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Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration

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ABSTRACT

Temperature and depth logging tags were implanted into adult eels released on Atlantic west coasts of France and Ireland to study their oceanic migration behavior. For three of the tags, 25 to 256 days after release there was a dramatic rise in temperature from 10 °C to 36 °C and the dive profile changed from depths of 300–1000 m to repeated ascents to the surface. This indicated that the eels carrying the tags had been eaten by a mammalian predator. Two of the tags had sufficient sampling rate to resolve the dives in detail. They recorded a total of 91 dives to maximum depths of 250–860 m lasting 11–12 min and with surface intervals of 5–7 min. More than two thirds of the dives included a rapid descent from approximately 500 m to 600–700 m. From this we infer that the predator was most likely a deep-diving toothed whale. The dives logged while the tags were inside the predator revealed that the temperature usually decreased during dives, and increased again during surface periods. The temperature drops during dives were probably caused by the ingestion of prey or water. These observations provide insights into the behavior of toothed whales foraging in the mesopelagic zone.

1. Introduction

Electronic tags have enabled remarkable progress in understanding the behavior of aquatic animals. In recent years, tag miniaturization has enabled their deployment on smaller animals, yielding insights into movement and ecology (Priede et al., 1991; Aarestrup et al., 2009; Rutz and Hays, 2009; Bograd et al., 2010). The use of increasingly sophisticated tags has also increased our understanding of the behavior of larger marine animals such as seals and whales, although the ethics, logistics and difficulty of performing attachment limits the type of tags that can be used (Cooke et al., 2004; Johnson et al., 2009).

In 2009 and 2010, a total of 156 European eels (*Anguilla anguilla* L.) were tagged with satellite and data storage tags in Ireland and France as part of the EU-project “European Eels in the Atlantic: Assessment of Their Decline” (Eeliad). This project has the objective to investigate the ecology and biology of European eels during their marine migration. This migration is a possible trans-oceanic transit to spawning grounds in the western Atlantic. Data have been recovered from 35 of those tags. All data sets start out showing a diving behaviour resembling that recorded in previous investigations of eel behaviour (Tesch, 1978; Aarestrup et al., 2009; Westerberg et al., 2014). In three of the tag records, however, the recovered data suggest that the eels were eaten at depth by marine mammals between 25 and 156 days after release. In each case, the evidence is clear and compelling: the clear patterns of eel diving behavior at depth are replaced abruptly by frequent surface oriented diving accompanied by a rapid rise in temperature above 30 °C.

2. Material and methods

2.1. Tag types and tagging method

Two different tag types were used; archival data storage tags (DST) and satellite pop-up archival tags (PSAT). Two of the eels were tagged with G5 long-life archival tags (Cefas Technology Ltd., http://www.cefastechnology.co.uk/) fitted with a chain of three cylindrical floats (Fig. 1). These were implanted intraperitoneally under anaesthesia. Total tag length was 14 cm with a diameter of 11 mm and with a net positive buoyancy of 9×10^{-3} N to enable surface drift. The tags were

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Fig. 1. The G5 data-storage tag.

programmed to record depth every 30 s (accuracy ± 10 m, resolution 0.3 m, maximum range 1000 m) and temperature every 5 min (accuracy ± 0.1 °C, resolution 0.03 °C, range -2 °C to 34 °C). The 66% response time of the tag's temperature sensor to a step change in temperature was 28 s in water. The first eel (length 83 cm, weight 1.1 kg, tag A05262) was released in Galway harbour, Ireland, 20th October 2009. The tag was recovered from the Isle of Coll, west of Scotland, in May 2010. The second eel (length 101 cm, weight 1.7 kg, tag A07062) was released in River Loire, France 24th November 2010 and was found in Bindal, Norway, in August 2012. All data were downloaded successfully from both tags.

The third eel was tagged externally with a satellite pop-up (PSAT) X-tag from Microwave Telemetry (http://www.microwavetelemetry.com/). This tag is 120 mm long with a maximum diameter of approximately 33 mm. Net buoyancy is approximately 0.025 N. After surfacing the tag continuously transmits the pressure and temperature time series via the Argos satellite system, as well as its current location. The resolution and accuracy of depth is at least ± 5.4 m and temperature ± 0.23 °C. The measuring range is similar to the archival tag, but the resolution of the transmitted dataset is at best 15 min, with gaps or a lower resolution where the data transmission is incomplete. This eel (length 93 cm, weight 1.9 kg, tag 49559) was released in Galway Bay, Ireland, 6th November 2010.

