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Predation on migrating eels (*Anguilla anguilla L.*) from the Western Mediterranean

H. Westerberg [a,*], E. Amilhat [b], M. Wahlberg [c], K. Aarestrup [d], E. Faliex [b], G. Simon [b], C. Tardy [e,f], D. Righton [g,h]

[a] *Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Freshwater Research, Stångholmsvägen 2, SE-178 93 Drottningholm, Sweden*
[b] *Cefrem, UMR 5110 CNRS-Université de Perpignan Via Domitia, F 66860 Perpignan, France*
[c] *Department of Biology, University of Southern Denmark, DK-5230 Odense M, Denmark*
[d] *Technical University of Denmark, National Institute of Aquatic Resources, Silkeborg DK-8600, Denmark.*
[e] *PSL Research University: EPHE-UPVD-CNRS, USR 3278 CRIOBE, 66860 Perpignan, France*
[f] *WWF-France, Paris, France*
[g] *Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft NR33 0HT, UK*
[h] *School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

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ABSTRACT

Nineteen female silver European eels (*Anguilla anguilla* L.) were tagged with satellite tags and released in the Gulf of Lion in the Mediterranean during the migration seasons 2013 and 2015. Sixteen tags transmitted data: five in the Atlantic Ocean, and eleven in the Mediterranean. Of those, 50% of migrating eels were consumed by marine mammals in each year, all in the Mediterranean. The diving behaviour recorded by the tags after the eels were consumed indicated that the most likely predators were deep diving toothed whales. Measurements of the acoustic target strength of the tag showed a negligible effect on the detectability by whale biosonar. Overall, the observed predation rate was similar to that reported for eels escaping into the Atlantic. However, unlike eels in the Atlantic, which are most vulnerable to predators in the first week of escapement as they traverse the continental shelf and before they reach the refuge of the deep ocean, eels escaping from the Mediterranean were predated in deep water, months after release, likely as a consequence of their migration within a relatively narrow and deep corridor in the Alboran Sea. This emphasises the challenge of accounting for natural mortality in management plans for the long-term recovery of the European eel.

1. Introduction

Freshwater eels (family *Anguillidae)* are facultatively catadromous: adults spawn in the ocean, with the larvae then migrating to coastal and inland waters to grow before they return as adults to spawn. The European eel (*Anguilla anguilla* L.) has a particularly long oceanic migration with leptocephali crossing the Atlantic Ocean from the Sargasso Sea (Schmidt, 1922) to occupy the European continental habitat for up to several decades before maturing and 'escaping' the coast or freshwater to begin their spawning migration back to the Sargasso Sea. The European eel population is generally thought to be panmictic, with successful spawners from the entire distribution contributing equally (Palm et al., 2009; Als et al., 2011).

In Europe, the European eel is distributed in coastal and inland waters from arctic Russia in the north to southern Morocco in the south and also occurs in the Baltic Sea, Iceland, Madeira, the Azores and the Canary Islands (Tesch, 2003). It is also found throughout the Mediterranean and Black Sea drainage areas. The Mediterranean region is characterized by numerous lagoons, recognized to be high productive ecosystems (Pérez-Ruzafa and Marcos, 2012). These lagoons are particularly important habitats for eels, with favorable conditions for growth (Marohn et al., 2013) leading to shorter generations times compared to northern Europe.

Although the Mediterranean region comprises a large part of the total eel population (Dekker, 2003), Ekman (1932) raised the possibility that, based on the unique hydrography of the Straits of Gibraltar, the Mediterranean Sea could act as a gigantic trap and prevent spawning eels from returning to the Sargasso Sea to spawn. For many years the

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* Corresponding author.
E-mail address: Hakan.westerberg@slu.se (H. Westerberg).

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contribution of the Mediterranean to the eel spawning stock was uncertain. Amilhat et al. (2016, 2017), using eels tagged with satellite transmitters, demonstrated that migrating eels do indeed pass through the Strait of Gibraltar to reach the Atlantic Ocean. No eels released from the Mediterranean (or other parts of Europe) have yet been tracked all the way to the Sargasso Sea. This is in part due to limitations of the tracking technology, but also because eels appear to face a number of threats as they escape the continental shelf to the ocean, including predation (Wahlberg et al., 2014; Righton et al., 2016).

Accounting for predation in natural environments is, however, challenging, since it requires either the sacrifice of a large number of predators (Hislop et al., 1997), or using observational techniques on prey species that may impede their ability to avoid predation. In the case of European eel, remains are only rarely found in stomach contents and only one account of predation of eels by whales has been published in the last 120 years (Vaillant, 1896). In contrast, records of predation of tagged fish (including eels) are increasingly common (Kerstetter et al., 2004; Wahlberg et al., 2014; Tolentino et al., 2017; Strøm et al., 2019) and can provide evidence of predation hotspots, predator guilds, and provide important insights into natural mortality of value to fisheries management (Strøm et al., 2019). To date, however, observations of predation on ocean migrating eels have only been used descriptively within tagging studies, yet they have great value in helping to generate estimates of predation rate and its possible impact on the spawning stock. The objective of this study, therefore, was to assess in detail the predation observed on Mediterranean eels, and to estimate the potential effect of this predation on the contribution of Mediterranean eels to the spawning stock.

2. Methods

2.1. Tags and tagging

Nineteen eels were tagged with pop-up archival satellite tags (PSAT) and released in the Gulf of Lion, northwestern Mediterranean Sea. They were caught in different lagoons on the French south coast (Table 1, Fig. 1). They were all large females with average total length 95.0 ± 5.5 cm, and average mass 2.0 ± 0.32 kg. The average ocular index (the size of the eye in relation to the length of the eel, Pankhurst, 1982), was 13.1 ± 1.4, while the silvering index (Durif et al., 2006) was stage IV or V. These indicators strongly support that all eels were ready for oceanic migration.

