The novel use of pop-off satellite tags (PSATs) to investigate the migratory behaviour of European sea bass *Dicentrarchus labrax* (L., 1758) in the Celtic Sea area

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ABSTRACT

A total of 12 adult European sea bass *Dicentrarchus labrax* were tagged with pop-off satellite archival tags (PSAT) in Irish coastal waters and in offshore waters in the north-east Celtic Sea between 2015 and 2016. Archived data were successfully recovered from five of the 12 tags deployed, three from fish released in inshore Irish waters and two from fish released offshore in the eastern Celtic Sea. All three fish tagged in inshore waters were found to undertake migrations into the open ocean coinciding with the spawning period. These fish also exhibited fidelity to inshore sites post-migration, returning to the same general location (within *c*. 73 km, which is roughly the predicted mean accuracy of the method) of their original release site. Although the number of tracks obtained here was limited, some degree of aggregation between inshore and offshore tagged fish in the eastern Celtic Sea was noted during the expected spawning period suggesting PSATs can provide new information on specific spawning locations of European sea bass.

Keywords: biotelemetry; European sea bass; PSAT; site fidelity; spawning; Celtic Sea

INTRODUCTION

Extensive tag–recapture studies of adult European sea bass *Dicentrarchus labrax* (L. 1758) (order Perciformes, family Moronidae) in British waters have revealed an annual pattern of feeding in inshore waters in summer and migration to offshore waters during winter and spring for spawning (Holden & Williams, 1974; Kelley, 1979; Pawson *et al.*, 1987, 2007, 2008; Fritsch *et al.*, 2007). In Irish waters, results from mark–recapture tagging studies of *D. labrax* during the 1970s along the south Irish coast showed a highly localized distribution of the species, with all recaptures being made in inshore waters (Kennedy & Fitzmaurice, 1972). More recently, annual site fidelity in inshore areas was identified by acoustic tracking (Doyle *et al.*, 2017). Pawson *et al.* (2007) reported *D. labrax* released from inshore waters on the west coast of Wales, U.K., recaptured in inshore waters of the south-western Irish coastline, providing evidence of more extensive movements of sea bass. Moreover, *D. labrax* undertake considerable migrations over short periods of time with recaptures reported 2 months post-release up to 1200 km away (Pawson *et al.*, 2007). These studies suggest that *D. labrax* originating from inshore Irish waters may undertake long range migrations across open waters, but to date no definitive data are available to support such claims.

Dicentrarchus labrax behaviour has been studied using data storage tags (DST), particularly for offshore migrations, which are currently beyond the detection range limits of acoustic tags and receivers (Heupel *et al.*, 2006). The environmental data recorded by these surgically inserted DSTs can be used upon a fish's recapture to model and map its most likely post-release migratory track (Woillez *et al.*, 2016). Due to the prohibition of commercial *D. labrax* fishing in Irish inshore waters since 1990 (Inland Fisheries Ireland, 2014) and minimal landings from the E.U. commercial fleet in Irish offshore waters (ICES, 2014), this method of tagging is ineffective due to potentially low recovery rates. As a result, methods of telemetry which do not rely on the recovery of the tag are more applicable. Though traditionally fitted to larger species such as sailfish *Istiophorus platypterus* (Shaw 1792) (Hoolihan & Luo, 2007) and bluefin tuna *Thunnus thynnus* (L. 1758) (Abascal *et al.*, 2016), advancements in tag technology have resulted in streamlined, lightweight pop-off satellite archival tags (PSAT) that gather information on specific environmental variables that can subsequently be used to estimate the geolocation of individual fish (Walli *et al.*, 2009). Unlike traditional DSTs, PSATs are programmed to detach at a pre-defined date and time, transmitting archived data *via* the ARGOS satellite network (Coyne & Godley, 2005). This is a method of biotelemetry that is particularly useful in fisheries where the possibility of tag recovery is low. The objective of this study was to evaluate the use of PSATs as a method of tracking adult *D. labrax* migration from Irish coastal waters and offshore waters of the north-east Celtic Sea and to investigate whether successful implementation of this technology could be used to identify spawning locations and post-spawning migration to inshore feeding sites in the Celtic Sea region.

MATERIALS AND METHODS

FISH SAMPLING

The *D. labrax* tagged in this study were obtained during a systematic and extensive sampling programme undertaken over 2 years on the south-east coast of Ireland aimed at understanding the behaviour and migration of *D. labrax* from Irish waters and the Celtic Sea. This involved conventional, acoustic and satellite tagging and tracking and biological analyses of *D. labrax*. Only larger fish (>42 cm LF believed to be adult fish; Inland Fisheries Ireland, 2014) were selected for PSAT tagging as these were considered more physically capable of carrying an externally mounted tag.

Approval to undertake research on the species was obtained by the Sea Fisheries Protection Authority (SFPA). Based on extensive local angling and commercial fishing knowledge prior to 1990, sampling was conducted in areas where the chances of encountering large adult *D. labrax* were likely to be high. Seine netting (net specifications: 100m long × 4 m deep; wings=42m of 210/30 × 80mm stretched mesh knotted nylon; cod end=16m of 210/12 × 20mm stretched mesh knotless nylon) was undertaken in the Cullenstown, Co. Wexford in April 2016, with eight fish tagged over 3 days. Inshore trawling took place on board the M.F.V. Boy River in the Waterford Estuary using a small otter trawl with a headline height of 3 m in February of 2016, with one fish tagged at this location. Tows varied between 10 and 20min in duration.