2.2. Reconstruction of geographic position of predation

We used the temperature record from the two archival tags to calculate the location where they had surfaced after the predation event. First, on the basis that isotherms run approximately in the east–west direction in the northeast Atlantic, latitude was estimated by comparing the recorded night-time water temperature to sea surface temperature (SST) from satellite observations on the current date. Data was downloaded from the Group for High Resolution SST (https://www.ghrsst.org/data/) choosing the L4 gridded SST product with the highest available resolution for the area. Second, because the tag became heated above the ambient water temperature by daylight radiation as it drifted, local noon in UTC (Coordinated Universal Time) could be estimated from the mid-point of the (generally) symmetrical heating curve, enabling estimation of longitude. The surfacing position of the PSAT is the first location received by the Argos system and was accurate to better than 250 m.

2.3. Analysis of predator diving behaviour

For the archival tag data, dive parameters for the predator were calculated for all dives following the first ascent after predation of the eel. The deep, presumably foraging, dives of the predator typically reached 600 m. The onset and end of dives was defined by a threshold depth of 20 m following Aguilar de Soto et al. (2008). The low temporal resolution of the PSAT data made detailed analysis of single dives impossible. For this dataset, the only parameters of use were the total time in the predator, the body temperature and the maximum and minimum depth, all of which are given with great uncertainty due to the low sampling rate of this tag.

Hydrography for the time and area where the predation events took place were taken from Argo buoy profile data (http://www.argo.ucsd.edu/index.html, available at http://www.coriolis.eu.org/). Argo is a global array of 3560 free-drifting profiling floats that measures the temperature and salinity of the upper 2000 m of the ocean. The nearest Argo profile to the position and time of the predation event was selected for comparison between diving activity and temperature and salinity stratification.

3. Results

3.1. Predation

Of the eels tagged and released in Ireland and France 2009–2010, from which data was recovered, eight (or approximately 25%) exhibit depth and temperature information consistent with predation. Of these, five events occurred on the continental shelf and post-predation data were consistent with the eels being eaten by surface or bottom-dwelling predatory fish. The remaining three cases occurred in deep water (>600 m) over the continental slope and can be inferred to be predation by marine mammals.

Fig. 2 shows the approximate positions of the events. Table 1 gives the particulars of time and depth of the predation, maximum recorded temperature while in the predator and the total time between ingestion and voiding of the tag. For brevity the different events will be referred to by the predator number given in Table 1.

3.2. Dive profiles

Outside the shelf and before the predation events the diurnal vertical migrations and range of all the eels were consistent with previous observations of ocean-migrating eels (Tesch, 1978; Aarestrup et al., 2009; Fig. 3). Fig. 4 gives an overview of the three predation events shown on approximately the same scale. Data

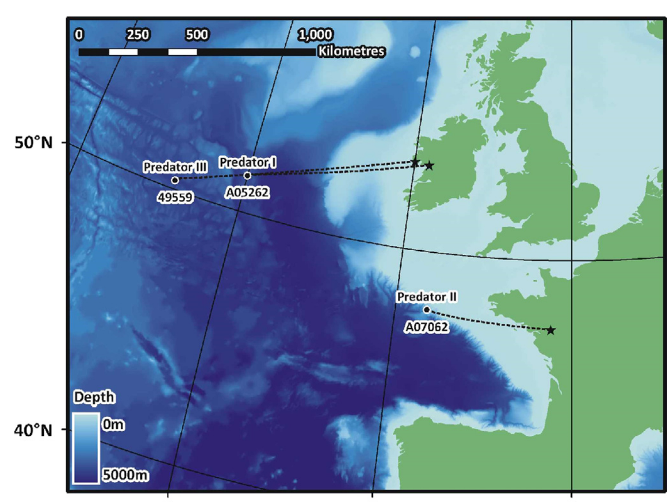

Fig. 2. The positions where three tagged European silver eels were released (star) and putatively consumed by predators (circle).

Table 1
Particulars of the predation events of three tagged eels. DST: data storage tag; PSAT: satellite tag; UTC: Coordinated Universal time. The time and depth of the predation event are given, as well as the maximum temperature logged by the tag and the duration during which the tag was inside the predator.

