

# Validation of pop-up satellite archival tags (PSATs) on Atlantic cod (*Gadus morhua*) in a Greenland fjord

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## ABSTRACT

Traditional tagging techniques are simple and cost-effective, but inferences require recaptures and data on movement/migration are limited to a start and end position at unpredictable intervals. Pop-up satellite archival tags (PSATs) offer other opportunities, as they provide positions at pre-programmed times and collect on-route data, which can be used to describe position, behavior, and habitat preferences. Species suitability should, however, be documented prior to large-scale studies using PSATs. We deployed PSATs on six relatively large (total length 84–125 cm) Atlantic cod (*Gadus morhua*) in inshore West Greenland waters. Three tags were physically recovered, providing high-resolution data on depth and temperature (readings every 3 s), while three tags did not report (recovery rate = 50 %). To evaluate the tag's applicability on Atlantic cod, we made a detailed behavioral analysis by defining swimming behavior, occupied water types and depth phases, which were cross-evaluated in relation to depth, temperature and water stratification to identify behavioral patterns. Distinct and shared patterns in swimming behavior were evident and we found no signs of impaired swimming behavior except for an adaptation period lasting up to 39 h after release. Generally, the three cod were pelagic and preferred waters ranging 2–5 °C. When encountering colder water masses these were avoided. During late summer/early autumn, increased vertical activity could in some cases be linked to darkness and a high-activity event could be linked to possible predator avoidance. All combined, we conclude that PSATs are suitable to monitor natural behavior on large specimens of Atlantic cod for periods of at least four months.

## 1. Introduction

Historically, Atlantic cod (*Gadus morhua*), referred to as cod hereafter, has been a key commercial species in West Greenland, with annual landings regularly exceeding 300,000 t during the 1950s and 1960s (Horsted, 2000). A combination of changes in climate, overfishing and stock migration caused a rapid stock decline and ultimately the collapse of the stock in West Greenland in the 1970s (Hovgård and Wieland, 2008). For the past two decades, the fishery for cod in Greenland has increased, yet annual landings only occasionally exceeded 50,000 t

(ICES, 2021). In offshore waters in West Greenland, the cod stock remains severely depleted, and a successful rebuilding plan should be based on robust, high-quality scientific advice (ICES, 2021). Yet, essential knowledge of the species' biology, especially their migrating behavior, is still lacking, making it difficult to correctly assess stock dynamics of cod in Greenland waters.

A shared characteristic of the yearly scientific advice for the three cod stocks in Greenland, given by the International Council for Exploration of the Sea (ICES), is the need for a better understanding of stock connectivity (ICES, 2021). The critical aspect is that the morphologically

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indistinguishable cod stocks mix in unknown proportions and pass through management areas in association with egg/larval drift, feeding, and spawning (Brickman et al., 2007; Christensen et al., 2022; Storr-Paulsen et al., 2004). This mixing needs to be quantified to accurately estimate stock status and thus produce more precise scientific advice. Migration patterns in marine fishes are often studied through tagging, ranging from traditional plastic tags to state-of-the-art electronic data recorders. In Greenland, > 100,000 T-bar anchor tags have been successfully deployed on cod in the last century (Hansen, 1949; Storr-Paulsen et al., 2004), leading to a well-documented understanding of the overall migration patterns (North/South, West/East, in-/off-shore). Still, with only a start and end position, the vertical and horizontal behavior in-between is unknown, and recaptures are naturally limited to fishing areas.

Several tags on the market can be used to investigate fish behavior and migration, but pop-up satellite archival tags (PSATs) do not rely on the recapture of the tagged fish to retrieve the data (Thorstad et al., 2013). PSATs record light, depth (through pressure) and temperature and transfer data via an Argos satellite, following tag release after a pre-programmed time-period. However, if the tags are physically recovered, the internal data of the tag ensures a complete data series of much higher resolution than if summaries of the data are transferred by Argos. Furthermore, data sets based on Argos transmissions are often fragmented, and gaps of several hours/days occur due to transmission failures. PSATs have been used successfully to obtain unique insights into the swimming behavior of both large and medium-sized marine fish such as Atlantic halibut (*Hippoglossus hippoglossus*), Atlantic bluefin tuna (*Thunnus thynnus*), European eel (*Anguilla anguilla*) and Atlantic salmon (*Salmo salar*) (Aarestrup et al., 2009; James et al., 2020; Lutcavage et al., 1999; Rikardsen et al., 2021). Also, a single tagging study with PSATs has been made on the Atlantic cod's congener the Pacific cod (*Gadus macrocephalus*) (Bryan et al., 2021). That study had successful tagging for up to 12 months, but also showed high mortality which was suspected to be caused by internal injuries due to barotrauma, especially for specimens caught in trawls (Bryan et al., 2021). For our study, we wished to explore the applicability of PSATs on Atlantic cod in Greenland for specimens that are caught as gently as possible. This will allow us to evaluate PSATs as a tool to investigate this species' natural swimming and migration behavior. If successful, there is a suite of relevant applications in relation to stock connectivity between in Greenland and Iceland, but also in other North Atlantic cod stocks where stock mixing occurs (Hüssy et al., 2016; Nordeide and Båmstedt, 1998).

For our study our goal was to deploy PSATs on cod and recover the tags so that behavioral patterns can be inferred from high-resolution data. The Kapisillit area in Nuup Kangerlua (Godthåbsfjorden) is ideal for such a study as cod here are known, from traditional tagging studies, to be resident (Hansen, 1949). Also, the innermost part of the area is the largest known inshore spawning ground for cod in Greenland (Hansen, 1949; Storr-Paulsen et al., 2004). Investigating the swimming behavior of cod here will therefore also provide novel insights into their behavior in terms of temperature and depth preferences in this biologically important area. Furthermore, unlike other more difficult-to-access locations where large cod occur in Greenland (e.g., offshore waters), tag retrieval is realistic in the Kapisillit Fjord. Specifically, the aims of the study are: 1) To deploy PSATs on large cod caught without barotrauma and retrieve the tags physically using a homing pinger; 2) To give a detailed description of behavioral patterns in terms of depth and temperature; and 3) To evaluate if PSATs are applicable to large cod over long time-periods (months).

## 2. Methods

### 2.1. Sampling procedure

Six cod between 84 cm and 125 cm total length (TL) were tagged in early June 2018 in the Kapisillit Fjord, an inner branch of Nuup

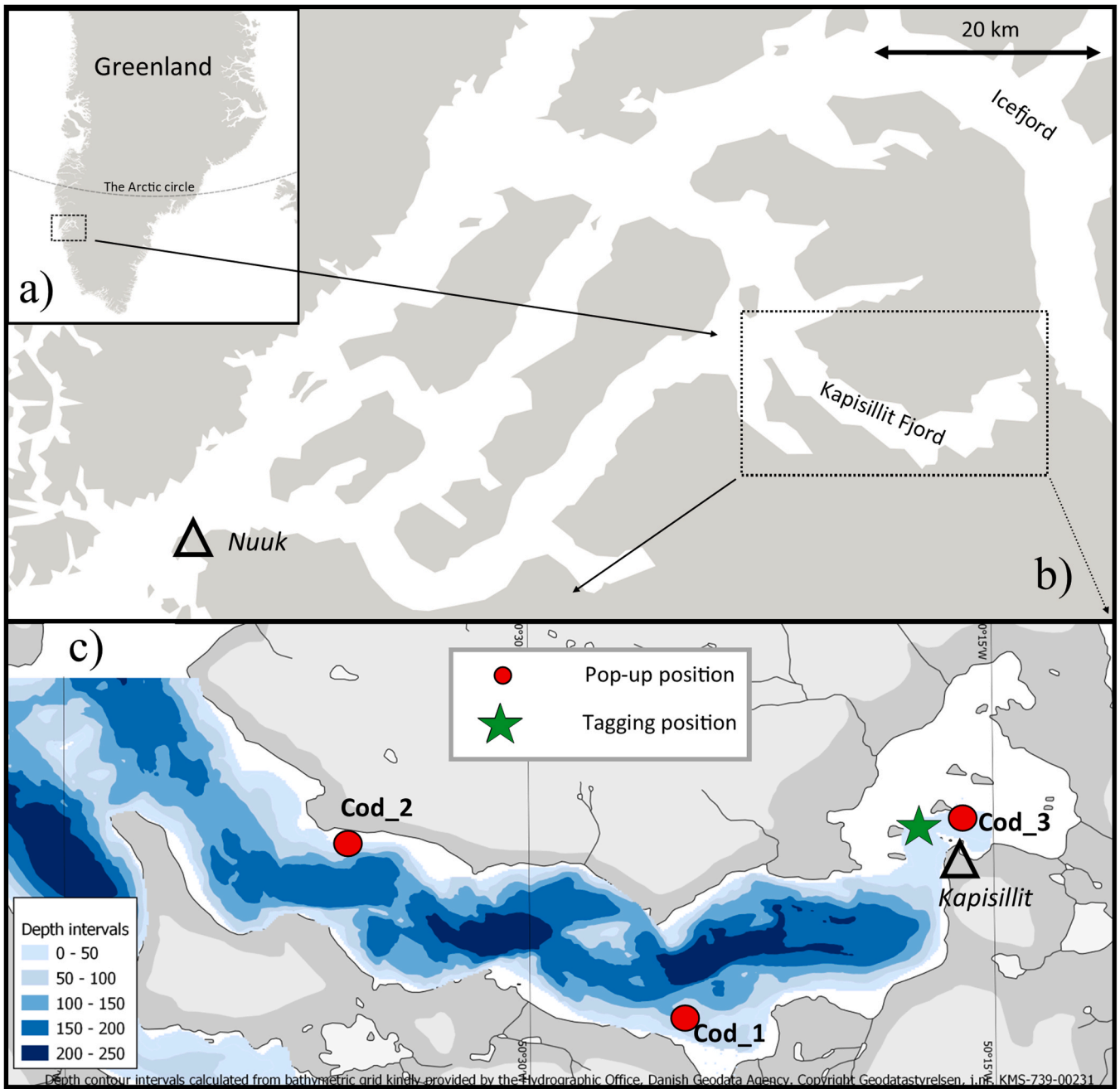
Kangerlua near the settlement of Kapisillit at 64.4°N south of the Arctic Circle (Fig. 1). From the release of sperm or eggs, four of the six specimens were sexed, and based on their size, all were considered sexually mature (see overview of tagged fish in Table 1). Two individuals were caught at 30 m depth using a fishing rod (Cod\_1–2), and four (Cod\_3–6, Table 1) were sampled in collaboration with a commercial fisher using a pound net anchored to the shore. To avoid capture-induced barotrauma, the specimens caught on a fishing rod were held at a depth of 10 m for approximately 5 min before being brought to the surface. Cod in the pound net were raised slowly towards the surface (~1 m min<sup>-1</sup>) from ~30 m depth and experienced neither barotrauma nor mechanical stress before being netted. Each cod was transferred to a 1.5 × 1.5 m plastic tub with seawater and observed for 10–15 min. If the cod maintained balance and did not bleed, e.g., from the gills, it was considered suitable for tagging. Before tagging, TL was measured to the nearest cm.