The tag used in the study was the Microwave Telemetry X-tag (http://www.microwavetelemetry.com/x_tag). These tags have a length of 12 cm, maximum diameter of 3.3 cm, and a buoyancy (negative weight in water) of 2.6 g. The weight in water of an eel is approximately 4% of the weight in air (Webb and Weihs, 1994). This means a buoyancy change of 3–4% due to the tag. The X-tags were attached dorsally with a 3-point attachment (as described in Økland et al., 2013). Before tagging, eels were anaesthetized using Aqui-S® (https://www.aqui-s.com/78-aqui-s/24-joomla) at a concentration of 20 mg/L until they lost equilibrium. The handling time for eels was a few minutes and the eels were

Table 1
Data for all released eels. The lagoons where the eels were caught were Salses-Leucate (A), Guissan (B), Thau (C) and Petite Camargue (D). The fate of the eel/tag was: scheduled pop-up (S), predation by non-mammal predator (P), predation by marine mammal (MM), no data (N) and unknown cause (U). The area where the tag surfaced was: Mediterranean Sea (1) and Atlantic Ocean (2).

Tag number	Capture location	Release date	Release pos	Length (cm)	Weight (kg)	Ocular index	Surface date	Drift (d)	Data (%)	Popup position	Fate	Arera
133979	A	09-12-2013	42.80 N, 3.04 E	95.2	1.62	14.3	09-06-2014	0.0	38%	36.25 N, 13.82 W	S	2
133980	A	09-12-2013	42.80 N, 3.04 E	90.8	2.09	13.5	26-03-2014	0.0	61%	34.93 N, 09.14 W	P	2
133981	A	09-12-2013	42.80 N, 3.04 E	93.4	1.63	10.7	03-03-2014	4.2	47%	36.41 N, 01.24 W	MM	1
133982	A	09-12-2013	42.80 N, 3.04 E	96.0	1.85	10.5	27-04-2014	4.1	39%	37.43 N, 02.09 E	MM	1
133983	A	09-12-2013	42.80 N, 3.04 E	99.8	2.63	12.7	24-03-2014	4.3	34%	35.86 N, 01.44 W	MM	1
133984	A	09-12-2013	42.80 N, 3.04 E	86.5	1.46	12.9	06-01-2014	4.2	86%	40.75 N, 03.18 E	MM	1
133985	B	10-12-2013	42.09 N, 3.11 E	98.7	2.24	12.4	09-06-2014	0.0	24%	38.75 N, 00.76 E	S	1
133986	B	10-12-2013	42.09 N, 3.11 E	91.8	1.68	14.6	09-06-2014	0.0	36%	34.96 N, 10.71 W	S	2
152916	C	08-12-2015	42.39 N, 3.70 E	99.0	2.17	12.7	30-03-2016	4.2	39%	36.19 N, 02.55 W	MM	1
152917	C	08-12-2015	42.39 N, 3.70 E	104.0	2.00	13.6	08-03-2016	4.2	58%	35.03 N, 02.39 W	MM	1
152918	C	08-12-2015	42.39 N, 3.70 E	96.0	1.91	11.2					N	
152919	D	08-12-2015	42.53 N, 4.10 E	94.6	2.13	15.2	12-03-2016	4.2	73%	38.24 N, 00.67 W	MM	1
152920	D	08-12-2015	42.53 N, 4.10 E	81.0	1.73	13.5		0.0		37.97 N, 12.85 W	S	2
152921	A	08-12-2015	42.87 N, 3.07 E	100.5	2.26	13.5	02-04-2016	4.1	65%	36.38 N, 07.73 W	S	2
152922	A	10-12-2015	42.87 N, 3.07 E	91.4	1.70	12.5					N	
152923	A	10-12-2015	42.87 N, 3.07 E	100.0	2.45	15.8	beached	?	3%	35.28 N, 03.68 W	U	1
152924	A	10-12-2015	42.87 N, 3.07 E	92.2	1.80	13.5	15-12-2015	15.7	66%	40.06 N, 01.62 E	U	1
152925	A	15-01-2016	42.87 N, 3.07 E	94.0	1.64	11.6					N	
152926	A	15-01-2016	42.87 N, 3.07 E	101.0	2.23	13.4	06-03-2016	4.2	56%	36.77 N, 02.06 W	MM	1

