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Overwintering behaviour of yellow-stage European eel (*Anguilla anguilla*) in a natural marine fjord system

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A R T I C L E   I N F O

A B S T R A C T

Like many animals, northern temperate eel can enter a hibernation-like state and become dormant during the winter. Knowledge of overwintering behaviour in eel is sparse and mainly based on anecdotal observations and a few experimental studies on thermal tolerance. We studied European eel (*Anguilla anguilla*) overwintering behaviour in a Skagerrak fjord in Southern Norway, during three consecutive years, using an array of acoustic receivers and acoustic tags with depth and temperature sensors. We obtained results from 55 yellow eel, of which 19 were studied for one winter, 35 for two winters and one for three winters. Dormancy was inferred to begin in September for the earliest individuals and lasted until May for the last, with the majority of eel dormant from at least late October–November until mid-April. The timing of dormancy was mainly related to photoperiod and less to temperature. More than 50% of eel became dormant when day length was <9 h and became active when day length was >14 h. Approximately 10% of eel remained active during the winter and 31% of eel changed their pattern between consecutive years. Some dormant individuals exhibited activity periods that interrupted their dormancy. Eel in the outer fjord nearer the open sea became dormant before eel in the inner more freshwater part of the fjord, and were dormant longer.

1. Introduction

The winter season poses several challenges for aquatic animals, such as low light, short days (at high latitudes), low prey abundance, low temperature and, in some systems, low oxygen (Shuter et al., 2012). Some species are adapted to these conditions and continue acquiring energy during the winter. Others subsist mainly on energy stores and reduce their activity (Shuter et al., 2012). Foraging during the winter is more common in juvenile than adult fish because they have lower energy stores and a higher metabolic rate (Shuter and Post, 1990; Ultsch, 1989). Winter foraging is also more common at high latitudes where winters are long, and the risk of starvation is higher. In temperate environments, it is common for fish to enter a period of dormancy: a hibernation-like state, in which organisms are inactive, cease feeding, and have a low metabolic rate (Speers-Roesch et al., 2018; Ultsch, 1989). Fish that exhibit dormancy take shelter, minimize movements, and rely on lipid reserves accumulated during the previous feeding

season (Shuter et al., 2012; Reeve et al., 2022). Overwintering may involve different levels of activity, from sleep through quiet wakefulness to alert, and active (Crawshaw, 1984). Some species exhibit facultative dormancy while, for others, dormancy is obligatory.

The European eel (*Anguilla anguilla*) is widely distributed from north Africa and the Mediterranean to northern Norway. The species is tolerant of large differences in temperature. Eel are catadromous, but some individuals skip the freshwater phase and reside in marine coastal habitats or brackish water lagoons and estuaries (Tesch, 2003; Daverat et al., 2006). Eel reduce their activity as temperature decreases during the winter (Bertin, 1951; Dannevig, 1945; Tomie et al., 2017; West-erberg and Sjöberg, 2015). Apart from a few experimental studies on eel thermal tolerance (Dannevig, 1945; Sadler, 1979; Walsh et al., 1983), observations of winter dormancy in the wild are anecdotal. Eel are rarely observed during the winter. It is assumed that they bury themselves in the sediment or hide in crevices (Bertin, 1951; Tesch, 2003). Most of the commercial catches during the fall are silver eel, which argues that they

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are active during this period of the year whereas other life stages are less so (Durif and Skiftesvik, 2019; Durif and Elie, 2008). A study in the freshwater Lake Mälaren in Sweden confirmed that most eel reduced their activity during the winter (Westerberg and Sjöberg, 2015), but it is unknown whether eel residing in the marine environment also display this behaviour or migrate to freshwater for overwintering as do some American eel (*Anguilla rostrata*) (Thibault et al., 2007). The mechanisms that trigger the initiation and termination of dormancy are poorly known, but are hypothesised to be related to temperature, photoperiod, food availability and body condition (Andrews et al., 2019; van Deurs et al., 2010; Winslade, 1974).

The objective of this study was to describe the general overwintering patterns of eel residing in a marine environment and to evaluate the influence of temperature and day length on the timing of dormancy. To this end, we used data from yellow-stage European eel tagged with acoustic transmitters whose movements were recorded by an array of stationary receivers extending from freshwater to saline environments in a fjord system in southern Norway.