### 2.2. Tagging procedure

Each cod was externally tagged with a PSAT (MiniPAT, Wildlife Computers; length x diameter, weight: 124 mm × 38 mm, 60 gr.). The PSAT was equipped with two nylon strings mounted to a silicone plate (30 × 10 mm), which was attached to the fish by injecting plastic-coated stainless-steel strings (0.2 mm in diameter) across the dorsal musculature ~5 mm below each side of the first dorsal fin (Fig. 2a). A similar methodology has been successfully applied for mounting PSATs on Pacific cod, Atlantic salmon and European sea bass (*Dicentrarchus labrax*) (Bryan et al., 2021; Hedger et al., 2017; O'Neill et al., 2018; Rikardsen et al., 2021). Before release, tagged individuals were observed for approximately 5 min to ensure they kept their balance (Fig. 2b and c). All fish were released at the same location in the Kapisillit Fjord (Fig. 1). The tagging procedure followed national laws and regulations applying for the Greenland Institute of Natural Resources (GINR) within Greenland waters.

### 2.3. Tag settings and recovery

In the Tag Agent software provided by Wildlife Computers, tags were programmed in terms of tagging duration and the expected physical conditions experienced by cod. Tags were programmed to release after ~134 days-at-liberty (DAL), which allowed us to recover them in mid-October. This was presumably well before the area's seasonal sea ice formation. A tagging duration of 134 days automatically generated a recommended sampling interval for Argos transferred data, to be every 450 s. Further gaps in the final dataset were dependent on how successful the Argos transmission was. Each tag's sampling interval was every 3 s, making the internally archived data much greater. This high-resolution internal data only became available if the tag was physically recovered. PSATs can automatically release if prolonged inactivity occurs, which could indicate a dead individual. We did not enable this setting as it was unknown if and for how long a cod might remain inactive or nearly inactive at a given depth, e.g., by resting just above the bottom. Tags were programmed to release (and thereby initiate transmission) if they floated at the surface for more than 24 h, e.g., if the tag detached prematurely from the fish. Data Product Settings encompassing 'daily series', 'time series' and 'summary messages' were activated to 'always be generated'. The histogram bin limits for temperature were set to -2.0, -1.0, 0.0, 1.0, 2.0, 4.0, 6.0, 8.0, 10.0, 12.0, 15.0 and 45.0°C and 10.0, 20.0, 40.0, 70.0, 100.0, 200.0, 300.0, 400.0, 500.0, 700.0, 1000.0, and 2000.0 m for depth. The homing pinger was activated to allow for physical location of the tags when at surface. To find the floating tags, their approximate direction/location was first detected by an Arrow Yagi antenna and an AOR AR8200 (WB RCVR Handheld 500k/3000 MHz) wide range receiver. Subsequently, the tags were located by sailing (or walking on shore) in transects around the last known position received via Argos, adjusting the direction according to the acoustic signal, until the tag was visually spotted.



**Fig. 1.** Tagging location. a+b: The fjord system (Nuup Kangerlua) in West Greenland showing the Icefjord and the Kapisillit Fjord. c: Tagging location, location of capture (Cod\_3, longline) and Argos pop-up positions (Cod\_1 and Cod\_2, pop-up) in the Kapisillit Fjord.

**Table 1**

Overview of PSATs deployed on cod in the Nuup Kangerlua (Godthåbsfjorden) near Kapisillit. DAL is ‘days at liberty’ and NC refers to ‘No Contact’. Positions are given in decimal degrees. Cod\_1–2 were caught on fishing rod and Cod\_3–6 in pound net.

ID	TL (cm)	Sex	PSAT PTT	Date of			DAL (days)	Position of	
				deployment	progr. pop-off	reporting		deployment	pop-up (argos)
Cod_1	125	M	173877	04.06.18		16.10.18	134	64.395; -50.418	
Cod_2	84	M	173880	05.06.18		16.10.18	133	64.438; -50.601	
Cod_3*	91	F	173882	05.06.18	15.10.18	01.10.18	119	64.438; -50.267	
Cod_4	93	NA	173878	05.06.18		NC	-	64.436; -50.302	
Cod_5	104	F	173879	05.06.18		NC	-	NC	
Cod_6	94	NA	173881	05.06.18		NC	-	NC	

\* tag recovered by fisher



## 2.4. Analyses

### 2.4.1. Horizontal movements

Horizontal migration distance was calculated as the shortest distance (not crossing land) between the tagging position to the first available Argos position of class 2 or 3 (which have a 500 m accuracy; Douglas et al., 2012). Geolocation was attempted using only the light data, as we lacked other supportive data to calibrate this, such as depth and water temperature profiles from across the fjord.

### 2.4.2. 'Depth phases' and vertical activity

From depth-time plots for each cod, so-called 'Depth phases' were visually defined as coherent time periods (>5 days) with an overall constant swimming depth. For each 'Depth phase', the average depth and average temperature were calculated, together with coherent standard deviations. For these calculations, data from transition periods (<8 days) between 'Depth phases' were excluded. To evaluate patterns in vertical activity in relation to season, day-vs-night and tide, the depth variances in 1-hour time intervals were calculated and plotted as log-transformed values for each fish throughout the tagging period. The variance,  $\sigma^2$ , was calculated as

$$\sigma^2 = \frac{\sum_{i=1}^n (X_i - u)^2}{n}$$

where  $X_i$  is the single depth reading,  $u$  is the average depth over 1 h and  $n$  is the number of depth readings in the given time period.

### 2.4.3. Swimming behavior

In each 'Depth phase', the vertical 'Swimming behavior' (SB) was categorized based on the frequency of so-called 'Ascents' and 'Descents'. 'Ascents' were defined as rapid vertical upward movements followed by similar rapid downward movements of more than 1 m. 'Descents' were defined as the opposite. SB could also be characterized by periods of relatively low vertical activity (<1 m changes) or by almost constant swimming depth. In total, five different SBs were defined:

- SB1: 'Ascents' and 'Descents' occur with approximately equal frequency (Fig. 3a).
- SB2: 'Descents' occur most frequently (Fig. 3b).
- SB3: 'Ascents' occur most frequently (Fig. 3c).
- SB4: Little vertical activity with few or none 'Ascents'/'Descents' (Fig. 3d).
- SB5: Swimming at constant depths interrupted by rapid depth changes (Fig. 3e).

For all individuals, each day was visually assigned an 'SB' independently by two of the authors (JN and RH) based on the frequency of 'Ascents'/'Descents'. In case of disagreement, the assignment was re-evaluated by both authors and agreed upon. On days with multiple SBs being exhibited, the dominant SB was chosen. If several days had an almost equal duration of different SBs, the days were split to allow both SBs to be represented in the results. An example of this could be if July 1st to July 3rd had 51 % SB1 and 49 % SB2. One day would then be designated as SB2 and the two others as SB1.