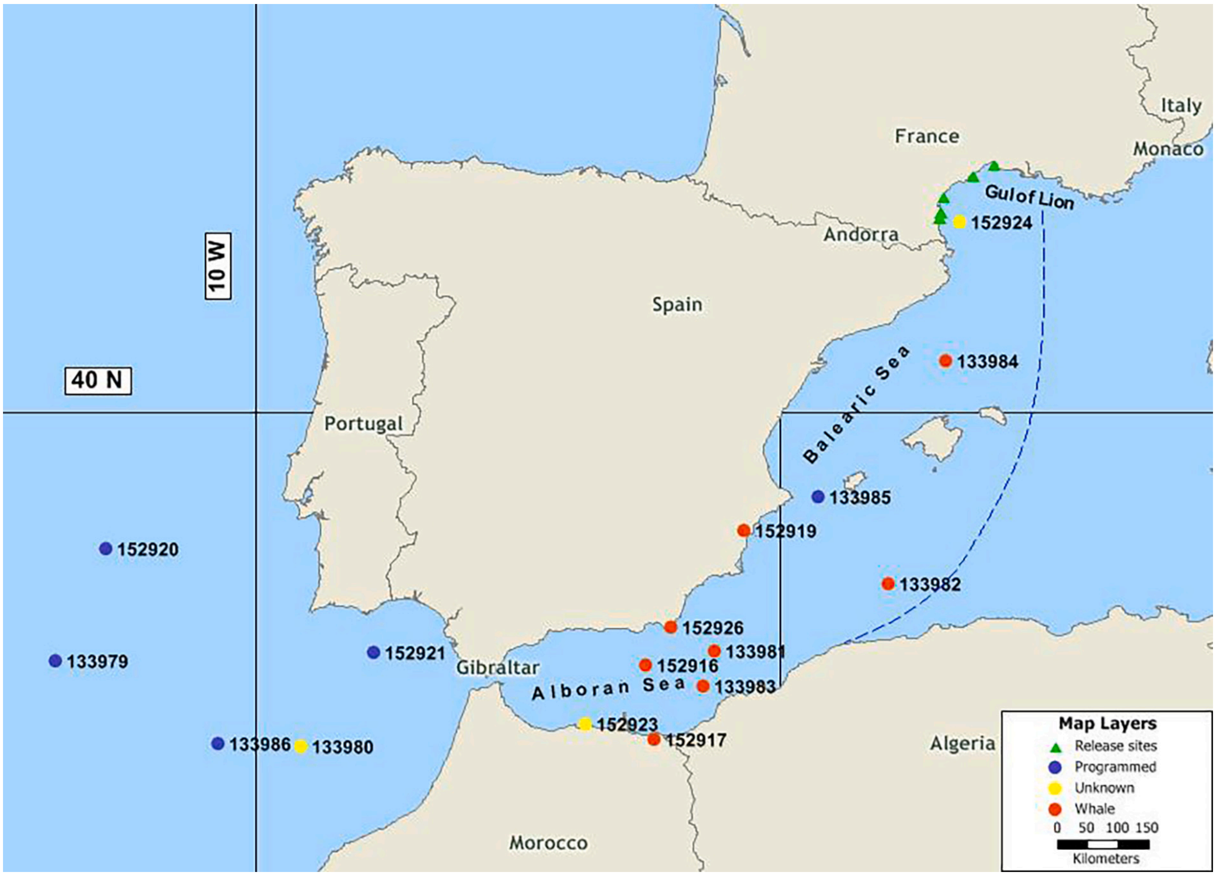

Fig. 1. Release and pop-up positions of the 19 PSAT tagged eels from the 2013 and 2015/16 studies. Green points show the release sites. The symbols show the end positions corrected for drift of all the tags, colour-coded according to the cause of ending. The dashed blue line indicates the approximate eastern limit of the eel trajectories. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recovered in 300 L holding tanks for one day before release. Procedures were conducted in accordance with the guidelines of the French Ethical Committee for animal experiments. Tagging was conducted by trained and licensed scientists working under the authority and approval of the *certificat d'experimenter sur les animaux vertébrés vivants* (experimental animal certificate) number 66.0801 (Elisabeth Faliex) of the CEFREM, University of Perpignan and number 2012-DY-2934-00007 (Kim Aarestrup) of DTU, Denmark.

2.2. *Tag data & programming*

The tags measure pressure, temperature and light irradiance at 2-min intervals. Light is used for an onboard calculation to estimate daily location based on the times of sunrise and sunset. The temperature resolution of the X-tag is ±0.15 °C, which is of the same order of magnitude as the entire temperature range of the weak thermal stratification in the upper 1000 m in the Mediterranean. Resolution of the depth sensor was 0.7 m.

Although data are stored at high resolution onboard the tag, only a limited subset of the data collected and stored by the X-tags can be transmitted via the Argos satellite system after the tag has surfaced. Furthermore, the proportion of transmissible data that is received by Argos varies depending on environmental conditions and battery power at time of transmission. Under ideal conditions, the daily maximum and minimum light level and the light-based estimated of daily location are transmitted to the Argos system, while temperature and pressure values are transmitted up to a maximum resolution of a 15 min interval. If the rate of change in depth or temperature between data points were greater than the maximum set by the data compression system of the PSAT a provisional, lower, value, termed 'delta values', was transmitted (see https://www.microwavetelemetry.com/compression_techniques_used_in_standard_rate_tags?s=delta%20limit for details). In addition to transmitting archived data, the X-tags also transmit their geographic position (the real-time 'Argos position') at the time of transmission.

Tags were programmed to pop-up after six months in the 2013 release (tag numbers 133979–86), and eight or ten months (tag numbers 152916–20, and 152921–26 respectively) in the 2015 release. However, the X-tag has a fail-safe release which is triggered if the pressure remains constant for a given period, or if the tag exceeds a threshold depth (set at 1400 m). The purpose of the failsafe is to retrieve the data even if a tagged fish dies, or if there is a risk that the tag will become physically damaged. When the seabed is shallower than 200 m, eels often rest at the seabed during the day (Westerberg et al., 2007; Righton et al., 2016), so data transmission was programmed to take effect after 4 days of unchanging depth to prevent premature pop-up of tags from eels remaining close to the seabed or surface in the first few days of release (as for Righton et al., 2016). A consequence of this programming is that a delay of four days before data transmission begins also occurs if the tag is separated from the eel prematurely and starts drifting at the surface, which introduces uncertainty into the pop-up location of the tag.

2.3. *Geolocation*

Anguillid eels exhibit a very strong diel vertical migration, moving to shallower depths by night and returning to deep water by day. The times of rapid descent and ascent have been shown to coincide with the times of sunrise and sunset (Righton et al., 2016; Wu et al., 2018; Chang et al., 2020). This allows estimation of the daily time of local noon, which after correction for the equation of time gives the longitude along the trajectory, while temperature data were used to estimate latitude (as for Righton et al., 2016).