2. Materials and methods

2.1. Study area

Sandnesfjord together with Songevannet and Nævestadfjord form a ~15 km long coastal fjord system located in southern Norway (Fig. 1). A 1.5 km long and 3 m deep channel, Lagestraumen, physically separates these two areas, which display contrasting salinities (Tjomsland and Kroglund, 2010). Driven by tidal influences and significant freshwater input from the Storelva River and other sources, this fjord has a highly dynamic and vertically layered salinity profile, with average salinities
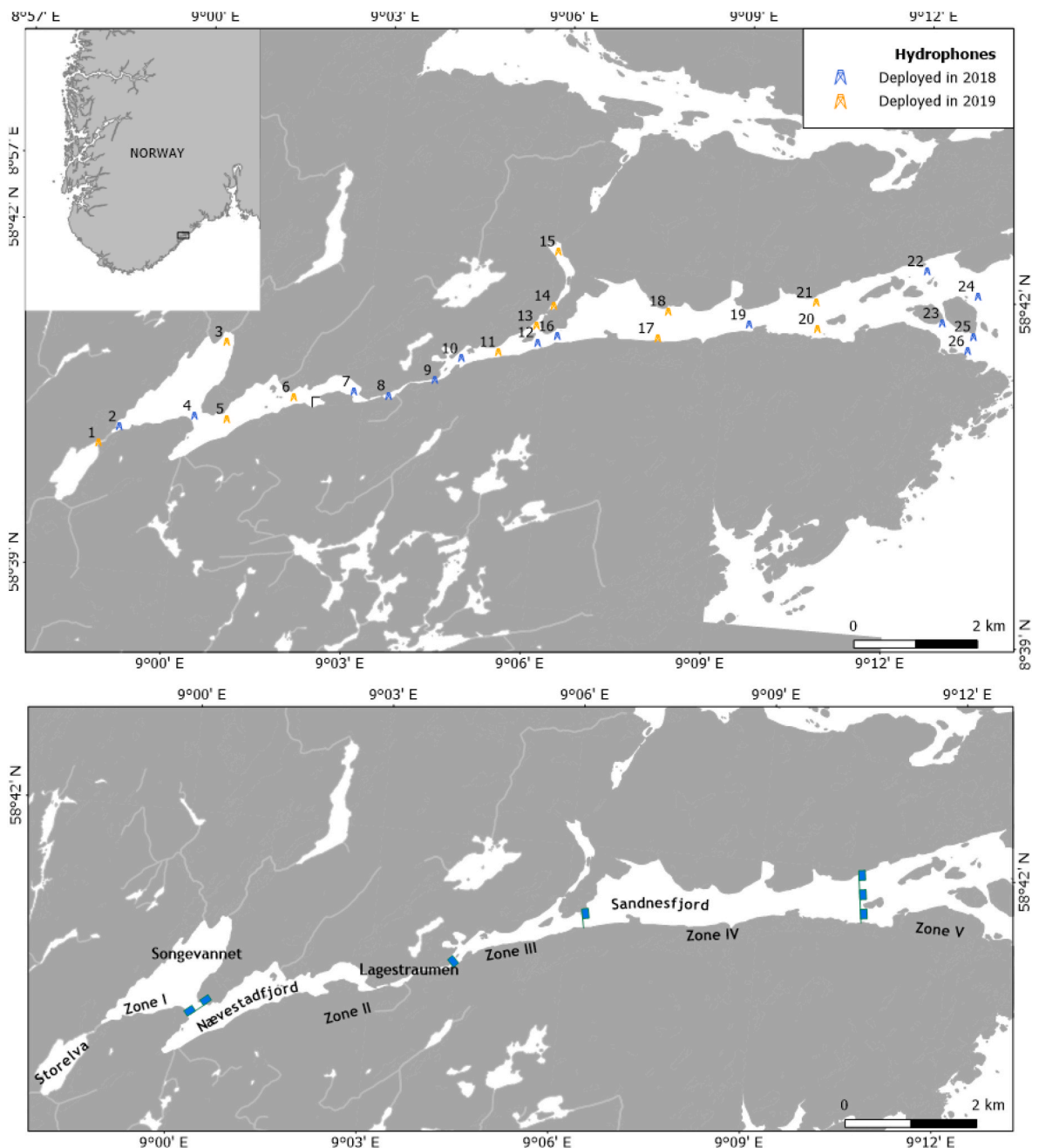

Fig. 1. Study area in Sandnesfjord, Southern Norway. Deployed receivers are numbered from 1 to 26. Different fjord zones (I–V) are identified by blue gates. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

increasing from Songevannet to the outer reaches of the fjord system (Tjomsland and Kroglund, 2010; Kroglund et al., 2011).

Freshwater is only found in the surface waters of Songevannet and Nævestadfjord, and the extent of it varies seasonally. The study area was divided into five zones based on salinity and fjord topography (Fig. 1): Zone I (Songevannet) – layered salinity marine water zone with fresh water occurring in the surface layers; Zone II (Nævestadfjord)– layered salinity marine water zone with freshwater occurring near the surface only seasonally; Zone III – layered salinity marine water zone with direct brackish water inflow from Zone II through the "Lagestraumen" tidal stream and a tributary fjord in the north; Zone IV - layered salinity marine water zone with no direct brackish water inflow; Zone V - layered salinity marine water zone, with opening to the ocean. Flowing between Zones II and III is the "Lagestraumen" tidal stream where the currents turn daily with the tides during periods with limited freshwater discharge from Storelva River. Depth varies, often on small spatial scales, throughout the fjord system with densely vegetated shallow habitats situated close to trenches down to 70 m deep. Eel are abundant throughout the fjord system, usually associated with the bottom of the fjord as they are caught with fyke nets (Durif and Skiftesvik, 2019).

2.2. Receiver array

An array of 14 acoustic telemetry receivers (VR2W, Innovasea Systems Inc., US), which were previously used for studying Atlantic cod (*Gadus morhua*) movements (see Kristensen et al., 2021), was used for this study from August 2018 to August 2021 (Fig. 1). Twelve additional receivers were deployed in September 2019 to increase the coverage (Fig. 1). The receivers were deployed along the salinity gradient from Storelva River to the open sea and attached to moorings at about 2.5 m from the surface with the hydrophone facing down. Data were downloaded and receiver batteries replaced in early August each year.