### 2.4.4. Water type

Changes in swimming depth were associated with changes in temperature depending on the cod's position in the water column and the characteristics of the water column. The tagged cod encountered both fully mixed and strongly stratified water columns with a distinct thermocline. Additionally, the fjord showed strong horizontal gradients and presence of pronounced temperature fronts mainly due to an intrusion of cold, even subzero, water. Based on the change in temperature associated with different SBs, we designated six depth-temperature

relationships that define the 'Water type' (WT) occupied by the cod:

- WT1: Stratified water column with a distinct thermocline, where swimming depth and temperature are correlated, so that 'Ascents' are associated with a temperature increase and 'Descents' are associated with a temperature decrease (Fig. 4a). This is consistent with the cod being inside the thermocline.
- WT2: Stratified water column with a distinct thermocline, but only 'Ascents' are associated with a temperature change (increase), whereas 'Descents' do not result in a temperature change. This is consistent with the cod being just below the thermocline (Fig. 4b).
- WT3: Stratified water column with a distinct thermocline, but only 'Descents' are associated with a temperature change (decrease) whereas 'Ascents' do not result in a temperature change. This is consistent with the cod being just above the thermocline (Fig. 4c).
- WT4: No change in temperature regardless of large depth changes of e.g., > 10 m (both 'Ascents' and 'Descents'). This is consistent with the cod being in a fully mixed water column or mixed waters typically below a thermocline (Fig. 4d).
- WT5: The water column is highly stratified with a warm surface layer and a subsurface temperature minimum associated with glacial water masses (Mortensen et al., 2013). This is the cold-water intrusion of waters around 0 °C. The depth of the intrusion can vary, but the closer to the surface it is, the more compressed the thermocline/stratification in the warmer waters above it becomes. This results in rapid temperature changes (>3 °C) even when swimming at a constant depth. The cod can be either in the warm water above the intrusion (WT5a, Fig. 4e+f+g) or below the intrusion (WT5b, Fig. 4h). In the latter case, 'Ascents' are associated with a decline in temperature. We found no incidents of cod staying inside the cold-water intrusion.

All analyses of swimming behavior and water types were done visually in the software Instrument Helper (version 3.0) provided by Wildlife Computers.

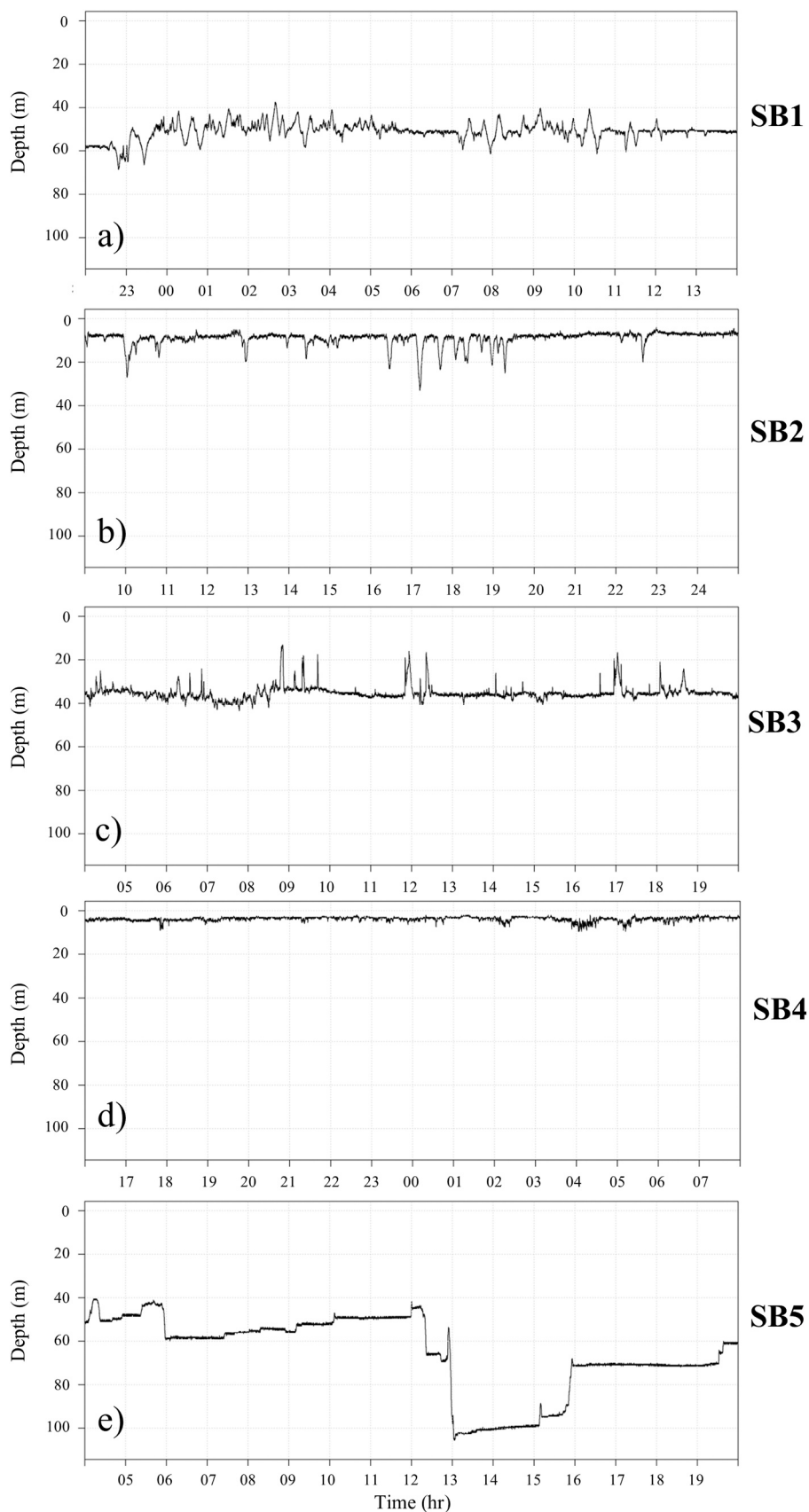
## 3. Results

### 3.1. Tag recovery

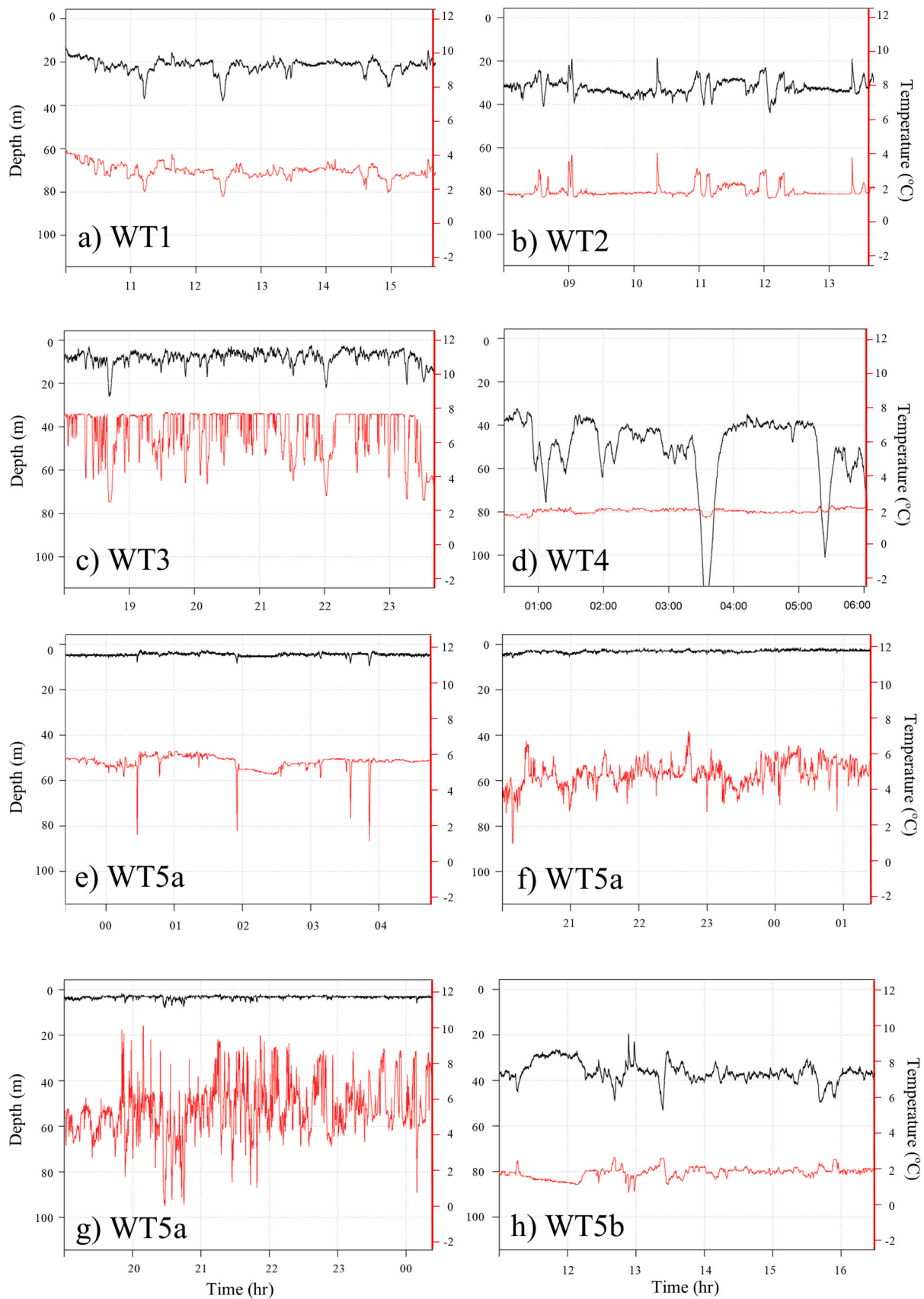
We retrieved data from three of the six deployed tags. One tag was recovered by a local fisher catching Cod\_3 on a long line on October 1st, 2018 (DAL=119 days). Two other tags released as scheduled and reported positions the following day on October 16th, 2018 (Cod\_1 and Cod\_2, DAL=134 and 133, Table 1). The last three tags did not report any data (Cod\_4–6). The two reporting tags were physically recovered using the activated pinger signal. Locating the tags in the fjord took considerable effort (one full day of searching for each tag) in good weather conditions with calm waters. One tag was found floating while the other had washed up on a beach. From each of the three tags, the internal data consisted of 3.4–3.8 million data points of depth, temperature, and light level, respectively, which were available for analysis. For Cod\_3, a visual inspection of the tag location showed minimal skin abrasion surrounding the tag (Fig. 2e and f). Underneath the tagging plates, the skin had disappeared, and muscle tissue was exposed to the plate. The stomach contents of Cod\_3 consisted of remnants of pelagic Atlantic herring (*Clupea harengus*) and other unidentifiable fish.