Predator	Tag ID	Tag type	Predation date	Time (UTC)	Depth (m)	Max temp (°C)	Duration (h)
I	A05262	DST	12-Jan-10	04:50	550	36.5	15.9
II	A07062	DST	19-Dec-10	06:20	470	36.4	44.1
III	#49559	PSAT	10-Apr-11	11:30	700	37.1	35.5

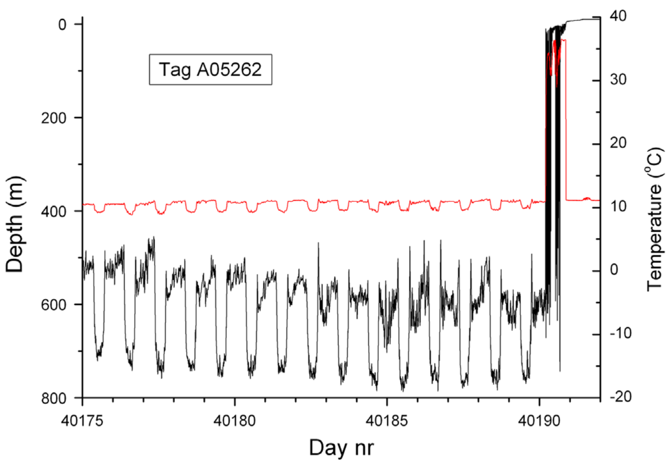

Fig. 3. Extended view of the event denoted Predator I in the text, showing the regular diurnal behaviour of the migrating eel before predation.

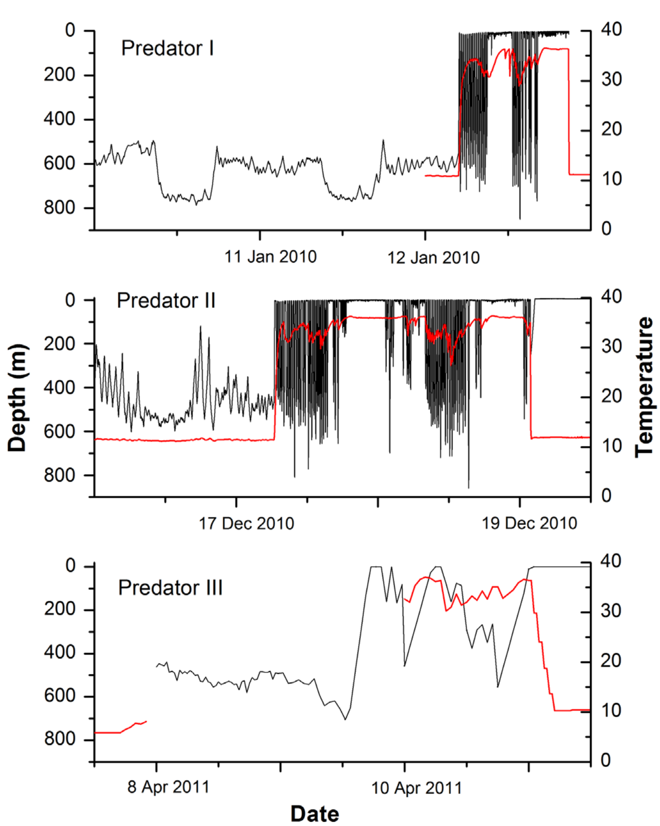

Fig. 4. Overview of depth (black) and temperature (red) time-series from the three predation events. In the Predator III event, the data were provided by pop-up satellite tag and, while the general pattern of depth reflects pre-and post-predation events. The precision of the depth data transmitted by the PSAT can be distorted by the data compression algorithms used.

from the PSAT tag ingested by predator III does not provide the same level as detail as from the recovered DSTs because the sampling rate during the event is relatively coarse at 30 min. In addition, the complicated data compression that the PSAT tag uses is not able to cope with the rapid diving behavior of the predator and so the only reliable data points are the measurements of depth and temperature every 6 h.

Both predators I and II show a similar diving behaviour with bouts of deep dives. The median duration of such dives was 11–12 min and the interval at the surface between dives varied between 5 and 7 min. The average depths of the deep dives differ by approximately 125 m between predators I and II (Fig. 5a and b). The frequency distribution of depth of dives is bimodal with an approximate division around 250 m, with the deeper dives centered at 600–700 m (Fig. 5a). The statistical parameters for all dives are given in Table 2.