2.3. Fish sampling and tagging

Eel (*N* = 100) were tagged in 2018 and 2019 on three occasions throughout the fjord system (Table 1). The fish were captured by an experienced commercial eel fisher using fyke nets. Eel were anaesthetized immediately after capture using a 1:1 mixture of clove oil and ethanol (40 mL/L). Eel were measured (total length, pectoral fin length, and eye diameters) to determine sex and silver stage (Durif et al., 2005, 2009). All tagged eel were female (body length >500 mm) and all were classified to be yellow eel, except one individual that was at the silver stage.

Acoustic transmitters equipped with temperature and pressure sensors (V9TP or V13TP, Innovasea Systems Inc., US) were implanted through a 10 mm surgical incision into the intraperitoneal cavity of each eel (Baras and Jeandrain, 1998; Durif et al., 2003; Thorstad et al., 2013). The incision was closed with 2–3 sutures (Novosyn braided, coated, absorbable thread). The surgical procedure took less than 5 min per fish. All tagged eel were released at the site of capture within 10 min after they recovered from anaesthesia. Transmitters emitted a signal at 110–250 s intervals at a frequency of 69 kHz. The tags were cylindrical, the V9TP model with diameter of 9 mm, length of 44 mm, mass of 6–3 g

Table 1

Overview of eel (*Anguilla anguilla*) tagged in Sandnesfjord, Norway. n = sample size, TL = total length, SD = standard deviation, FII = yellow eel growth stage, FIII = premigration stage, and FV = migration stage (according to Durif et al., 2005). Proportion of tagged eel detected by the receiver array is also given.

Release date	*n*	TL (mm) ±SD	Stage	Proportion of detected eel
9-Aug-18	29	650 ± 70	FII, FIII	72%
11-Oct-18	22	650 ± 50	FII, FIII	100%
17-Sep-19	49	640 ± 70	FII, FIII, FV	94%
Total	100	650 ± 60	FII, FIII, FV	89%

(3.5 g in water) and estimated lifetime of 675 days, and the V13TP model with diameter of 13 mm, length of 48 mm, mass of 13 g (6.5 g in water) and estimated lifetime of 1484 days. Temperature measurement accuracy and resolution given by the manufacturer for both transmitter models was ±0.5 °C and 0.1 °C, respectively. Depth measurement accuracy and resolution given by the manufacturer for V9TP and V13TP transmitters at room temperature were ±1 m and 0.3 m, and ±3.4 m and 0.3 m, respectively. Maximum potential depth that could be recorded by each of the transmitter models was 68 m. Negative depth values were occasionally recorded in shallow areas and these were replaced with 0.01 m.

2.4. Determination of dormancy

We opted for a broad definition of dormancy, inactive for a period of at least seven days. Our purpose was to describe a general pattern for overwintering behaviour of eel in the marine environment which included dormant periods, disappearances (from the receiver array) and active periods. The actual physiological state of eel was not known. The period from September 1st to May 1st was analysed. Eel activity was assessed from logged detections of transmitter depths (*i.e.,* their vertical movements and the receiver where they were detected, following the approach taken by Villegas-Rios et al. (2020)). Dormant, disappeared and active eel were determined using the following criteria:

- Eel were considered dormant when detected at the same depth (±1 m for V9TP transmitters and ±3.4 m for V13TP transmitters), by the same receiver for at least seven days (Fig. 2a, b, e), (following from the criteria for dormancy applied by Westerberg and Sjöberg (2015)).
- Some eel remained undetected for several weeks. If such disappearances occurred within the inactive period of nearby eel, and reappearance occurred at the same receiver, we interpreted these disappearances to be episodes of dormancy, assuming that they had disappeared because they had found a shelter which blocked the transmission of the acoustic signals from the tag.
- Eel were defined as active when detected at different depths (Fig. 2) (e.g. in neither of the above categories).

2.5. Data analysis

We analysed dormant and disappeared eel separately and together. Eel with ambiguous behaviour - brief periods of activity in between episodes of dormancy or disappearances - were removed from the analyses (n = 7). Dormancy and disappearance episodes are identified in all the Figures. To identify differences in overwintering patterns within the fjord, we applied a Principal Component Analysis (PCA) on the following variables: total eel length, Julian day (when dormancy started and ended), day length (in hours, when dormancy started and ended), T° (temperature when dormancy started and ended). Plots were labelled according to the fjord zone where eel overwintered and according to disappearance/dormancy assignment.