### 3.2. Acclimatization period and horizontal movements

Initially in the tagging period, all cod exhibited an acclimatization period. After being released, each cod immediately descended to 70–90 m, which corresponded to the bottom depth on the echosounder. They then showed little activity before slowly returning to shallower depths (<20 m) over time periods of 7–39 h, whereafter a more active swimming behavior was initiated (Fig. S1). Due to this acclimatization



**Fig. 3.** Swimming behavior (SB). a: SB1 = ‘Ascents’ and ‘Descents’ occurring equally frequent. SB2 = ‘Descents’ occurring most frequently. SB3 = ‘Ascents’ occurring most frequently. SB4 = little vertical activity. SB5 = periods of constant depths abruptly by rapid depth changes.



**Fig. 4.** Water type (WT). Water types occupied by the cod. a: in the thermocline (WT1). b: Below or just below a thermocline (WT2). c: Above or just above a thermocline (WT3). d: Mixed water (WT4). e-g: Increasingly extreme stratification above intrusion of cold water (WT5a). h: Water below intrusion where ‘Ascents’ can be linked to temperature decrease and ‘Descents’ to temperature increase (WT5b). For all plots, the red line shows temperature and is linked to the red y-axis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

period, data from the first two tagging days were omitted for further analysis.

At the end of the tagging period, Cod\_1 and Cod\_2 reported 10.6 km and 15.2 km from the original tagging location, respectively, and Cod\_3 was caught on a long line, 1.7 km from the tagging location (Fig. 1). For all three cod, the daily minimum travelling distance was 14–114 m d<sup>-1</sup>. Geolocation in the tagging period was not possible for several reasons. Firstly, the light data showed little daily variation until mid-August, making it impossible to estimate the exact time of sunrise, sunset and noon, which are used for determining approximate latitudinal position (data not shown). Secondly, the apparent site fidelity displayed by the cod during the tagging period meant that their horizontal movement did not exceed the uncertainty associated with light-based geolocation estimates (Lisovski and Hahn, 2012). Although geolocation by light-levels

has been a powerful tool for estimating the spatial movement of other fish species (e.g. Strøm et al., 2018; Walli et al., 2009), no further analysis was made in this study concerning light-based geolocation.

### 3.3. Depth phases and vertical activity

Cod\_1 had only one depth phase mainly staying in relatively deep and cold water (<3.0 °C,  $\bar{x}$ =32.8 m, Fig. 5a) with a weak, increasing depth trend and a moderate vertical activity throughout the period (mean±SD of the daily depth variance was 5.6 ± 12.9 m<sup>2</sup>, Table 2, Fig. S2a). There were no diel patterns in vertical activity (i.e., differences in activity levels between day and night) until mid-August, wherefrom the highest activity levels were measured during daytime (08:00–19:00, Fig. S2a). This diel trend became stronger throughout autumn.

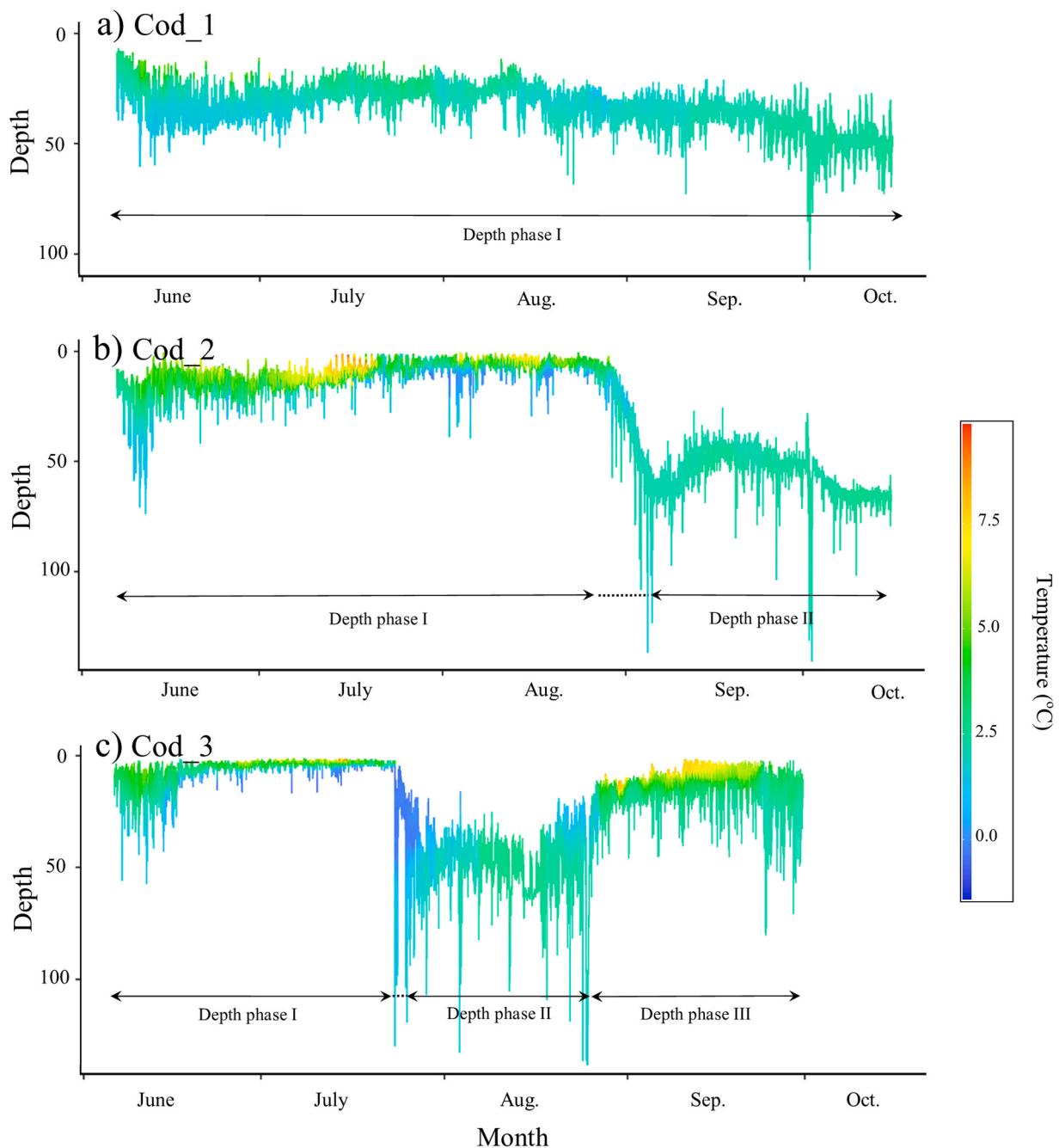


Fig. 5. Depth and temperature. Profiles of depth and temperature for each cod in the tagging period. Notice that Cod\_3 was caught by a fisher on October 1st 2018 which is prior the programmed tag-release. Individual depth phases (arrows) and transition periods are indicated (dotted line).