In Fig. 5 the distribution of the maximum depth of dives is compared to the stratification of temperature and salinity in the vicinity of the predation event. The distribution of deep dives of both predator I and II have a maximum close to the salinity minimum at the boundary between East Atlantic Subarctic Intermediate Water and Mediterranean Outflow Water (van Aken, 2000). A detailed comparison is not possible as there is a time difference from the measurements of the Argo profiles and the predation events of 8 d and 5 d for predator I and II, respectively. There is also a difference between the position of the ARGO profile and the probable position of the predation events on the order of around 100 km.

A frequent feature during the deep dives was a deceleration at some mid-depth followed by acceleration to the maximum depth of the dive. Such 'sprint dives' (sensu Aguilar de Soto et al., 2008) were seen in both predator I and II. Fig. 6 provides examples of this behaviour. In 73% of the deep dives of predator I and 63% for II the maximum speed after a slowdown increased by $>50\%$ to 1.5–2.5 m/s. For predator II most of the dives without a sprint were to depths less than 400 m. On a few occasions the predator ascended briefly before the final downward sprint.

3.3. *Internal temperature measurements*

Following predation, the initial large increase in temperature of the tag is caused by the rapid heating of the tag as it equilibrates to the stomach temperature of the predator, slightly delayed by the insulation of the body wall of the eel. The later, small changes in temperature are more directly related to the temperature of the stomach or gut contents and probably reflect ingestion of food of the ambient temperature. In many cases a drop in temperature was seen in connection with a dive. Fig. 7 shows the maximum drop over 5 min that was recorded during the deep dives of the two predators. Excluding the 2 first hours after the ingestion of the tag the temperature drop exceeded 0.5° in 56% and 44% of the dives of predator I and II, respectively. Fig. 7 also shows the diving activity of the predator in relation to the local daylight cycle.

Two large temperature drops was seen in predator I during a long period without deep dives while the predator stayed at the surface. One similar sudden temperature drop without clear connection to a dive was also seen in predator II (Fig. 8).

4. Discussion

4.1. *Predation by a marine mammal*

The logical conclusion of this study is that the tagged eels described here were eaten immediately prior to the rapid temperature increase and ascent to the surface. Based on the latitude and longitude estimated from the temperature record immediately after