Logistic regression was used to explore whether the start and end of dormancy was associated with specific environmental factors. The probability that an eel was dormant was modelled according to water temperature (measured by the transmitters) and day length (calculated based on latitude and date). Data from all three years were combined. Dormancy periods were considered as independent observations since the same eel could display different behaviours between years. The probability of an eel waking from dormancy was also modelled using the same explanatory variables. Duration of dormancy was compared between the inner part (Zones I-II) and the outer part of the fjord (Zone III-V) using a linear model. Final models were validated using standard procedures (Zuur et al., 2010). Data exploration, visualization and analyses were done in R version 4.0.3 (Team, 2021). In the figures, the timing of dormancy is depicted using the number of days after August
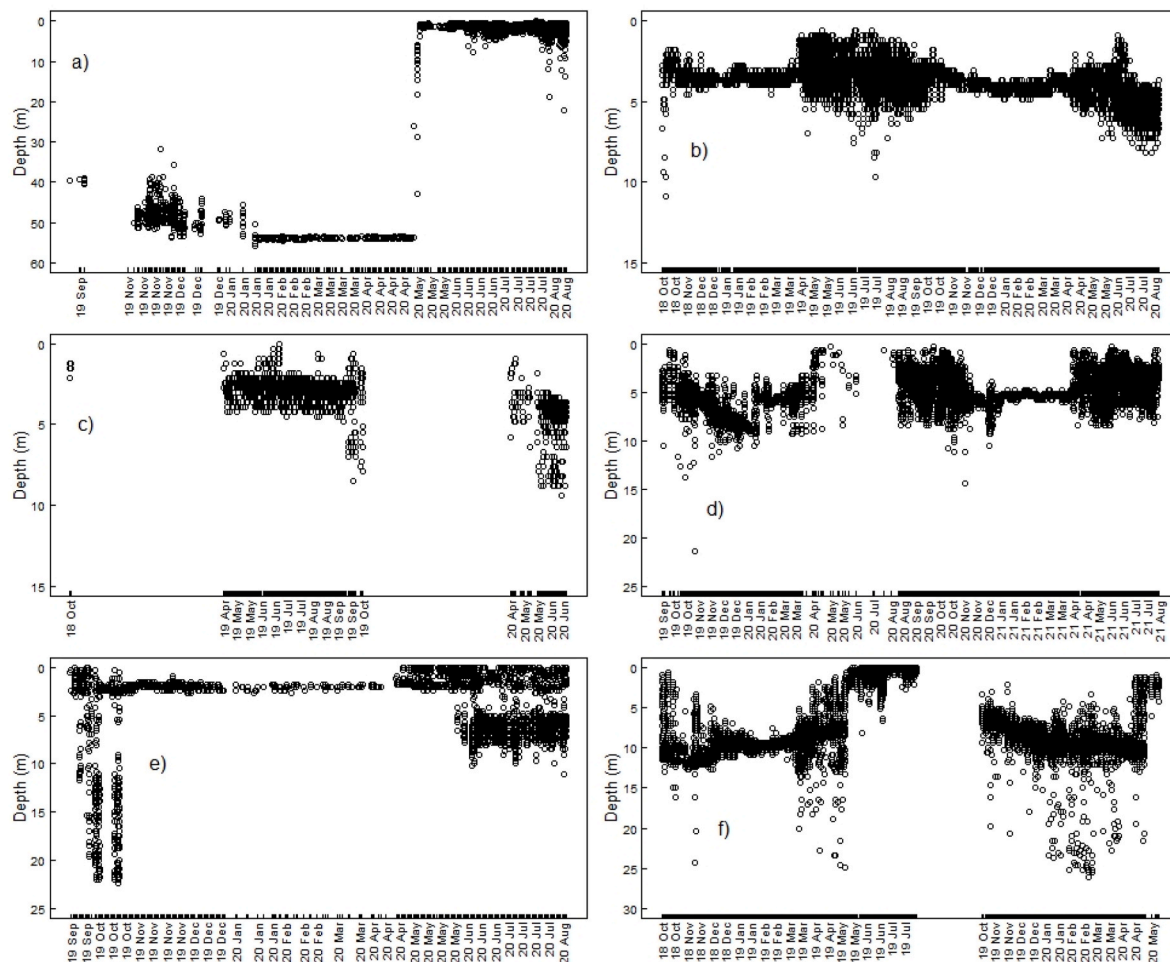
Fig. 2. Examples of depths (black circles) experienced by individual yellow eel (*Anguilla anguilla*) tagged with acoustic transmitters. a) deep-water dormancy episode, which was preceded by periods of disappearance and activity; b) dormancy during two consecutive years with decrease in variation of depth use; c) disappearance from the receivers during the two consecutive winter periods; d) constant activity during the first winter period, but not during the second; e) dormancy and a preceding high-amplitude depth variation in autumn; and f) constant activity during the two winter periods.

1st rather than Julian days to avoid discontinuous axes between December and January. Maps were made using Manifold System 8.0 using Shape files downloaded from the NVE database (Norwegian Water Resources and Energy Directorate).

3. Results

3.1. Detection summary

Some eel turned silver during the study period. This was inferred from their abrupt change in behaviour: diel vertical migrations and subsequent escapement from the fjord. These data were excluded. A total of 1 028 318 (temperature) and 1 029 780 (depth) eel detections, were recorded by 25 receivers during the study period. No eel transmitters were detected at the innermost freshwater site or in the outermost part of the fjord (receiver 1 and zone V, Fig. 1). Nine of the 100 tagged eel were never detected by any of the receivers. Two eel were removed from the dataset because they had either expelled the transmitter or died 1–2 months after tagging (the transmitter was detected at constant depth). Eel with <10 detections during the study period were excluded. This resulted in a final sample of 55 eel representing 92 individual overwintering/study periods across the three years.

3.2. Behaviour of eel

There was no detectable effect of the tagging procedure on eel behavior; all showed motor activity. Some eel resumed swimming right after tagging and release, whereas some were only briefly detected and then disappeared (Fig. 2). Out of 92 overwintering periods, 11% were active (six eel) – that is, these eel maintained activity throughout the winter (Figs. 2 and 3). The rest of the periods (89%) corresponded to dormancy (61%), or disappearances (39%). Some eel displayed spurts of activity between episodes of dormancy. These temporary active periods lasted between one day to a few weeks and included vertical movements of up to 5–6 m. Seven eel displaying these ambiguous behaviours were not included in the statistical analysis.

Most eel (64%) were observed for two winters (one eel, #15175, for three winters, Fig. 3). However, they did not necessarily display the same behaviour during those two years (Figs. 2 and 3). For instance, some eel were dormant during the first winter, but were active during the second winter, and vice-versa (Fig. 2d). Of the 36 eel with data on two or three consecutive winters, 69% displayed the same behaviour during consecutive years.