In 5 of 16 cases, pop-up location was transmitted within a few hours of the tag reaching the sea surface. However, most pop-up locations (11) were uncertain due to the delayed transmission of data caused by the programming of the failsafe feature of the X-tag. To account for this, the location of tags at pop up were estimated by using the first 24 h of real-time Argos positions to calculate surface drift, and therefore to back-calculate the position four days earlier. Where possible (approximately a third of the cases) the light-dependent geolocation performed by the tag during this drift was of help. It was not possible to use the data to find the position where the predation took place as the movements of the predator between ingestion and evacuation of the tag were unknown.

2.4. Predation

The primary indication of a predation event involving a marine mammal was the sudden rise in temperature, from approximately 13 °C in the Mediterranean water to more than 30 °C. The time and depth where the eels were eaten were estimated at the moment when the first temperature rise towards 30 °C was observed. The uncertainty in the estimates depended on the sampling periods of temperature and depth, which were not necessarily the same due to the transmission algorithm of the X-tag. The time of evacuation of the tag from the predator was, similarly, identified by the sudden drop in temperature below 30 °C, followed by drift at the surface. In addition to the identification of predation using the temperature time-series, the recorded pattern of depth also changed abruptly, indicating predation. Although the diving activity of predators that followed could not always be fully resolved, due to the occasional low sampling rate of pressure, the moment of predation could often be discerned by the abrupt end of eel diel vertical migrations. When predation was not mammalian, this change in diving pattern or maximum daylight level also enabled identification of predation events such as by sharks or endothermic fishes as bluefin tuna (*Thunnus thynnus* L).

2.5. Acoustic reflectivity measurement

To investigate the possible effect of the tag on the detectability of the eel by toothed whale biosonar, a measurement of the target strength (TS) of an X-tag perpendicular to the long axis was made using an approximately 50 kHz signal, mimicking a click in the frequency range used by toothed whales when searching for food (Au and Suthers, 2014). The measurements were made at a frequency of approximately 50 kHz and calibrated against a 5 cm steel sphere with known TS of −38 dB. Details of the calibration are provided in the Supplementary Material. A diagram of the experimental arrangement is shown in Fig. S13.

To calculate the target strength of eels tagged in our study, we used the length-TS regression for eels obtained by McCarthy et al. (2008), given as:

$$\mathrm{TS} = 0.2381{*}\mathrm{L}{-}52.296$$

where L is length in mm and $\mathrm{R}^2 = 0.59$.

This regression was calculated from measurements using a split-beam echosounder beam operating at 120 kHz, directed horizontally towards eels ($n = 30$, length range 40–95 cm) swimming past the beam (McCarthy et al., 2008).

3. Results

3.1. Data recovery

Of the 19 tags released in the Gulf of Lion, 16 transmitted their archived data. Five of these (31%) surfaced in the Atlantic, one prematurely and four at the programmed date. Of the eleven that surfaced in the Mediterranean (69%) only one tag (133985) released at the programmed date, while the other ten popped-up before the scheduled date. Data recovery from the tags was, in general, low compared to the expected data recovery (the average was 46% of the expected recovery of data at 15 min sampling interval, range 3–86%, Table 1). Transmitted data were therefore at irregular sampling intervals or had gaps.

3.2. Fate of eels

Out of the five tags that were attached to eels that reached the Atlantic Ocean, one was predated and swallowed by an ectothermic predator, just west of the Strait of Gibraltar. Of the ten tags that surfaced prematurely in the Mediterranean, eight provided datasets that were consistent with mammalian predation as an end point: the recorded temperature suddenly increased above 30 °C and dive patterns changed abruptly with frequent visits to the sea surface (as for Wahlberg et al., 2014). The marine mammal predation events are detailed in Table 2, and depth and temperature plots of all predations are in Supplementary Material, Fig. S1-S11. The weight of eels predated by the marine mammals was slightly larger (mean 2.01 ± 0.37 kg) than the overall mean 1.97 ± 0.32 kg), but this difference, and the difference in length, was not statistically significant (*t*-test $p > 0.7$).

Data from the other two tags released in the Mediterranean were inconsistent with predation: tag 152924 remained at a constant depth and at the same temperature as the ambient water for 7 h before suddenly surfacing five days after release (suggesting mortality without predation, as for Righton et al., 2016), while the dataset from tag 152923 was fragmented with a 20-day gap before it started transmitting from a beach in Morocco, preventing any interpretation or analysis.

The overall predation for the 16 tags that transmitted data in the experiment was 56% (9 eels), of which eight occurred in the Mediterranean Sea and can be strongly linked to marine mammals. No marine mammal predation was recorded for the five eels reaching the Atlantic, but one by an ectothermic predator.

3.3. Geographic aspects

The estimated surfacing locations of all the tags are shown in Fig. 1. As soon as the eels left the continental shelf, they started a regular diurnal vertical migration, swimming deep during daytime and shallower at night as they migrated towards the Straits of Gibraltar. An example of diurnal vertical migration behaviour is illustrated in Fig. 2, for the tagged eel 133983. All eels moved south or southwest off the Spanish coast, without large deviations to the east, and when they approached Africa they turned west towards the Strait of Gibraltar.

The mean duration between dates of release and predation was approximately 3 months (89 days, range 51–140 days), and eels travelled on average 620 km (range: 200 to 950 km) from the point of release during this time. Assuming there was no significant movement post-predation, most marine mammal predation events (7 out of 8) took place in the Alboran or south Balearic Sea (Fig. 1). However, there is some uncertainty associated with the location of the predation event due to the likely movement of the predator between ingestion and evacuation (time between ingestion and evacuation range from 11 to 334 h, median time 43.5 h). This adds to the uncertainty related to the post-evacuation drift of the tag at the sea surface before the first Argo location (median estimated drift distance 42 km, maximum 200 km).