**Table 2**

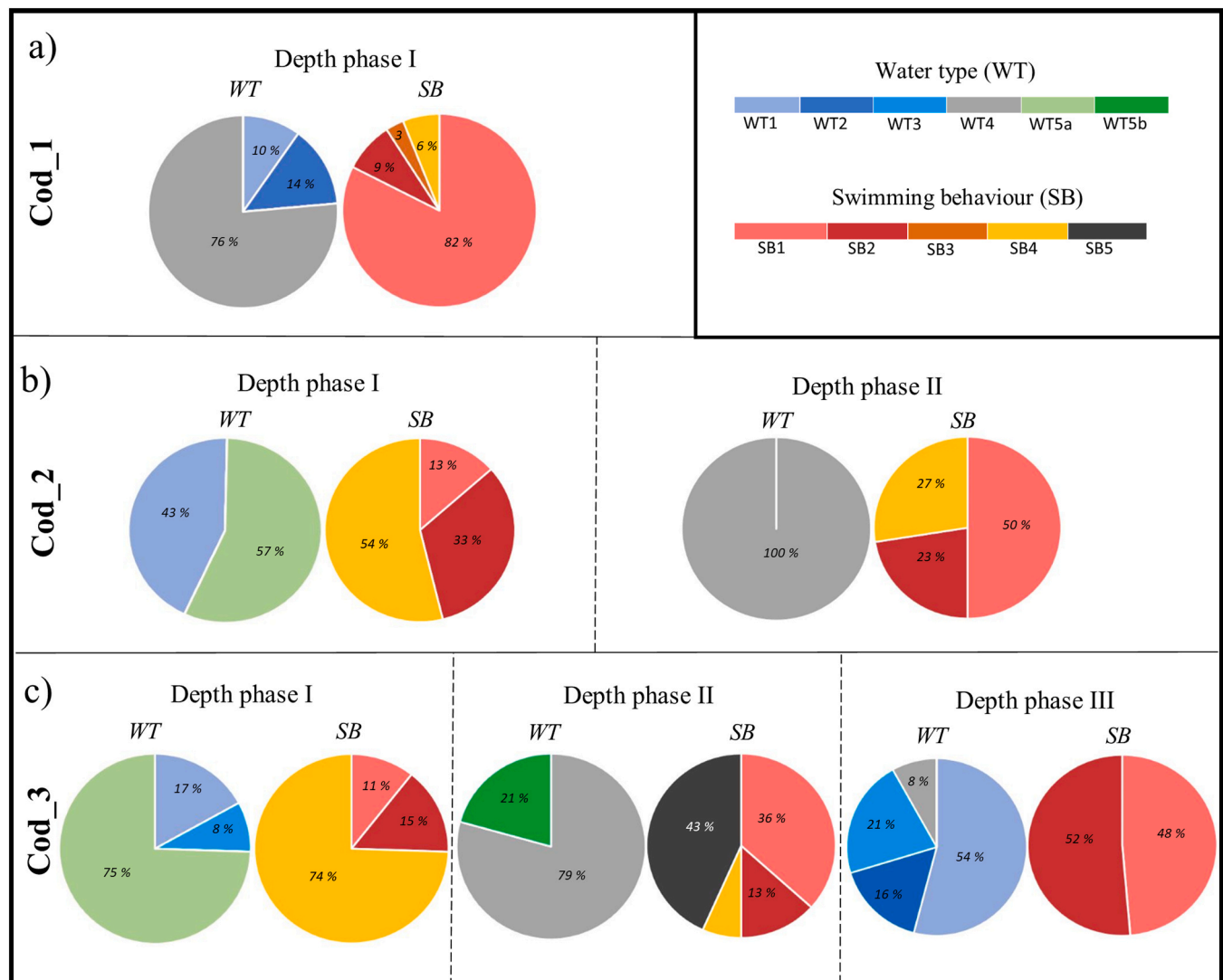
Depth, temperature, and variance for each Atlantic cod in their respective depth phases (DP). For Cod\_2 and Cod\_3, depth phase I and II were separated by a transition period (tr).

	DP	Dates	App. no of weeks	Depth (m)		Temperature (°C)		Variance ( $\sigma^2$ ) mean±SD
				mean±SD	range	mean±SD	range	
Cod_1	I	07/06–16/10	17	32.8 ± 8.5	6–107	2.1 ± 0.4	0.9–6.9	5.6 ± 12.9
Cod_2	I	07/06–28/08	11	9.9 ± 6.4	1–74	4.5 ± 1.5	-0.4–11.0	2.7 ± 12.3
	tr.	29/08–05/09	1					
Cod_3	II	06/09–16/10	5	55.1 ± 9.8	25–163	2.4 ± 0.2	1.5–2.8	7.9 ± 48.0
	I	07/06–23/07	6	5.6 ± 4.2	1–57	4.0 ± 1.2	-0.7–10.2	2.9 ± 10.7
	tr.	24/07–27/07	0					
	II	28/07–25/08	4	46.6 ± 14.9	4–185	1.9 ± 0.9	0.0–3.5	23.2 ± 72.8
	III	26/08–01/10	5	13.9 ± 7.3	1–80	4.3 ± 1.6	0.6–8.4	12.8 ± 31.1

Cod\_2 had two depth phases lasting eleven and five weeks, respectively (Table 2). ‘Depth phase I’, was mainly in warmer and shallow waters (>3.0 °C,  $\bar{x}$ =9.9 m, Fig. 5b) and was characterized by a low vertical activity ( $2.7 \pm 12.3 \text{ m}^2$ , Table 2, Fig. S2b). ‘Depth phase II’ occurred in colder and deeper waters (<3.0 °C,  $\bar{x}$ =55.1 m, Fig. 5b) with a higher average vertical activity than the previous phase ( $7.9 \pm 48.0 \text{ m}^2$ , Table 2 Fig. S2b). During the first two weeks of ‘Depth phase I’, Cod\_2 had increased nocturnal activity, but for the remaining part of

the tagging period, there were no diel patterns in vertical activity levels (Fig. S2b).

Cod\_3 had three depth phases lasting six, four and five weeks, respectively (Table 2). ‘Depth phase I’ was in warmer and shallow water (>3.0 °C,  $\bar{x}$ =5.6 m, Fig. 5c). Since Cod\_3 showed almost complete inactivity except for the first two weeks of ‘Depth phase I’, the entire phase was characterized by low vertical activity ( $2.9 \pm 10.7 \text{ m}^2$ , Table 2, Fig. S2c). ‘Depth phase II’ was in colder and deeper water (<3.0 °C,  $\bar{x}$ =46.6 m), and the fish exhibited the highest variance in vertical



**Fig. 6.** Swimming behavior and water type composition. Overview of composition of the five different swimming behaviors (SB) in relation to the six different water types (WT) in each depth phase for each cod.

activity among all cod of this study ( $23.2 \pm 72.8 \text{ m}^2$ ). 'Depth phase III' occurred in warmer and shallower water ( $>3.0 \text{ }^\circ\text{C}$ ,  $\bar{x}=13.9 \text{ m}$ ) with high vertical activity ( $12.8 \pm 31.1 \text{ m}^2$ ). Unlike 'Depth phase I', there were no signs of a cold-water intrusion during this last depth phase. No distinct diel activity patterns were found before early September, wherefrom the vertical activity was highest during the night (Fig. S2c).

By evaluating the vertical activity hour-by-hour throughout the tagging period in relation to the tidal cycle (see Fig. S2), we found no patterns in the vertical activity related to the tide for any of the cod.

### 3.4. Swimming behavior and water type

During the six distinct depth phases identified, the swimming behavior differed considerably in relation to the types of water mass e.g., stratified/non-stratified or above/below an intrusion of colder water of around  $0 \text{ }^\circ\text{C}$ .

During 'Depth phase I', Cod<sub>1</sub> was mainly in a mixed water mass (WT4 = 76 %, Fig. 6a), which occurred from mid-July and throughout the remaining tagging period. In the first part of the tagging period and until mid-July, Cod<sub>1</sub> mostly occupied water within or near a thermocline (WT1 + WT2 = 24 %). 'Ascents' and 'Descents' typically ranged from 10 to 30 vertical meters and generally occurred equally frequent (82 %, SB1). Swimming behaviors such as SB2 (8 %) and SB3 (3 %) were sporadically observed until mid-August, whereafter only SB1 was exhibited. Cod<sub>1</sub> was inactive 6 % of the time (SB4, Fig. 6a).

During 'Depth phase I', Cod<sub>2</sub> was predominantly in a thermocline (WT1 = 43 %) and 'Descents' of 5–20 vertical meters dominated the vertical activity (SB2 = 33 %, Fig. 6b). There were also periods where 'Ascents' and 'Descents' occurred equally frequent (SB1 = 13 %). From early July until late August, Cod<sub>2</sub> primarily occupied waters above an intrusion of cold water (WT5a = 57 %). By then Cod<sub>2</sub> was mostly vertically inactive (SB4 = 54 %, Fig. 6b). In 'Depth phase II', Cod<sub>2</sub> was only in mixed waters (WT4 = 100 %) and the swimming behavior was dominated by SB1 and SB2 (50 % and 23 %, respectively, Fig. 6b). Cod<sub>2</sub> had a transition period of about one week between the two depth phases, where multiple distinct 'Descents' of around 50–90 m were performed (Fig. S3).