During dormancy, eel were usually stationary at depths between two and 10 m (96.5% of detections at < 10 m), which corresponded approximately to the same range as during the rest of the year (99.8% of detections at < 10 m). However, four dormant individuals were registered at 15, 19, 51 and 53 m.
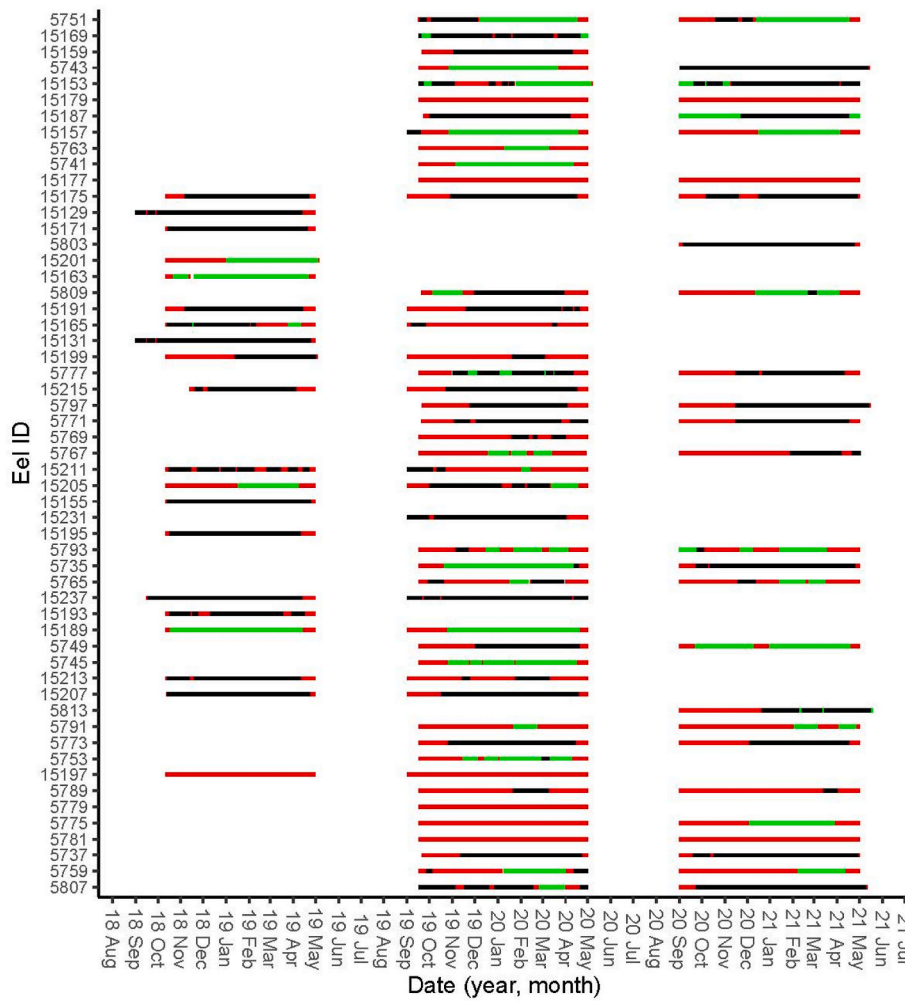
Fig. 3. Activity timelines of European eel (*Anguilla anguilla*) (*N* = 55) tagged with acoustic transmitters. Red line – activity; green line – no depth variation (interpreted as a dormancy event); black line – disappearance (interpreted as a dormancy event). Individual eel are sorted along the y-axis by total length from 530 mm (ID 5807) to 820 mm (ID 5751 and 15169). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The average duration of dormancy (including dormancy and disappearances) was 138 days (min: 35 and max: 224 days, Fig. 3). The duration of dormancy was more strongly correlated with the start date than the end date (start date: R^2 = 0.60; end date: R^2 = 0.27); the later the dormancy started, the shorter it lasted. The start date was more variable (range = 158 days, Fig. 4) than the end date (range = 92 days, Fig. 4b). By October–November, most individuals (>50%) had entered dormancy (Fig. 4). In mid-April, most eel (>50%) had become active again, but during the last two years some eel were still dormant until May (Fig. 4).
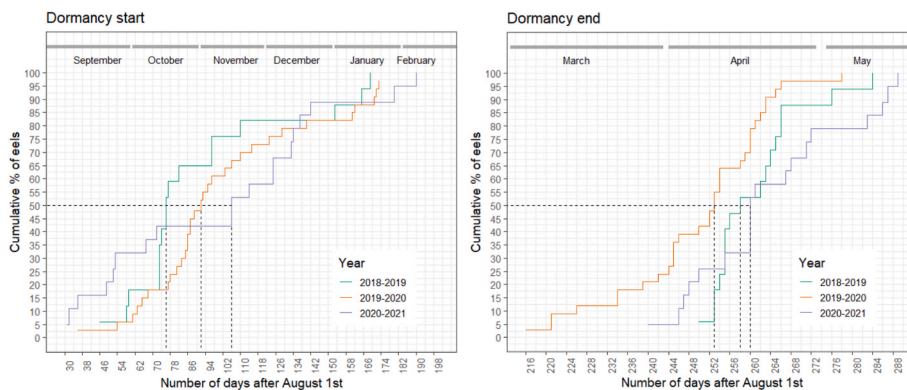