3.4. Characteristics of predation by marine mammals

Most (75%) of the eels that were eaten were taken during daylight and within the depth range occupied by the eels during the day (approximately 450 to 700 m, Fig. 3), at which depth the total daylight irradiance would have been less than 0.01% of the surface values. An example of predation is shown in detail in Fig. 4. The tagged eel

Table 2
Parameters recorded during the period when the tag was in the marine mammal. Depth values are minimum values subject to the limitations of sampling rate and occurrence of "delta limited" values. The dive cycle is estimated from periods with sampling period shorter than 60 min.

Tag	Predation		Sampling period	Dive cycle	Max temp	Max depth	Evacuation	Duration
number	date/time	depth	minutes	minutes	°C	m	date/time	hours
133981	28-02-2014 23:50	330	30	60	37.3	700	03-03-2014 00:55	49.1
133982	13-04-2014 18:30	460	15	60	35.4	595	27-04-2014 15:15	332.7
133983	23-03-2014 08:30	550	60	–	36.9	550	24-03-2014 05:05	20.6
133984	06-01-2014 09:10	560	60	–	34.9	660	06-01-2014 20:15	11.1
152916	28-03-2016 08:10	610	60	–	37.4	420	30-03-2016 03:40	43.5
152917	07-03-2016 20:50	195	15	40	36.9	470	08-03-2016 11:45	14.9
152919	08-03-2016 15:30	530	20	65	36.6	560	12-03-2016 00:00	80.5
152926	04-03-2016 08:00	515	20	65	36.9	660	06-03-2016 03:15	43.2

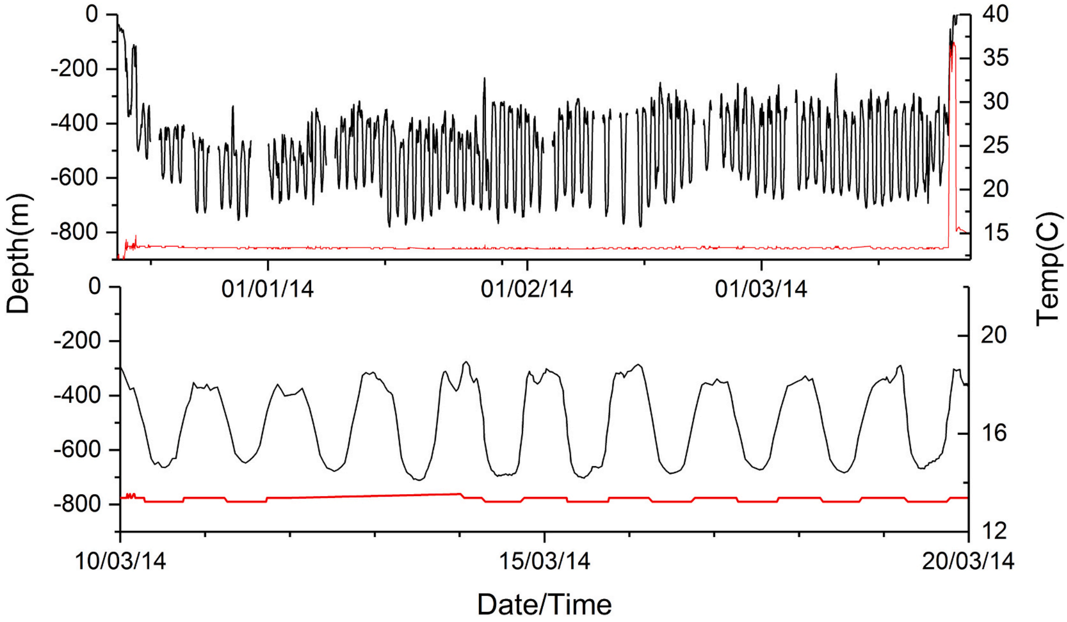

Fig. 2. Swimming depth and experienced temperature of eel 133983. Upper panel shows the entire time series, with diurnal vertical migration typical for eel migration in deep water, ending with a marine mammal predation. The lower panel expands a section of the time-series to illustrate the regularity of the diel vertical migrations. The black lines shows depth data with 5 points adjacent averaging. The red lines shows the water temperature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(152919) is swallowed at approximately 530 m depth and the tag immediately records a sudden warming accompanied by a change in diving pattern to surface oriented diving. The tag continues to record throughout the time within the predator, providing information on foraging and diurnal changes in activity. Prey ingestion is seen as a decrease in temperature when cold prey reaches the stomach and intestine during periods of deep diving (as for Wahlberg et al., 2014). In this example, the predator shows regular periods of rest at the surface each night during the four days the tag remains in the predator (starting around 20:00–23:00 in the evening and lasting to 05:00–07:00 in the morning). During those periods the temperature gradually increases to 36.5 °C. Similar resting periods during the night were seen for tag 133983, 152916, 152926 and possibly for tag 152917 (Figs. S5, S7, S10 and S8 respectively).

Considering the maximum depths and dive cycle durations observed in connection with the predation events (Table 3) as well as the distribution of marine mammals in this part of the Mediterranean (Notarbartolo di Sciara and Birkun Jr, 2010), the most likely candidate predators were sperm whales (*Physeter macrocephalus*), Cuvier's beaked whales (*Ziphius cavirostris*) or long-finned pilot whales (*Globicephala melas*). The long duration of the dive cycle for the tags 133982, 133981, 152919 and 152926 (Figs. S2 to S4, S1, S9 and S10) makes it most likely that the predators were sperm whales.