Cod<sub>3</sub> had the most diverse swimming behavior of the tagged cod. During 'Depth phase I', the cod occupied water inside or close to a thermocline for the first two weeks (WT1 + WT3 = 25 %, Fig. 6c), while it exhibited both 'Ascents' and 'Descents' (SB1 + SB2 = 26 %). After that, Cod<sub>3</sub> swam above a cold-water intrusion for the rest of 'Depth phase I' (Fig. 5c) and became almost vertically inactive (WT5a = 75 %, SB4 = 74 %, Fig. 6c). The transition from the first phase to 'Depth phase II' occurred abruptly and was characterized by multiple large vertical 'Ascents' and 'Descents' ( $>100 \text{ m}$ ) over four days, primarily in cold water around  $0 \text{ }^\circ\text{C}$  (Fig. 5c, Fig. S4). In 'Depth phase II', Cod<sub>3</sub> was mainly in mixed water (WT4 = 79 %) or waters below a cold-water intrusion (WT5b = 21 %, Fig. 6c). In this phase, swimming at constant depths, interrupted by rapid vertical shifts, was dominating (SB5 = 43 %), followed by SB1 (36 %) and SB2 (13 %, Fig. 6c). On three occasions, Cod<sub>3</sub> rested on the bottom for up to ~24 h, with the tidal cycle visible in the depth data (Fig. S5). In 'Depth phase III', Cod<sub>3</sub> remained near a thermocline, being either within (WT1 = 54 %), just above (WT2 = 16 %) or below it (WT3 = 21 %), while the swimming behavior was either SB1 or SB2 (Fig. 6c). During the last two weeks of the tagging period, a total of 34 distinct descends of 10–30 m were made and followed by time periods of 2–40 min at a constant depth before Cod<sub>3</sub> ascended to the original depth (Fig. S6). These were presumably dives to the bottom. Cod<sub>3</sub> was caught on a benthic long line on October 1st during one of these distinct descends.

### 3.5. The high-activity event

A distinct high activity behavior occurred on October 1st to 2nd for Cod<sub>1</sub> and Cod<sub>2</sub> starting around noon and lasted for ~26 h. During this

period, the behavior was characterized by the highest vertical activity level for the entire tagging period. In more detail, more than 30 distinct 'Ascents' and 'Descents', which ranged from approximately 20 to 160 vertical meters, were performed by both fish (Fig. 7a and b). During this event, the highest recorded vertical swimming speed of  $0.9$  and  $1.0 \text{ m s}^{-1}$  was measured for both Cod<sub>1</sub> and Cod<sub>2</sub>. Cod<sub>3</sub> was caught on a benthic long line also on October 1st, but the fish did not show any increased vertical behavior before it was hooked (Fig. 7c, Fig. S5).

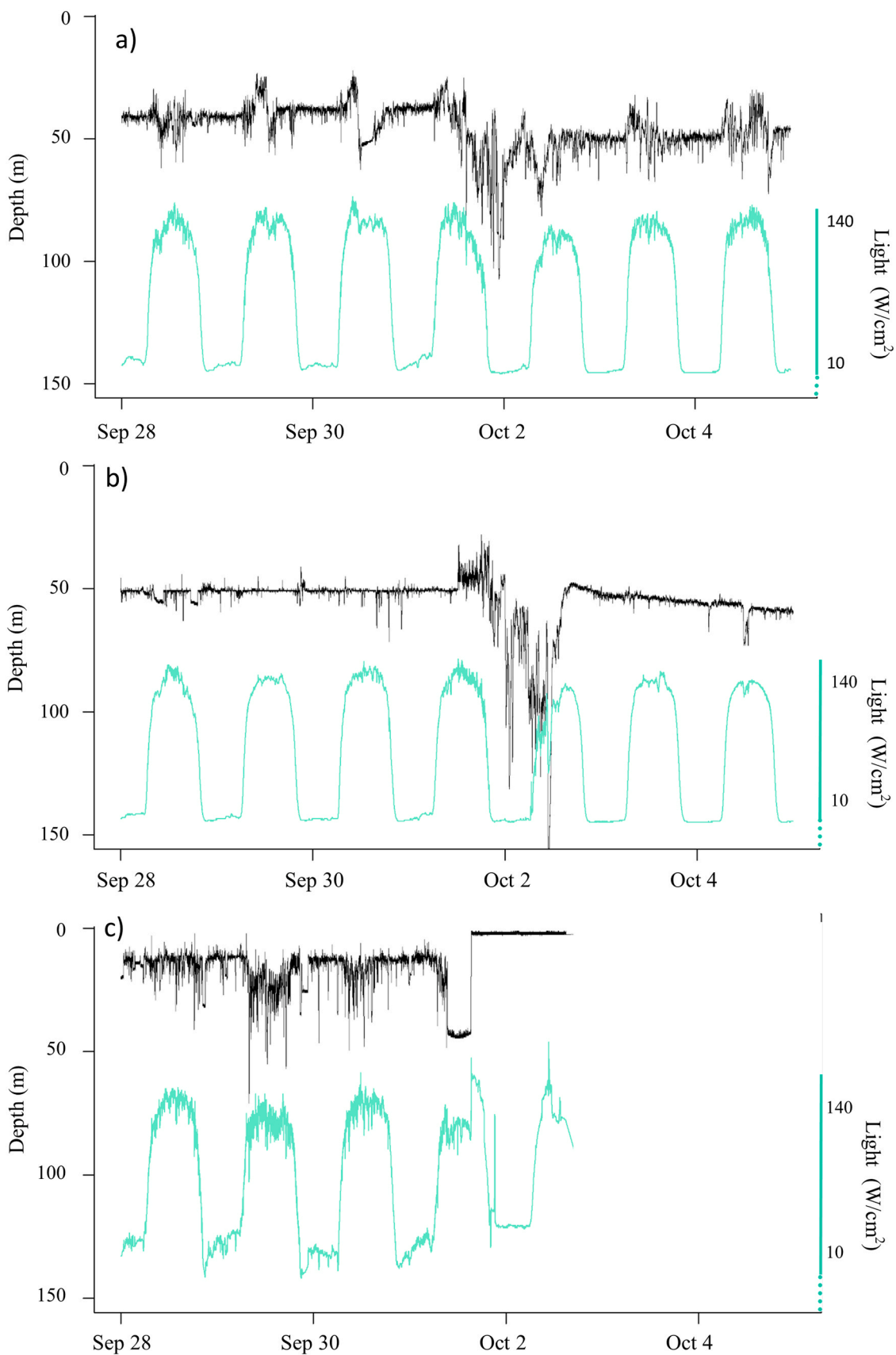
## 4. Discussion

### 4.1. The applicability of PSAT on cod

We deployed six PSATs on Atlantic cod and successfully retrieved three. The success rate, data quality and little physical impact on the single recaptured specimen (Fig. 2d and e) demonstrate that PSATs under the given conditions can provide detailed biological insights into natural cod behavior over at least four months. To further assess this, we scrutinized the swimming behavior based on 3.4–3.8 million coupled depth and temperature measurements from each of the three cod. Such high-resolution data series provide unprecedented details on the vertical behavior of Atlantic cod. At first glance, the three cod had rather different swimming behavior, but similarities within vertical activity patterns in specific water types were evident. Due to these similarities in swimming behavior, we conclude that the three cod behaved naturally in the tagging period and that PSATs are applicable with an acceptable level of discomfort to the fish. Swimming tunnel experiments have shown increased metabolic costs for cod tagged externally with dummy tags resembling PSATs (Steinhausen et al., 2006). Steinhausen et al. (2006) reported, that the critical swimming speed, a standard measure to assess swimming capabilities of fish (Plaut, 2001), decreased by 10–13 % due to increased drag from the tag. The cod in our study had a body mass of 7–19 kg (cf. length-weight relations for cod, Froese and Pauly, 2022). This makes the PSATs for our cod 3–6 times lighter in terms of the tag-body mass ratio, compared to the cod examined by Steinhausen et al. (2006). We therefore consider the effect of PSATs on cod in this study to be less than described by Steinhausen et al. (2006). Most PSAT studies have reporting rates of ~70 % (Musyl et al., 2011), which is higher than the 50 % in this study. However, we do not consider our missing tags to be due to mortality caused by barotrauma or stress from carrying the tags. If any such reasons had caused Cod<sub>4–6</sub> to die before tag release, PSATs would at some point reach the surface due to decomposition of the fish and establish satellite contact (see Bryan et al., 2021). A more likely explanation could be linked to the freshwater outflow from a river in the inner part of Kapisillit Fjord. This freshwater outflow allows ice to be formed in the innermost parts of the fjord in the early winter. In 2018, ice was formed extraordinarily early, and the innermost part of the fjord was frozen in mid-October, which coincided with tag's programmed release dates. If the tags of Cod<sub>4–6</sub> released under the ice, they might have been trapped here in a layer of freshwater causing the tags to detect they were in a non-saline environment. Such circumstances would start unsuccessful data transmission until out of battery (like they do during normal transmission when exposed to air at the surface). Another possibility for these tags not reporting could be due to predation (see below).

### 4.2. Biological insights into cod in the Kapisillit Fjord

From the available high-resolution data on depth and temperature, we found clear individual differences as well as similar behavioral patterns among the tagged cod. For Cod<sub>1</sub> and Cod<sub>3</sub>, there were no distinct differences in day vs night activity until mid-August/early September (Fig. S2a+c). This matches with the onset of astronomical twilight at this latitude ( $64^\circ\text{N}$ ) and suggests that during autumn, real darkness had a suppressing effect on the vertical activity, whereas increased activity was linked to the presence of light for these two fish (Fig. S2a+c, see also



**Fig. 7.** The high-activity event. Depth and light levels in the days around October 1st, which was when Cod\_1 (a) and Cod\_2 (b) had the highest activity levels. Cod\_3 (c) showed no increased activity on October 1st before being caught on long line. For all plots, the blue line shows light level and is linked to the blue y-axis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 7a for examples of increased daily activity). A similar diel pattern has been shown for cod tagged with acoustic tags during the autumn in northern Norway (Løkkeborg and Fernö, 1999). For Cod\_2, however, a higher nocturnal activity occurred only during the first 10 days of the tagging period (June), whereafter there were no differences between day and night for the remaining tagging period. Such opposing patterns could be caused by individual differences in feeding preferences which in the Kapisillit area could encompass many different prey items in both benthic and pelagic environments (Grønkjær et al., 2020; Hedeholm et al., 2017).