Fig. 4. Dormancy behaviour of eel tagged with acoustic transmitters monitored between August 2018 and August 2021. The dashed lines represent the median number of days for the end of dormancy. Day one was assigned as August 1st. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Only one eel overwintered in the innermost part of the fjord (Zone I). The percentage of eel that started their dormancy was related to a decrease in day length and temperature and an increase in Julian days (Fig. 5). The percentage of eel that ended their dormancy increased with an increase in all three variables: Temperature, day length and Julian days (Fig. 5). Eel located in the mid and outer parts of the fjord (Zones III and IV) became dormant before eel in the inner (more freshwater) part of the fjord (Zone II). The reverse occurred for the end of dormancy: eel located toward the inner freshwater zone (Zone II) were the first to become active again. This pattern was consistent between years (Fig. 5). Length of eel increased toward the outer part of the fjord (Fig. 5). Duration of dormancy was significantly longer in the outer part of the fjord: by 54 days on average (t = 5.16, P < 0.0001, linear model estimate).

Only day length was significant as an explanatory variable (Table 2). When including eel that has disappeared, almost all models were significant, except for the temperature variable in the combined temperature and day length model (Table 2). Dormancy occurred at a wide range of water temperatures (6.5–15 °C, Fig. 6). Overall, day length showed a better fit than temperature for explaining overwintering patterns (Fig. 6). The estimated number of hours of daylight corresponding to

half of the eel entering dormancy (start) or awakening (end) are 9.4 and 14.1 h respectively (Table 3).

4. Discussion

Low temperatures induce inactivity, fasting and a low metabolic rate in fish (Shuter et al., 2012; Speers-Roesch et al., 2018). For eel, this occurs at about 5 °C. Below that temperature, oxygen consumption decreases and eel enter metabolic torpor (Walsh et al., 1983; Reeve et al., 2022). Eel in our study rarely experienced such low temperatures. Sandnesfjord is a temperate marine environment in which dynamic water mixing occurs throughout the year due to ebb and flood tides resulting in higher average and more variable water temperatures compared to inland waters at the same latitude (Tjomsland and Kroglund, 2010). Despite these relatively mild temperature conditions, eel were inactive at approximately the same time in both study years. Overall, overwintering pattern in Sandnesfjorden varied little from year to year: from October–November to mid-April, and were best predicted by day length (Table 3). Temperature had much less power than day length in explaining the timing of the inactive period, which we refer to as dormancy. We conclude that eel may enter dormancy even under mild
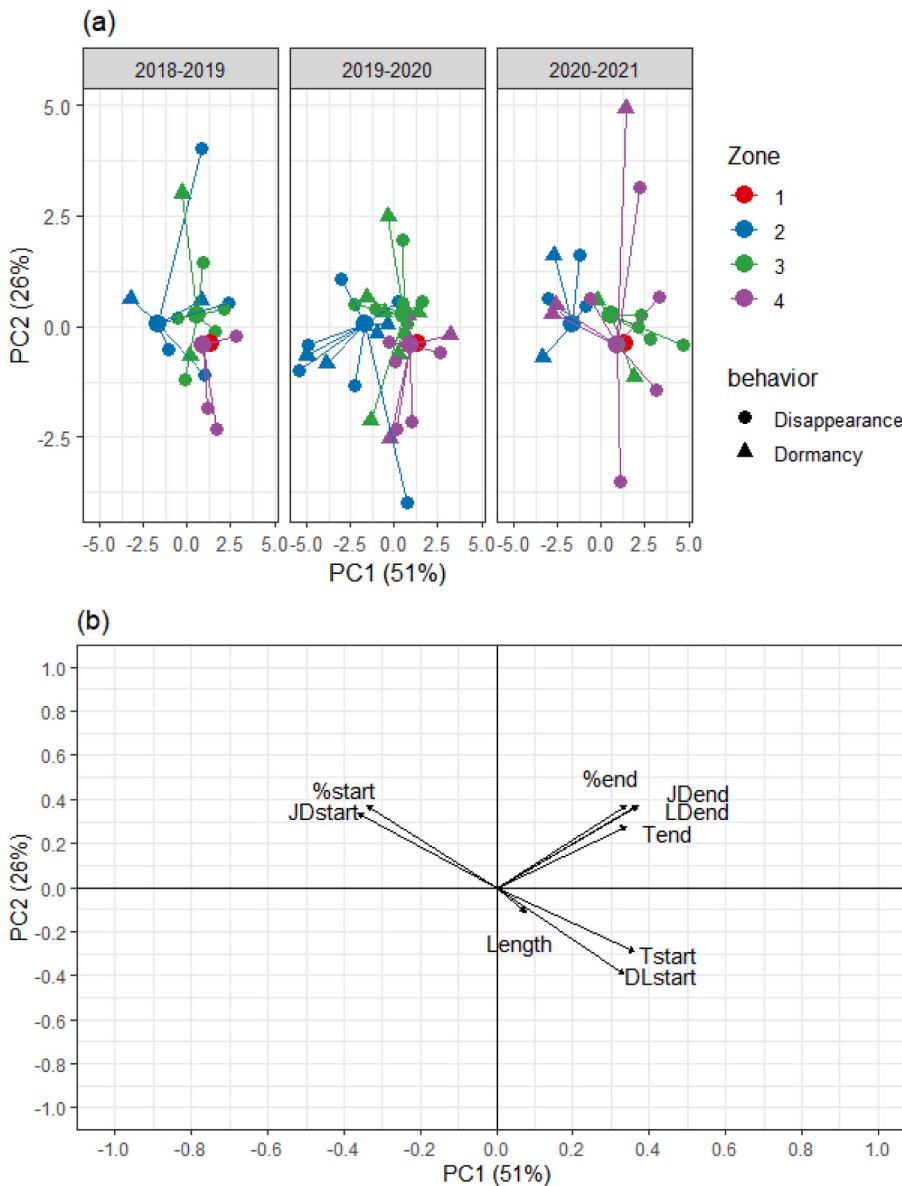