3.5. *Acoustic reflectivity of eels and satellite tags*

Based on the regression in McCarthy et al. (2008), the mean target strength (TS) of the eels that were predated in the Mediterranean would be −25 dB with a range − 23 to −28 dB. This is well above that of squid (−38 to −44 dB for 22–26 cm large squid, Madsen et al., 2007), which is the main food of sperm and pilot whales. The measured TS of the X-tag was −41 dB, which is at least 13 dB (or contributing about 5% to the acoustic energy) below that of the smallest eel. The addition of the tag makes, therefore, only a minor contribution to the detectability of the eel by whale biosonar.

4. Discussion

European eels face a number of threats as they migrate to the spawning area, including hydropower turbines, irrigation dams, fishing and predation. Our results, while comprising a relatively small sample size, show that half of migrating silver eels released on the French Mediterranean coast were predominantly consumed by marine mammals, despite their occupation of the predation refuge of the mesopelagic layer of the Mediterranean Sea. Oceanic predation of pelagic fish is generally poorly understood due to difficulties in sampling this life-history stage. For this reason, the data provided by this study are of

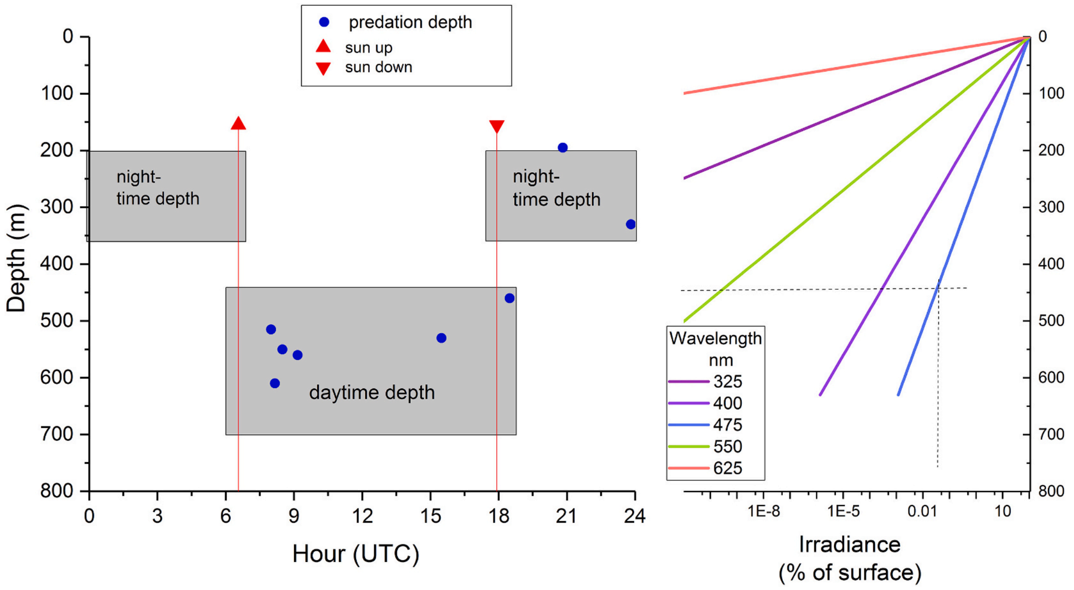

Fig. 3. Intercept depth (blue dots) of all whale predations as function of time of day. The sunrise and sunset are indicated for March 1 in the SW Mediterranean. The grey boxes show the range of the daytime and the night-time swimming depth of the 8 eels preceding predation. Right panel shows daylight irradiance for different wavelengths in percent of the surface irradiance. Dotted lines show minimum daytime depth of the eel and maximum percentage irradiance in the visible specrum. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

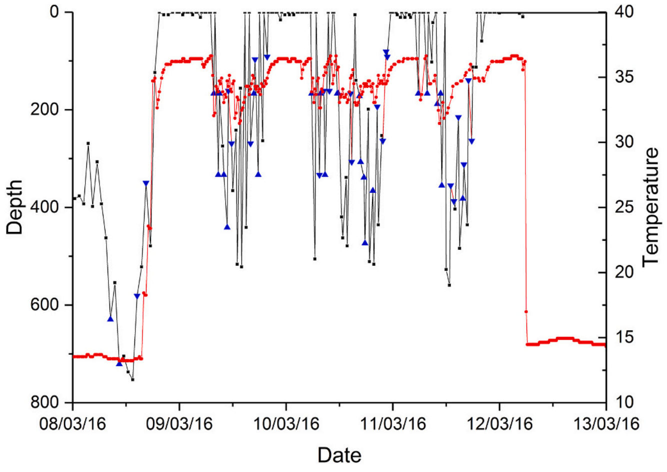

Fig. 4. Depth and temperature data for the predation/ingestion period for the eel tag 152919. The black line and symbols show the depth data, with black squares showing measured depth and blue triangles showing ‘delta depth’ values which are estimated and recorded by the tag when vertical movement rate exceeds the ability of the tag to record a measured value. The red line shows the temperature. Note the alternating foraging and rest periods, visible both in diving activity and stomach temperature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

value in determining not just the type of predator of greatest threat to eels in the Mediterranean, but also the locations and timing of predation.

4.1. Predation rates

Overall, the predation rate for eels tagged in the Mediterranean was similar to that reported for eels escaping from catchments directly into the Atlantic Ocean or North Sea (Righton et al., 2016), at approximately 50% of all eels tagged. In general, predation rates in migrating diadromous fish can be very high, either as juveniles (Thorstad et al., 2012) or as adults (Lacroix, 2014; Strøm et al., 2019), which is generally considered to be a consequence of the increased risks that individuals take or experience as they move between freshwater and marine habitats. Indeed, in a study of migration of silver American eel in the St Lawrence system, Béguer-Pon et al. (2014) reported that only 4 of 180 internally tagged eels were detected at the terminal listening array situated at the exit to the Gulf of St Lawrence, and suggested that marine predation was likely to have made a significant impact on escapement. This finding was supported by a follow up study (Béguer-Pon et al., 2018), in which annual escapement rates were low (between 9% to 20%

Table 3
Whale species regularly occurring in the Mediterranean Sea with literature data about maximum diving depth and typical duration of foraging dives in the Mediterranean.