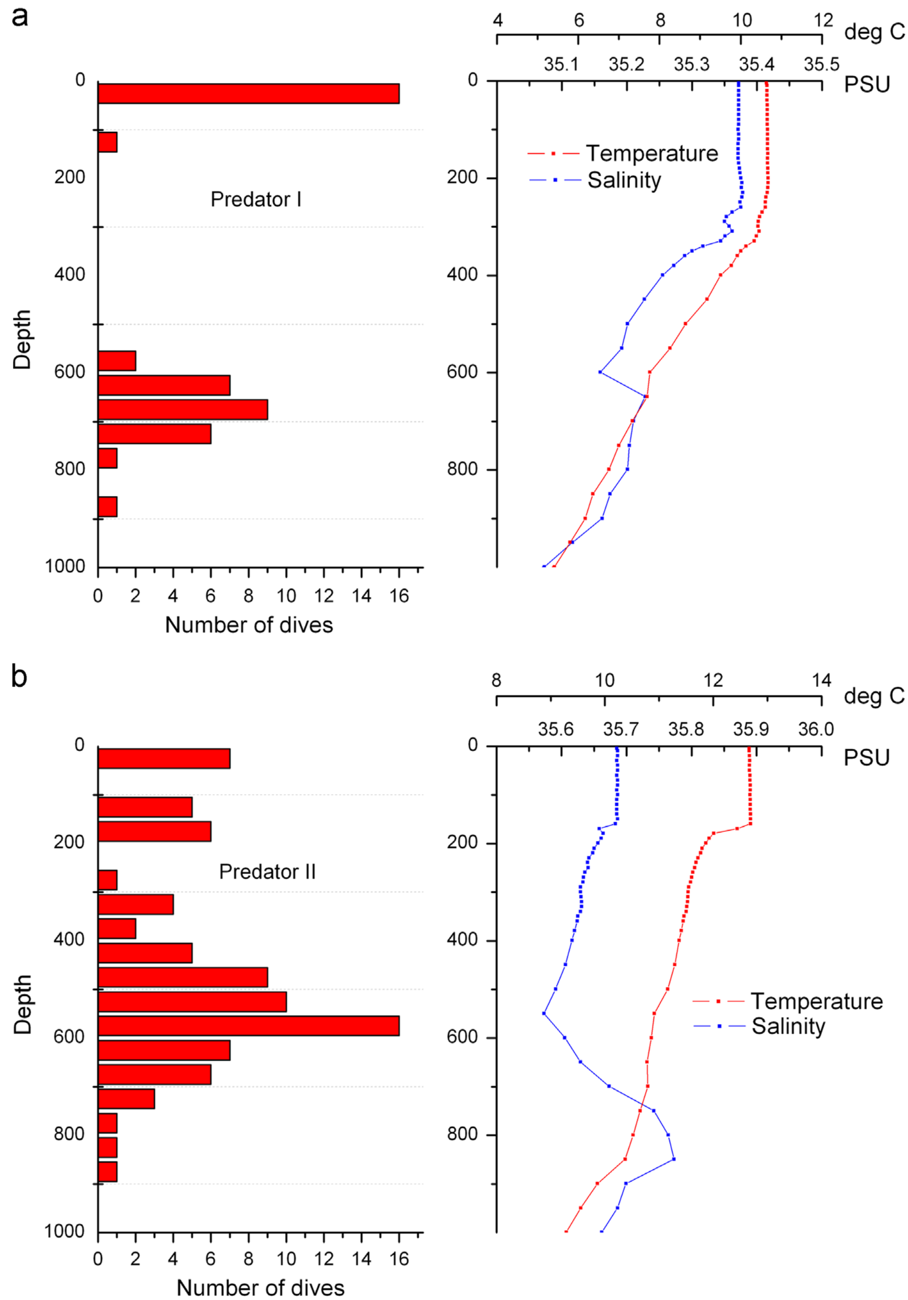

Fig. 5. Frequency histogram of all dives > 20 m and the temperature and salinity profiles from the nearest Argo buoy (for details, see text) for predators I (a) and II (b).

the tag was expelled, predation occurred in the mesopelagic zone of oceanic waters, over seabed depths of > 3000 m.

Predation of tagged animals is not unprecedented and has been used to infer mortality rates (Hays et al., 2003). The regular dives from the surface and the sustained high temperatures suggest that the eels were eaten by marine mammals. Among the marine mammals in the vicinity of the predation event, candidate predators are grey and harbor seals as well as tens of species of toothed whales (primarily delphinids, beaked whales and sperm whales). The two seal species found in the area are not known to dive to such large depths as recorded here; neither are the patterns of shallow dives observed in the tag data typical for either species (Tollit et al., 1998; Bech et al., 2000).

The most likely predator, therefore, is a toothed whale, even though eel carcasses are only rarely found in stomach contents of whales and only one account of predation of eels by whales has been published in the last 120 years (Vaillant, 1896). Especially for two of the tags, the dive tracks obtained are of very high quality and from an undisturbed predator. Among the toothed whale species found in the area whose diving behavior has been studied, the dive characteristics recorded by the data storage tags (Figs. 5 and 6) was most similar to that described for short-finned pilot whales *Globicephala macrorhynchus* (Aguilar de Soto et al., 2008; Johnson et al., 2009; Jensen et al., 2011), a species known to feed mainly on squid (Bernard and Relly, 1999; Hernandez-Garcia and Martin, 1994; Spitz et al., 2011). There are however other possibilities, e.g., other delphinids, whose diving behaviour has not been studied. Nonetheless, the dive data recorded by the tag bear striking similarities to the data published in Aguilar de Soto et al. (2008), and in particular the 'sprint dives' at the end of descents, which were obvious in more than 60% of the dives reported here, when the vertical swimming speed increased to 1.5–2.5 m/s in downward 'sprints' before the return to the surface.

Table 2
Dive parameters for deep and shallow dives. The duration of dives was calculated as the total time deeper than 20 m. Vertical velocity was calculated over 60 s intervals and centered at the midpoint of the interval. Mean and maximum vertical speed for a dive was based on all points where depth > 20 m during that dive. Sdv.: standard deviation. Med.: Median.