Fig. 5. a) Plot of individual scores of the Principal component analysis (PCA) carried out on data from overwintering eel in Sandnesfjord (Norway). Zones are numbered from 1 (innermost part of the fjord) to 4 (outermost part of the fjord). Centroids were calculated to group individuals from these four different fjord zones. Individual eel are also labelled according to their overwintering behaviours (disappearance or dormancy). b) Plot of the variables used in the PCA, JD: Julian days (s: start and e: end), %s: Proportion of individuals that started overwintering, %e: Proportion of individuals that ended overwintering, DL: day length (s: start and e: end), T: temperature (s: start and e: end), Length is the body length of eel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Overview of the logistic regressions carried out on data from overwintering eel in Sandnesfjord, Norway. The proportion of eel that became dormant (start) or awoke from dormancy (end) according to either day length or temperature or the combination of both variables. Two groups of eel were tested according to how dormancy was defined by either including disappearances or not (dormancy). AIC: Akaike Information Criteria.

Model	Z value	P	AIC
Dormancy (n = 27)			
$\%_{start} \sim$ day length	−2.153	0.03	24
$\%_{start} \sim$ temperature	0.1537	0.12	29
$\%_{start} \sim$ day length + temperature	−1.642 (day length)	0.10	25
	−0.330 (temperature)	0.74	
$\%_{end} \sim$ day length	2.194	0.028	22
$\%_{end} \sim$ temperature	1.863	0.062	29
$\%_{end} \sim$ day length + temperature	1.602 (day length)	0.11	23
	0.632 (temperature)	0.53	
Dormancy and disappearances (n = 69)			
$\%_{start} \sim$ day length	−3.758	0.00017	54
$\%_{start} \sim$ temperature	−2.999	0.0027	74
$\%_{start} \sim$ day length + temperature	−2.657 (day length)	0.0079	56
	0.106 (temperature)	0.915	
$\%_{end} \sim$ day length	3.365	0.00077	58
$\%_{end} \sim$ temperature	3.061	0.0022	72
$\%_{end} \sim$ day length + temperature	2.342 (day length)	0.019	60
	0.483 (temperature)	0.63	

temperature conditions (in our study this could occur at temperatures around 14 °C), and that timing of entering dormancy is correlated with photoperiod or ecological processes associated with photoperiod.

Similar overwintering periods were observed in eel tagged with data storage tags in Lake Mälaren in Sweden (Westerberg and Sjöberg, 2015): between early November until the end of May. Since both study locations are at approximately the same latitude (58.7° and 59.4°) and have similar photoperiods, this is consistent with our observations that eel may enter a state of dormancy even at mild temperatures and that this is correlated with day length. Westerberg and Sjöberg (2015) also reported that the start of dormancy was associated with a wide range of temperatures (4.5–12.4 °C, our study: 6.5–15 °C) and attributed this to a residual effect of tagging. In other words, tagging surgery and handling caused the eel to be inactive for a period. However, in our study, tagging had little effect as eel rapidly resumed normal activity after the procedure. Thus, we argue that overwintering levels of activity occur even

Table 3

Day length (number of hours of daylight ± standard error) estimated for 25% (L25), 50% (L50), and 75% (L75) of eel (*Anguilla anguilla*) to enter dormancy (start) or to awake (end). Estimates are based on logistic regressions of the percentage of dormant (or awakened) eel according to day length.