Common name	Scientific name	Max dive depth (m)	Dive cycle (minutes)	Reference
Fin whale	*Balaenoptera physalus*	470	13	Panigada et al. (1999)
Sperm whale	*Physeter macrocephalus*	830	55	Watwood et al. (2006)
Cuvier’s beaked whale	*Ziphius cavirostris*	1888	58	Tyack et al. (2006)
Killer whale	*Orcinus orca*	265		Bowers and Henderson (1972)
Long-finned pilot whale	*Globicephala melas*	825	15	Verborgh et al. (2016)
Risso’s dolphin	*Grampus griseus*		7	Bearzi et al. (2011)
Rough-toothed dolphin	*Steno bredanensis*	>70	15	Jefferson (2018)
Bottlenose dophin	*Tursiops truncatus*	450	5	Klatsky et al. (2007)
Striped dolphin	*Stenella coeruleoalba*	700	5	Archer II (2009)
Short beaked common dolphin	*Delphinus delphis*		2	Bearzi et al. (2005)
Harbor porpoise	*Phocoena phocoena*	220	5	Bjørge and Tolley (2009)

over a four-year study period).

Of the 96 predation events reported for non-Mediterranean eels in Righton et al. (2016), only three could be attributed to whales (see Wahlberg et al., 2014 for more detail). Instead, the majority of predations occurred during the first week, predominantly on the continental shelf (<200 m water depth) and were attributable to surface-oriented fish or sharks and in one instance a seal. The majority of these events were categorized as 'suspected predation' and could not be attributed directly to a species group. High predation rates on the continental shelf has also been recorded for American eel (*Anguilla rostrata*, Lesueur). In this case the predators were assessed to be endothermic fish, probably porbeagle sharks, and the predation rate was >50%, e.g. Béguer-Pon et al. (2012). Manabe et al. (2011) also report predation on Japanese eel (*Anguilla japonica*, Temmninck & Schlegel) by an endothermic fish. Since the diel vertical migration behaviour of eels appears to be geared towards occupying a deep predation refuge during the day, the predation rate in the Mediterranean Sea was unexpected, because here eels can quickly access this refuge once they leave the coast. In contrast to in the Atlantic, all the predation on eels occurred in Mediterranean deep waters, on average 3 months after release, often at great depth where light levels were insufficient for visual predation. Approximately 90% of the predation was directly attributable to toothed whales.

The differences between rates of marine mammal predation in the Mediterranean compared to other oceanic parts of the European distribution area, can be linked to the abundance, as well as the spatial and temporal overlap of potential predators with eels as they migrate into the Atlantic Ocean. In terms of the assumed predator, the sperm whale density in the Atlantic and the Mediterranean Sea is similar based on published studies. Whitehead (2002) estimated for 1992 a density of $4.9{*}10^{-3}$ km^{-2} in the NE Atlantic, while Gannier et al. (2002), assuming an 8 km detection range in their acoustic surveys), estimated a density of $3{*}10^{-3}$ km^{-2} in the Mediterranean west of Sardinia during summer. However, the spatial overlap of eels and cetaceans may be very different. In the present study, eels traverse only a very narrow continental shelf compared to in the Atlantic, and because the western Mediterranean Sea in particular is a small and confined area, eels are likely funneled along a relatively narrow corridor towards the Gibraltar Strait, where some cetacean species congregate annually to feed. Despite swimming at depths that offers protection from visual predators, they are still vulnerable to deep divers that use biosonar (i.e. toothed whales). Thus, the high whale predation rate (7/8) observed in Alboran and south Balearic Sea could be explained by an increase in concentration of migrating eels as the Mediterranean narrows towards the Strait of Gibraltar during late winter, and/or a gathering of whales foraging in this area at this time (de Stephanis et al., 2008).

4.2. Predator identity and behaviour

The data from the tags provide strong evidence that the predator species inside the Mediterranean was a deep diving cetacean species. Eleven cetacean species are regularly present in the Mediterranean Sea (Notarbartolo di Sciara and Birkun Jr, 2010); these are listed in Table 3, together with their maximum diving depth and the characteristic duration between foraging dives, if known. The only other marine mammal permanently present in the area is the rare Mediterranean monk seal, which is a shallow diver and is primarily a benthic forager (Dendrinos et al., 2007), ruling it out by virtue of the depth at which the eels were eaten, even if the sampling period (sometimes 60 min) of some of the tag data prevented discrimination on the basis of dive duration. Where the duration of the dives could be estimated, the data incontrovertibly indicate deep-diving toothed whales, such as pilot whales, sperm whales or Cuvier's beaked whales.

For some tag datasets, the data provide poor resolution even over lengthy time-scales. During the ingestion period of tag 133984, for example, no surfacing was recorded during the entire 11 h the tag was in the whale. Similar long periods without apparent surfacing were seen for tag 133982 during periods with low sampling rate (e.g.13 h 15 April, Fig. S3). However, based on the maximum depth and the dive cycles during periods with 15 min sampling interval, it is possible to infer that this predator most probably was a sperm whale and that tag 133984 also was predated by a toothed whale.

