did not enter Strandfjorden while the monitoring system was in place (until June 2013), we cannot draw conclusions about homing to a local spawning area.

Furthermore, CSS herring may not be tightly linked to specific spawning locations along the coast, but may vary their preferred spawning grounds according to changes in environmental conditions. The winter 2012 to 2013 was particularly cold, with sea ice remaining until May, which could explain that only few fish (N = 3) returned to the specific Landvik system. Due to late ice cover, potentially returning herring may have spawned at different locations along the coast with more favourable environmental conditions.

Conclusion

Observations gathered by acoustic telemetry demonstrated individual transition of herring between habitats with different environmental conditions. These transitions were neither linked to biological characters such as size or age nor to environmental factors such as tidal cycle. Transitions between fully marine localities were also observed mostly during the night. For habitat transitions between marine locations, spawning is suggested as the primary driver. However, in the local Landvik system, evidence suggests that 3 putative herring groups exist (NSS, CSS and Landvik herring), which differ in their migratory behaviour as well as in their affinity to coastal waters. There was no clear evidence for either natal or repeated homing to this specific area; however, CSS and Landvik herring showed a tendency to stay near the coast. The present study reveals new aspects of herring migration dynamics by demonstrating spatial decisions made by individual herring at intermediate temporal (months) and spatial scales (km). Our work suggests that the capacity for individual behaviours in schooling fish may be underestimated.

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