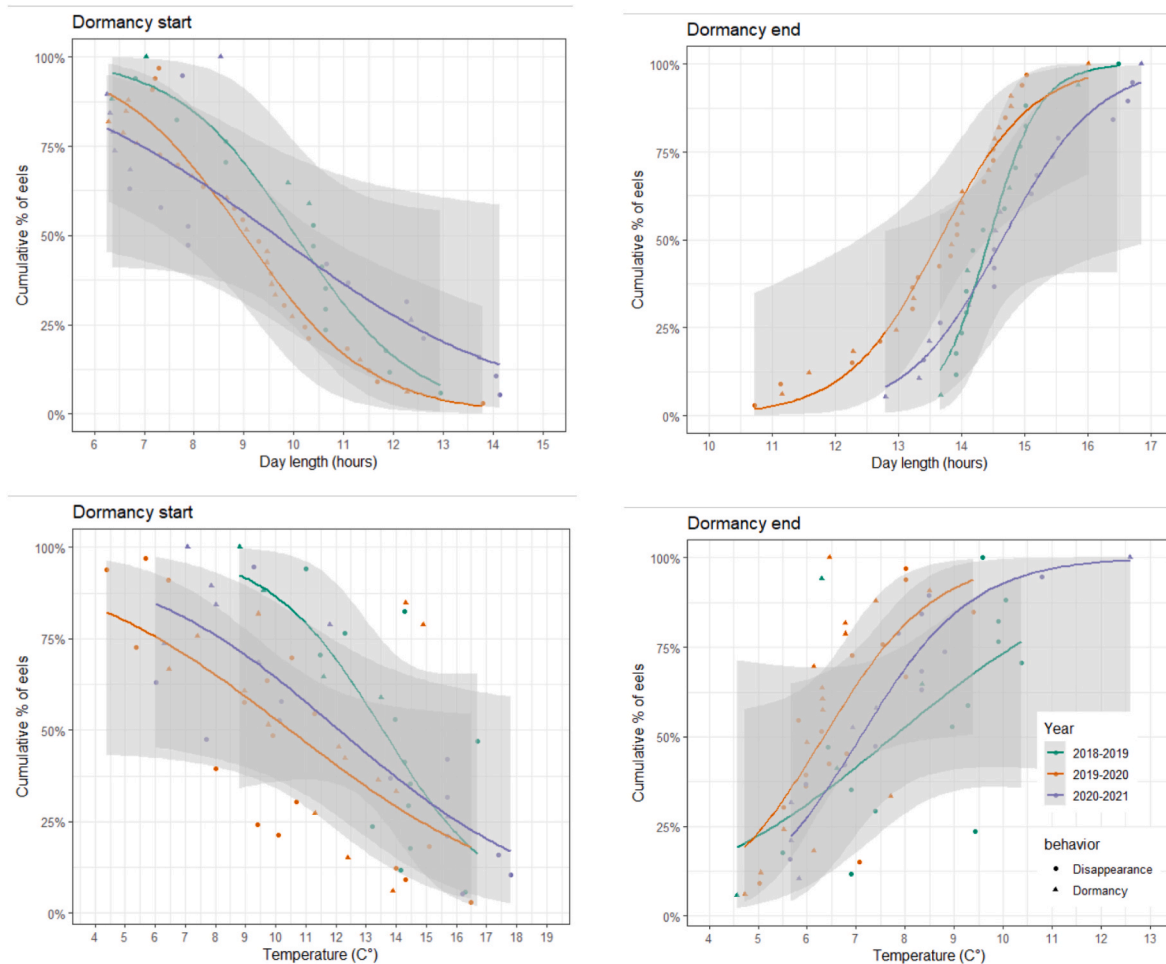|	DL25	DL50	DL75
Dormancy start	11.3 ± 0.7	9.4 ± 0.5	7.5 ± 0.7
Dormancy end	13.2 ± 0.4	14.1 ± 0.2	15.0 ± 0.3

Fig. 6. Timing of eel (*Anguilla anguilla*) dormancy according to photoperiod and temperature. The graphs show the proportion of eel that fell into dormancy (start) and awoke from dormancy (end). Logistic regressions were fitted to the data. Grey shading represents confidence interval of the GLM model using a binomial distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

at relatively mild temperatures. Whether light/day length is the trigger of overwintering behavior is unknown. However, it seems unlikely because eel often take refuge in the mud during the dormant period (Tesch, 2003). The trigger could also be one or more ecological processes that are correlated with photoperiod; for example, the decrease in productivity and subsequent disappearance of prey items during the winter (Larsen et al., 2004).

There was a clear difference in the timing of dormancy between zones II and III-IV (Fig. 5). Dormancy started later and ended earlier in the inner part of the fjord (zone II) and was also shorter by an average of approximately 54 days compared to the outer part of the fjord. This indicates that photoperiod is not the only factor modulating the timing and duration of dormancy. What the other factors are is unclear but may be related to seasonal changes in salinity. In mid-April – when eel awake from dormancy – river flow generally increases as snow melts. Thus, the increased freshwater input from Storelva river causes the salinity to decrease, initially, in zones I and II, then later in the outer fjord system (Tjomsland and Kroglund, 2010).

Dormancy of eel observed in this study seems to be facultative rather than obligatory; several eel (~11% of the overwintering periods) remained active, or were intermittently active, during the winter. The reasons why some eel remained active while other became dormant require further investigation, for example, at the physiological level.

Some caution is warranted regarding our interpretation that all disappearance episodes represent periods of dormancy. As the receiver area did not provide total coverage of the entire study area, we cannot exclude the possibility that some eel moved to areas between receivers in which they would not have been detected. However, nearly all the eel that disappeared reappeared at the same or a nearby receiver. This indicates that they stayed in the area but were not detected by the receivers. Temperate eel bury themselves into sediments or hide in crevices during winter (Bertin, 1951; Tesch, 2003; Tomie et al., 2017). As the transmissions of acoustic waves are blocked by rocks, and can be severely weakened by sediments and vegetation, it is possible that the signals emitted by transmitters of buried and sheltered eel had a reduced detection range and, therefore, were less likely to be recorded by the stationary receivers.

Our observations of the dormancy period are useful for deciding the timing of surveys for eel, at least in marine coastal areas. Logistic regressions may also be used to adjust abundance estimates – a posteriori – according to the time of the year. For example, a survey conducted when daylength is 10 h, should consider that approximately 50% of eel may be dormant. This would be especially important during annual surveys carried over several years at the same location as part of monitoring of this endangered species.

CRediT authorship contribution statement

Mehis Rohtla: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Even Moland:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Anne-Berit Skiftesvik:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Eva B. Thorstad:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Sebastian Bosgraaf:** Methodology, Investigation. **Esben M. Olsen:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Howard I. Browman:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Caroline M.F. Durif:** Writing – review & editing, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.108016.

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