4.3. Impact of tags on predation

The main food of the deep diving toothed whales is cephalopods, which are detected using echolocation (Madsen et al., 2007). The high incidence of predation on eels in the Mediterranean occurred at 500–800 m depth, where sperm whales and Cuvier's beaked whales echolocate for squid (Watwood et al., 2006), and where predation by visual predators is unlikely. A possibility that we considered was that a strong echo from the PSAT tag may have increased the probability that the eel was detected. However, our measurements of the acoustic reflectivity of the PSAT suggest that, at -41 dB, the tag had a target strength at least 13 dB below the TS of the eel. Furthermore, both the tag and eel were measured perpendicular to their long axis and, as the tag will tend to align with the eel during swimming the difference in acoustic reflectivity will tend to be independent of the orientation with respect to the whale. The tag is therefore unlikely to make the eels significantly more detectable by echolocating predators. This, and the lack of daylight, means that the high level of predation by whales is likely not an artefact of increased detectability as a result of the tag.

Nevertheless, while the tags may not increase the detectability of the tagged eels, the presence of a relatively large external tag may evidently increase the general risk of predation in other ways, such as post-release stress, a reduction in ability to avoid predation due to the effect of drag and, potentially, the release of an odour trail from the attachment wound (Jepsen et al., 2015; Tolentino et al., 2017). This will increase predation by all kind of predators, not just whales. The fact that eels search refuge in deep water during daytime means that the risk of predation by visual predators is minimized; on the other hand it also means that non-visual predators, as whales, goes undetected by the eels. Thus, while the predation rate may be increased for tagged eels we argue that the high prevalence of whale predation in the western Mediterranean compared to elsewhere is a strong evidence of the character of the mortality regime in the Mediterranean. In consequence, the predominance of predation by whales that we report here would be likely to have an important impact on the eels escaping the Mediterranean drainage areas for reproduction.

4.4. Consequences of whale predation on eels

In general, the magnitude of escapement of eels, i.e. the biomass of silver eels returning to the sea for reproduction, is poorly known (ICES, 2019). Furthermore, because the oceanic migration of eels is still poorly understood, the proportion of eels that escape to the sea that are able to contribute to spawning is completely unknown. Generating knowledge on predation rates and other aspects of natural mortality is therefore an important step in reducing this uncertainty. The Mediterranean basin is known to be an important area for eel production, although the only available modelling study of the eel production in Mediterranean lagoons (Aalto et al., 2015), estimated that the silver eel escapement for the period 2000–2012 was, depending of the assumptions, between 3800 and 7100 tons/year (7–12 kg/ha). Considering the rapid growth, shorter life cycle and large surface of suitable high productive habitats in the Mediterranean area (ICES, 2019), the eels from the Mediterranean region could potentially have a key role in the sustainability of the eel population. The reported catches from Mediterranean countries have for several decades been estimated as approximately half the total catch of the European eel (Fig. S12, supplementary material). The present tagging study shows that whale predation could be a significant source of mortality during silver eel migration in the Mediterranean Sea.

Although the number of tagged individuals was low, the predation rate was similar during both years of tagging. If the results are representative of the Mediterranean area, 50% of the migrating silver eels were lost while passing the Alboran and Balearic Seas. Cetaceans are present in the whole Mediterranean Sea, so unless the area in the westernmost part of the Mediterranean is particularly exposed to predation, the total loss could be even higher.

Of the eight eels consumed by marine mammals, sperm whales were likely responsible for five of them. A rough estimate of the number of sperm whales can be made for the summer distribution of acoustic 'sightings' west of Sardinia (Gannier et al., 2002). Approximately 1500 individuals were present in this area. Lewis et al. (2018) arrives at a similar abundance estimate (1678 whales) for the western Mediterranean. This means that if all predation was by those sperm whales, concentrating in the Alboran and Balearic region during the eel migration season, they would have an eel consumption of 1.3–2.4 ton/individual and year, using the escapement estimate above (corresponding to the order of magnitude 10 eels per whale and day). The daily food consumption of sperm whales has been estimated to be 300 and 200 kg/day for averaged sized female and males respectively (Kawakami, 1980). This means that eels constitute a minor part of between 1.2 and 3.3% of the diet of the sperm whales in the western Mediterranean. Such a low contribution to the diet indicates that the concentration of eel predations rather reflects a coincidence with a hot-spot for foraging on other prey than a specialization on eel, and is an effect of migrating eels converging in the narrowing area towards the Strait of Gibraltar. Similar reasoning would apply to pilot whales and Cuviers beaked whales, as potential predators of the eels in the present study, and a similar conclusion would be drawn.

Finally, the high rate of predation by whales raises several questions regarding its impact on the overall Mediterranean contribution to the eel spawning stock. Additional tagging experiments throughout the Mediterranean Sea should be undertaken to understand whether whale predation also is particularly high and consistent in general, and whether the 50% predation rate observed in this study is an underestimate of the total predation rate. Moreover, it would be valuable to understand the relative contribution of silver eels from the Atlantic and Mediterranean regions to eel spawning. More tracks of eels entering the Atlantic from both areas would be valuable, so as to gain a greater understanding of the relative impact of the various threats that eels face after escaping to sea (Righton et al., 2016). These results could provide important information to improve stock assessment and management of the European eel on its entire distribution range.

Data availability

The data underlying this article are available in the article and in its online supplementary material. PSAT records for predation events can be requested from the corresponding author.

CRediT authorship contribution statement

H. Westerberg: Conceptualization, Writing – original draft. **E. Amilhat:** Writing – review & editing, Funding acquisition, Project administration. **M. Wahlberg:** Methodology. **K. Aarestrup:** Writing – review & editing, Investigation. **E. Faliex:** Writing – review & editing. **G. Simon:** Writing – review & editing, Investigation. **C. Tardy:** Writing – review & editing. **D. Righton:** Writing – review & editing.

Declaration of Competing Interest

There are no conflicts of interest.

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Appendix A. Supplementary data

Details of swimming depth and temperature during all predation events (Figs. S1-11). Development of eel catches in Europe (Fig. S12). Description of method used for measurements of target strength (Figs. S13-16).

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