In general, cod are considered benthopelagic, which is why we expected to observe benthic behavior more frequently, as in other studies (e.g. Pedersen et al., 2008). We acknowledge that bottom topography can cause “forced” ascents/descents, which theoretically could be interpreted wrongfully as pelagic swimming. However, the rapid nature of the vast majority of these ascents and descents, observed during the most common swimming behaviors (i.e. SB1 and SB2, Figs. 3 and 6), suggest that the swimming of the tagged cod mostly was pelagic. From the temperature response in relation to depth changes, our results also show, that in the pelagic zone, the three cod were associated with the thermocline for most of the tagging period. The few times benthic behavior was observed was for Cod\_3, which on three occasions clearly rested near the bottom making tidal fluctuations visible in the recorded depth data (Fig. S5). Also, a behavior where descents were made to the bottom, which was then followed for time periods up to 40 min, was occasionally observed in the last weeks before Cod\_3 was caught on a long line (Fig. 7c, Fig. S6). Further, we did not observe any connection between tidal patterns and vertical activity levels throughout the tagging period (Fig. S2). This was surprising as we expected the tidal difference of 3–4 m to be of importance to prey availability, especially for pelagic swimming predators, as it has been shown for other marine predators (e.g. Brownscombe et al., 2014; Robles, 1987). Whether the tide was of little importance or vertical depth data are inappropriate for such analyses is not possible for this study to evaluate.

The swimming behavior was related to water mass stratification/mixing and temperature. During the summer period, Cod\_2 and Cod\_3 encountered intrusions of cold water ( $\sim 0^\circ\text{C}$ ), which they clearly seemed to avoid by residing in warmer water ( $>2^\circ\text{C}$ ) either above or below this intrusion. The avoidance is well exemplified by the two cod having very low vertical activity (SB4) when swimming above cold water (Figs. 5+6 and Fig. S4). At some point, both Cod\_2 and Cod\_3 sought warmer waters below the intrusion, although they did so quite differently (see Fig. S3 and Fig. S4). These specific situations of cold-water avoidance are key predictors of spatial behavior during the tagging period. During summer and early autumn, water around  $0^\circ\text{C}$  is not expected in the Kapisillit Fjord (Zamora-Terol et al., 2014). It could, however, be formed in another branch of the fjord with three marine-terminating glaciers (the Icefjord, Fig. 1, Mortensen et al., 2013). Consequently, the upper part of the water column is cold in the Icefjord, also during summer and autumn (Mortensen et al., 2011) and tongues of subzero waters do penetrate nearby fjord branches. These are referred to as cold-water intrusions and have previously been documented for the outer parts of the Kapisillit Fjord (Swalethorp et al., 2016). We strongly encourage future studies in inshore waters, such as studied here, to map hydrological conditions for the study area. Doing such could have increased our knowledge on the tagged cod’s horizontal movements in the tagging period.

The most distinct and coinciding behavior in the tagging period was the “high-activity event” exhibited by Cod\_1 and Cod\_2. Despite very different swimming behavior up to this event, both cod had a very sudden response on October 1st characterized by a pronounced vertical activity lasting for approximately one day (Fig. 7a+b). Cod\_3 did not show any increased activity prior to being hooked on that same day (Fig. 7c, Fig. S6), but the fisher reported that an unusually powerful and fast-swimming fish was hooked and within a few seconds, it raised the entire long line to the surface, whereafter the line broke. Only a portion

of the line and catch was therefore recovered (including Cod\_3, Fig. 2d). Interestingly, according to the fisher, most of the recovered catch were large cod bitten in half. This information combined (half bitten large cod and a fast-swimming powerful fish) limits the potential candidates in a Southwest Greenland fjord that could have caused the disturbance in the area. The most obvious candidates would be a Greenland shark (*Somniosus microcephalus*) or a large Atlantic halibut. However, neither of these are both fast-swimming and able to cut large fish in half. A more likely candidate could be the porbeagle (*Lamna nasus*) – a fast-swimming pelagic shark, which in recent years has been observed multiple times in Greenland inshore waters during the same times as our study. Since 2019, porbeagles have been caught annually in gill nets targeting cod or salmonids in West and East Greenland fjords during autumn ( $N = 8$ , GINR unpublished data, Fig. S7). Porbeagle environmental DNA have also been identified in offshore water samples from southern Greenland (Jensen et al., 2023) and a dissection of a porbeagle from South Greenland in 2019, showed Atlantic cod to be the main prey item (GINR unpublished data). Regardless of the predatory species, the tagged cod’s behavior reflects their capability to perform what appears to be a predator avoidance/escape. This example also indicates that the potential negative effects of the tag, even late in the period, were not severe enough to hamper an escape response or a prolonged intense vertical activity. This aligns with the observation of no skin stress on the recaptured Cod\_3 beyond the exact location of the silicone plates.

## 5. Conclusion

From the distinct behavioral similarities between three fish exposed to various hydrographic conditions, we conclude that PSATs can be used on large Atlantic cod and successfully record natural swimming behavior for 4–4.5 months. The tags can provide detailed information on swimming behavior and habitat preferences under the prerequisite that the cod are captured and released gently without any kind of barotrauma. Physical tag retrieval is desirable and possible but should only be considered an option in inshore/coastal areas, where waters are more likely calm and drifting opportunities limited. Short, but biologically informative, events like the predatory event or the outbreak from the cold-water intrusion could likely be missed had we not evaluated high-resolution data. Despite evaluating only three cod, we describe strong behavioral trends and suggest that the analytical framework can be used to quantify swimming behavior in future studies where similar high-resolution data are available.

## CRedit authorship contribution statement

Conceptualization: Rasmus Hedeholm, Helle Torp Christensen, Anja Retzel, Julius Nielsen. Data curation: Rasmus Hedeholm, Helle Torp Christensen, Julius Nielsen, Anja Retzel. Formal analysis: Julius Nielsen, Daniel Estévez-Barcia, Søren Post, Rasmus Berg Hedeholm. Funding acquisition: Rasmus Hedeholm, Helle Torp Christensen. Methodology: Julius Nielsen, Rasmus Hedeholm, Søren Post, Helle Torp Christensen, Anja Retzel, Lorenz Meire, Frank Rigét, John Frederik Strøm, Audun Rikardsen. Project administration: Julius Nielsen, Rasmus Hedeholm. Software: Julius Nielsen, Daniel Estévez-Barcia, Søren Post, Rasmus Berg Hedeholm. Visualization: Julius Nielsen, Rasmus Hedeholm, Søren Post, Helle Torp Christensen, Anja Retzel, Lorenz Meire, Frank Rigét, John Frederik Strøm, Audun Rikardsen. Writing – original draft: Julius Nielsen, Rasmus Hedeholm. Writing – review & editing: Julius Nielsen, Rasmus Hedeholm, Søren Post, Helle Torp Christensen, Anja Retzel, Lorenz Meire, Frank Rigét, John Frederik Strøm, Audun Rikardsen.

## Declaration of Competing Interest

The authors declare no competing interests.

## Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106782.