		Dives deeper than 250 m						Dives between 20 m and 250 m					
		Mean	Sdv	Med	Max	Min	N	Mean	Sdv	Med	Max	Min	N
Predator I													
Duration (min)	Dive	11.1	0.8	11	13	9.5	26	1.7	0.5	1.5	2.5	10	17
	Surface interval	6.1	6.1	2.9	5.0	17	26	28	46	8.5	149	2.0	16
Max depth (m)		674	62	675	852	557	26	35	20	32	110	23	17
Max speed (m/s)	Down	−2.7	0.4	−2.7	−2.2	−4.0	26	−0.4	0.3	−0.4	−0.1	−1.6	17
	Up	2.6	0.1	2.6	3.0	2.4	26	0.3	0.2	0.3	1.1	0.2	17
Predator II													
Duration (min)	Dive	12	1.6	12	15	8.5	65	5.3	3.1	6.3	11	1.5	18
	Surface interval	11	14	7.0	91	3.5	65	37	95	8.5	398	1.5	17
Max depth (m)		549	119	566	860	259	65	102	60	117	180	27	18
Max speed (m/s)	Down	−2.4	0.4	−2.4	−1.3	−3.5	65	−1.0	0.5	−1.2	−0.2	−1.7	18
	Up	2.5	0.4	2.6	3.1	1.4	65	0.7	0.3	0.7	1.1	0.2	18

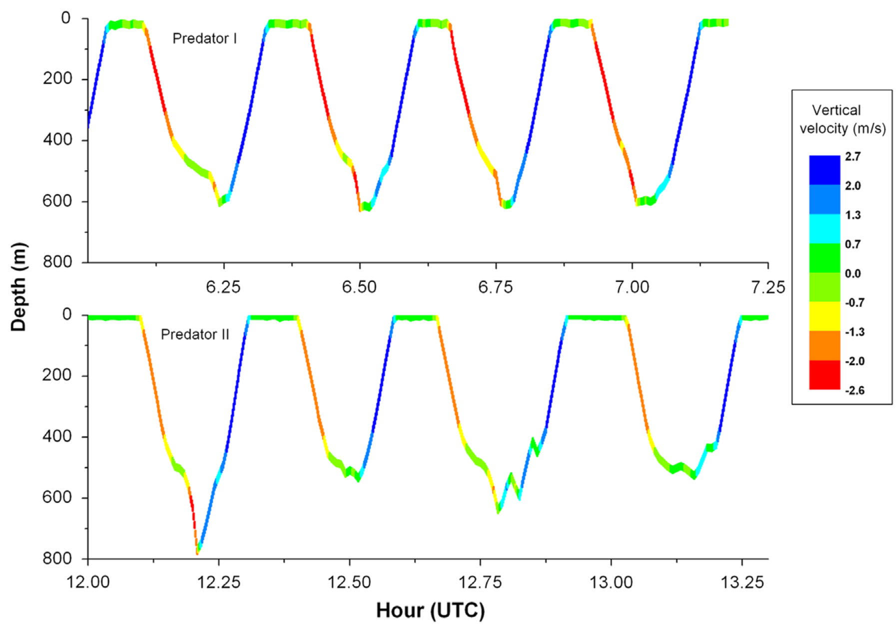

Fig. 6. Detail of series of deep dives with a sprint at the end of the descent.

4.2. Inferences from temperature data

After ingestion the recorded temperature rose quickly to 30 °C as the eels transferred from the cold ocean to the warm stomachs of the predators (Fig. 4). The recorded temperature then gradually increased over the next few hours, most likely because the tags' temperature sensors became increasingly exposed to the predators' stomach temperature as the eels were digested (Fig. 4). During this acclimation period, occasional small decreases in recorded temperature occurred during or immediately after deep dives (Fig. 4). In contrast, presumably once the eels were fully digested and the tags fully exposed, temperature changes during dives were more pronounced (Fig. 7). The most likely cause of these temperature drops is food consumption and water intake. 50% of the deep dives showed a drop larger than 0.5 °C (indicating a successful foraging event), which could give an indication of the success in foraging.