## References

- Aarestrup, K., Økland, F., Hansen, M.M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., Howey, P., Sparholt, H., Pedersen, M.L., McKinley, R.S., 2009. Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science* 325 (5948), 1660. <https://doi.org/10.1126/science.1178120>.
- Brickman, D., Marteinsdottir, G., Logemann, K., Harms, I.H., 2007. Drift probabilities for Icelandic cod larvae. *ICES J. Mar. Sci.* 64 (1), 49–59. <https://doi.org/10.1093/icesjms/fsl019>.
- Brownscombe, J., Gutowsky, L., Danylchuk, A., Cooke, J., 2014. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Mar. Ecol. Prog. Ser.* 505, 241–251. (<https://www.int-res.com/abstracts/meps/v505/p241-251>).
- Bryan, D.R., Mcdermott, S.F., Nielsen, J.K., Fraser, D., Rand, K.M., 2021. Seasonal migratory patterns of Pacific cod (*Gadus macrocephalus*) in the Aleutian Islands. *Anim. Biotelemetry* 9 (24), 1–18. <https://doi.org/10.1186/s40317-021-00250-2>.
- Christensen, H.T., Rigét, F., Retzel, A., Nielsen, E.H., Nielsen, E.E., Hedeholm, R.B., 2022. Year-round genetic monitoring of mixed-stock fishery of Atlantic cod (*Gadus morhua*); implications for management. *ICES J. Mar. Sci.*, fsac076 <https://doi.org/10.1093/icesjms/fsac076>.
- Douglas, D.C., Weinzierl, R., C. Davidson, S., Kays, R., Wikelski, M., Bohrer, G., 2012. Moderating Argos location errors in animal tracking data. *Methods Ecol. Evol.* 3 (6), 999–1007. <https://doi.org/10.1111/j.2041-210X.2012.00245.x>.
- Froese, R., Pauly, D., 2022. FishBase. World Wide Web Electronic Publication. ([www.fishbase.org](http://www.fishbase.org)).
- Grønkvær, P., Ottosen, R., Joensen, T., Reeve, L., Nielsen, E.E., Hedeholm, R., 2020. Intra-annual variation in feeding of Atlantic cod *Gadus morhua*: the importance of ephemeral prey bursts. *J. Fish Biol.* 97 (5), 1507–1519. <https://doi.org/10.1111/jfb.14520>.
- Hansen, P.M., 1949. Studies on the biology of the cod in Greenland waters. Bianco Lunos Bogtrykkeri.
- Hedeholm, R.B., Mikkelsen, J.H., Svendsen, S.M., Carl, J., Jensen, K.T., 2017. Atlantic cod (*Gadus morhua*) diet and the interaction with northern shrimp (*Pandalus borealis*) in Greenland waters. *Polar Biol.* 40 (7), 1335–1346. <https://doi.org/10.1007/s00300-016-2056-1>.
- Hedger, R.D., Rikardsen, A.H., Thorstad, E.B., 2017. Pop-up satellite archival tag effects on the diving behaviour, growth and survival of adult Atlantic salmon *Salmo salar* at sea. *J. Fish Biol.* 90 (1), 294–310. <https://doi.org/10.1111/jfb.13174>.
- Horsted, S.A., 2000. A review of the cod fisheries at Greenland, 1910-1995. *J. Northwest Atl. Fish. Sci.* 28, 1–109.
- Hovgård, H., Wieland, K., 2008. Fishery and environmental aspects relevant for the emergence and decline of Atlantic cod (*Gadus morhua*) in West Greenland waters. In: Kruse, G.H., Drinkwater, K., Ianelli, J.N., Link, J.S., Stram, D.L., Westgaard, V., Woodby, D. (Eds.), Resiliency of Gadid Stocks to Fishing and Climate Change. University of Alaska Sea Grant, pp. 89–110.
- Hüssy, K., Hinrichsen, H.-H., Eero, M., Mosegaard, H., Hemmer-Hansen, J., Lehmann, A., Lundgaard, L.S., 2016. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. *ICES J. Mar. Sci.* 73 (2), 293–303. <https://doi.org/10.1093/icesjms/fsv227>.
- ICES, 2021. Northwestern Working Group (NWWG). *ICES Sci. Rep.* 3 (52), 766. <https://doi.org/10.17895/ices.pub.8186>.
- James, T.L., Landsman, S.J., Ramsay, L.L., Giffin, M.D., Bris, A.Le., 2020. Migration patterns of Atlantic halibut captured in the southern gulf of st. Lawrence as assessed with pop-up satellite archival and floy tags. *Can. J. Fish. Aquat. Sci.* 77 (7), 1233–1242. <https://doi.org/10.1139/cjfas-2019-0262>.
- Jensen, M.R., Høglund, S., Knudsen, S.W., Nielsen, J., Møller, P.R., Rysgaard, S., Thomsen, P.F., 2023. Distinct latitudinal community patterns of Arctic marine vertebrates along the East Greenlandic coast detected by environmental DNA. *Divers. Distrib.* 29, 316–334. <https://doi.org/10.1111/ddi.13665>.
- Lisovski, S., Hahn, S., 2012. GeoLight - processing and analysing light-based geolocator data in R. *Methods Ecol. Evol.* 3 (6), 1055–1059. <https://doi.org/10.1111/j.2041-210X.2012.00248.x>.
- Løkkeborg, S., Fernö, A., 1999. Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environ. Biol. Fish.* 54 (3), 345–353. <https://doi.org/10.1023/A:1007504712163>.
- Lutcavage, M.E., Brill, R.W., Skomal, G.B., Chase, B.C., Howey, P.W., 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: Do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Can. J. Fish. Aquat. Sci.* 56 (2), 173–177. <https://doi.org/10.1139/f99-016>.
- Mortensen, J., Bendtsen, J., Motyka, R.J., Lennert, K., Truffer, M., Fahnstoc, M., Rysgaard, S., 2013. On the seasonal freshwater stratification in the proximity of fast-flowing tidewater outlet glaciers in a sub-Arctic sill fjord. *J. Geophys. Res. Oceans* 118 (3), 1382–1395. <https://doi.org/10.1002/jgrc.20134>.
- Mortensen, J., Lennert, K., Bendtsen, J., Rysgaard, S., 2011. Heat sources for glacial melt in a sub-Arctic fjord (Godthåbsfjord) in contact with the Greenland Ice Sheet. *J. Geophys. Res. Oceans* 116 (C1). <https://doi.org/10.1029/2010JC006528>.
- Musyl, M.K., Domeier, M.L., Nasby-Lucas, N., Brill, R.W., McNaughton, L.M., Swimmer, J.Y., Lutcavage, M.S., Wilson, S.G., Galuardi, B., Liddle, J.B., 2011. Performance of pop-up satellite archival tags. *Mar. Ecol. Prog. Ser.* 433 (1998), 1–28. <https://doi.org/10.3354/meps09202>.
- Nordeide, J.T., Båmstedt, U., 1998. Coastal cod and north-east Arctic cod - do they mingle at the spawning grounds in Lofoten? *Sarsia* 83 (5), 373–379. <https://doi.org/10.1080/00364827.1998.10413696>.
- O'Neill, R., Ó Maoiléidigh, N., McGinnity, P., Bond, N., Culloty, S., 2018. The novel use of pop-off satellite tags (PSATs) to investigate the migratory behaviour of European sea bass *Dicentrarchus labrax*. *J. Fish Biol.* 92 (5), 1404–1421. <https://doi.org/10.1111/jfb.13594>.
- Pedersen, M.W., Righton, D., Thygesen, U.H., Andersen, K.H., Madsen, H., 2008. Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. *Can. J. Fish. Aquat. Sci.* 65 (11), 2367–2377. <https://doi.org/10.1139/F08-144>.
- Plaut, I., 2001. Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 131 (1), 41–50. [https://doi.org/10.1016/S1095-6433\(01\)00462-7](https://doi.org/10.1016/S1095-6433(01)00462-7).
- Rikardsen, A.H., Righton, D., Strøm, J.F., Thorstad, E.B., Gargan, P., Sheehan, T., Økland, F., Chittenden, C.M., Hedger, R.D., Næsje, T.F., Renkawitz, M., Sturlaugsson, J., Caballero, P., Baktoft, H., Davidsen, J.G., Halttunen, E., Wright, S., Finstad, B., Aarestrup, K., 2021. Redefining the oceanic distribution of Atlantic salmon. *Sci. Rep.* 11 (1), 1–12. <https://doi.org/10.1038/s41598-021-91137-y>.
- Robles, C., 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68 (5), 1502–1514. <https://doi.org/10.2307/1939234>.
- Steinhausen, M.F., Andersen, N.G., Steffensen, J.F., 2006. The effect of external dummy transmitters on oxygen consumption and performance of swimming Atlantic cod. *J. Fish Biol.* 69 (3), 951–956. <https://doi.org/10.1111/j.1095-8649.2006.01143.x>.
- Storr-Paulsen, M., Wieland, K., Hovgård, H., Rätz, H.J., 2004. Stock structure of Atlantic cod (*Gadus morhua*) in West Greenland waters: implications of transport and migration. *ICES J. Mar. Sci.* 61 (6), 972–982. <https://doi.org/10.1016/j.icesjms.2004.07.021>.
- Strøm, J.F., Thorstad, E.B., Hedger, R.D., Rikardsen, A.H., 2018. Revealing the full ocean migration of individual Atlantic salmon. *Anim. Biotelemetry* 6 (1), 2. <https://doi.org/10.1186/s40317-018-0146-2>.
- Swalethorp, R., TG, N., AR, T., Møhl, M., Munk, P., 2016. Early life of an inshore population of West Greenlandic cod *Gadus morhua*: spatial and temporal aspects of growth and survival. *Mar. Ecol. Prog. Ser.* 555, 185–202. (<https://www.int-res.com/abstracts/meps/v555/p185-202/>).
- Thorstad, E.B., Rikardsen, A.H., Alp, A., Økland, F., 2013. The use of electronic tags in fish research – an overview of fish telemetry methods. *Turk. J. Fish. Aquat. Sci.* 896, 881–896. <https://doi.org/10.4194/1303-2712-v13.5.13>.
- Walli, A., Teo, S.L.H., Boustany, A., Farwell, C.J., Williams, T., Dewar, H., Prince, E., Block, B.A., 2009. Seasonal Movements, Aggregations and Diving Behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) Revealed with Archival Tags. *PLoS One* 4 (7). <https://doi.org/10.1371/journal.pone.0006151>.
- Zamora-Terol, S., Kjellerup, S., Swalethorp, R., Saiz, E., Nielsen, T.G., 2014. Population dynamics and production of the small copepod *Oithona* spp. in a subarctic fjord of West Greenland. *Polar Biol.* 37 (7), 953–965. <https://doi.org/10.1007/s00300-014-1493-y>.