During the time spent at the surface between diving bouts of each predator, the temperature of the tags increased to > 36 °C (Fig. 4). In predator I, there were two large reductions in

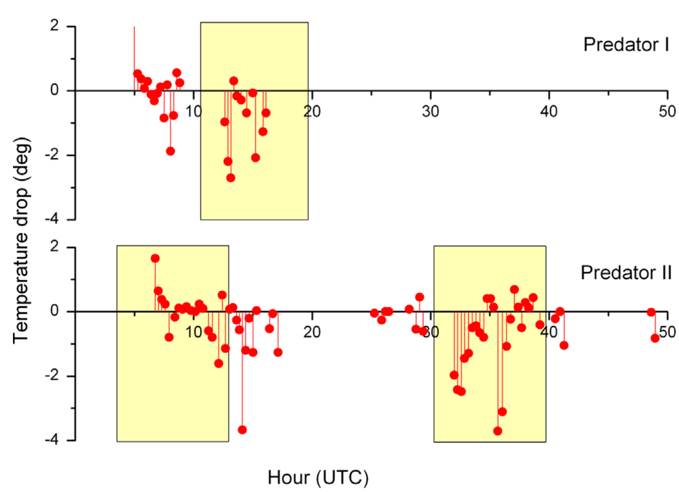

Fig. 7. Temperature drop recorded during successive deep dives. The yellow background shows the time of daylight at the date and longitude of the predation event. The origin of the time scales is at midnight the day of the predation event.

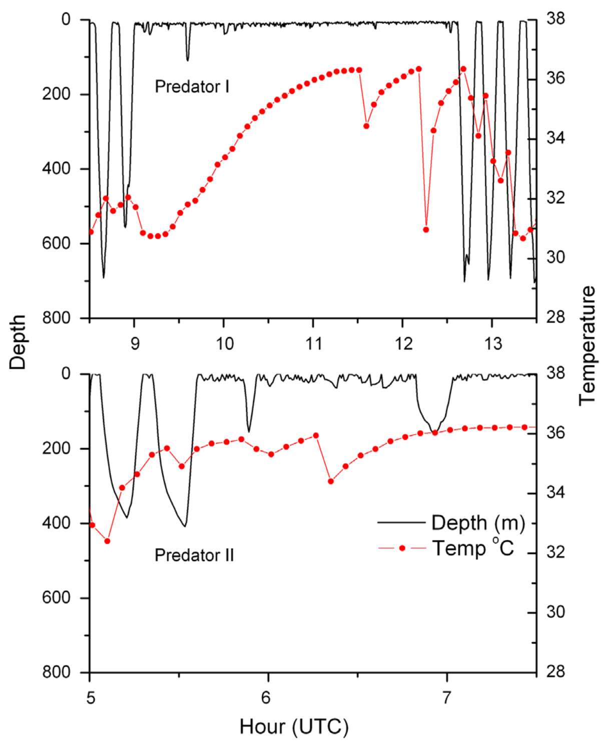

Fig. 8. Detail of resting periods at the surface showing sudden drops in temperature not related to diving activity.

temperature (> 1.5 °C, and > 5 °C) towards the end of the surface period between the first and second dive bouts, and in predator II, there were two temperature reductions of around 1 °C (Fig. 7). Pilot whales are not known to engulf prey at the surface, so these two drops may have been caused by ingestion of water, as has previously been reported from captive Odontocetes (Hui, 1981; Ridgway and Venn-Watson, 2010). The drops are similar in duration and the magnitude of temperature change to the ones reported during water intake in pinnipeds as observed using stomach temperature tags (Kuhn and Costa, 2006).

4.3. Diving and foraging ecology

The deep dives of both predators I and II are centered around and below a salinity minimum (Fig. 5a). This is the upper boundary of the high salinity Mediterranean outflow water. Presumably this is where food is accumulating. In a study of the spatial distribution of cetaceans in the strait of Gibraltar, de Stephanis et al. (2008) found that long-finned pilot whales mainly were found in deep waters where they likely were feeding in the Mediterranean Outflow Water.

The data presented here provides direct evidence of eel predation in deep oceanic waters. The data also show that archival tags can give detailed information on natural predatory events, similar to the direct observations obtained using temperature tags and video recordings in seals (Davis et al., 1999; Austin et al., 2006; Kuhn et al., 2009). The tag itself may have somewhat increased the target strength of the eel (but probably only to a minor degree), making it easier for the toothed whale to find and track it with its biosonar. In spite of this, our data provide the first direct evidence of eel predation in the deep ocean, previously only speculated upon. Further observations of oceanic prey and predators using tagging technology will increase our understanding of the dynamics of the deep-sea environment and thereby improve our ability to maintain the health of these ecosystems.

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