Targeted offshore sampling was undertaken on the R.V. *Celtic Voyager* during March 2016. Pelagic trawling (headline height 7 m) in an area of historic *D. labrax* catches resulted in the capture of a single specimen. The net was towed approximately 3–5 m off the seafloor at speeds ranging between 6·5 and 8·5 kmh−1 (*c*. 3·5–4·5 knots). Tow duration was between 20 and 40 min. Two further *D. labrax* were tagged and released in the eastern Celtic Sea during the annual Irish Groundfish Survey (IGFS) in November 2015. IGFS stations were fished during daylight hours to ensure standardization of results. At each survey station a 30 min trawl along the sea floor was conducted. The sampling gear used on the IGFS was the French grand overture verticale (GOV) net, designed to target species feeding on and above the seabed. The trawl headline height was 4·5 m and speed was maintained at *c*. 7·5 km h^{-1} (*c*. 4 knots) for the duration of the tow. The net spread was achieved through the use of Morgere FP 10 trawl doors mounted on either side of the net. Sensors were fitted to the net and trawl equipment to ensure that the net fished correctly (Marine Institute, 2012).

PSAT TAGGING PROCEDURE

Tagged fish were visually assessed for their suitability for tagging based on fish length and health status. The fish were placed in a holding tank–keep net to recover post-capture. A mixture of 2-phenoxyethanol and seawater (approximately 40 ml in 80 l of seawater) was used to induce anaesthesia. Once the fish had lost equilibrium and gill rhythm was slow but constant, it was placed in a trough lined with a sterile surgical drape. A dampened cloth was placed over the fish's head for sedation and a constant supply of seawater–anaesthetic mixture was passed over its gills. Fork length (L_F, cm) and mass measurements (g) were recorded. Mounting of the tag bridle was similar to the procedure described in Økland *et al.* (2013). The tag bridle was composed of two strips of hardened plastic (40 × 10 mm) with rubber backing plates, to prevent injury and irritation, connected *via* a braided section (75–100mm long) of marine-grade nylon. Medicated iodine solution was used to sterilize the area of needle insertion on the dorsal flanks. Two spinal cannulae needles (18G × 90 mm; BD; www.bd.com) were passed through the dorsal musculature of the *D. labrax* between the primary (spiny) and secondary (soft) dorsal fin. The exact site of needle insertion was identified by holding the backing plates in position and lining them up on either side of the dorsal flanks. Once inserted, the cannulae inserts were removed from the needles and a section of sterile 0·9 mm stainless steel wire was inserted into the needle hollows. The needles were then withdrawn, leaving the wire in place. The stainless steel wire was tightened by hand, with care taken not to overtighten. The bridle allowed for lateral movement of the tag while evenly distributing drag on the *D. labrax* (Fig. 1). The PSAT tag was then attached *via* a stainless steel clip to the marine-grade nylon section. The PSAT used in this study was the Desert Star Systems SeaTag-GEO (Desert Star Systems; www .desertstar.com) and was chosen due to its low weight (41·7 g in air) and its small float diameter (30 mm), making the lightest and streamlined PSATs available (Desert Star Systems, 2016).

Additional red and yellow Floy tags carrying an identification code in the form of "IRLXXXX" were inserted into the dorsal of each fish approximately 3-5cms in front of the PSAT bridle. Tagged specimens were then allowed to recover for up to 60 minutes prior to being released, once equilibrium and rhythmic gill movement had returned. Data for tagged sea bass is displayed in Table I.

The tagging and handlings procedures undertaken in this study were carried out under licence by the Health Products Regulatory Authority (Licence No.: AE19121/P001).

Fig. 1. *Dicentrarchus labrax* fitted with a Desert Star Systems SeaTag-GEO pop-up satellite tag (PSAT) and corresponding tag bridle with additional Floy tags for identification.

Table I. Pop-up satellite tag (PSAT) tagged sea bass *Dicentrarchus labrax* information and tag deployment dates

TAG ID	Capture method	Deployment date	Mass (g)	L_F (cm)	Mass ratio PSAT:fish (%)	Data successfully obtained?
148148	IGFS 2015	26/11/2015	3351	62.5	1.24	No
145137	IGFS 2015	26/11/2015	2696	56.5	1.55	Yes
145143	Inshore trawl	16/02/2016	2600	57	1.60	Yes
145142	Pelagic survey	17/03/2016	1295	46	3.22	Yes
145152	Seine netting	19/04/2016	3550	64	1.17	Yes
145141	Seine netting	19/04/2016	2360	52	1.77	No
145135	Seine netting	19/04/2016	2360	54	1.77	No
145144	Seine netting	19/04/2016	1960	53.5	2.13	Yes
145151	Seine netting	21/04/2016	2890	61	1.44	No
145149	Seine netting	21/04/2016	3730	66	1.12	No
145145	Seine netting	21/04/2016	3770	64	1.11	No
145146	Seine netting	20/04/2016	1920	51	2.17	No

L_F, fork length; IGFS, Irish Groundfish Survey.

TAG SPECIFICATIONS

Release dates and times for SeaTag-GEO PSAT detachment were user defined with offshore tagged *D. labrax* programmed to detach during the assumed peak spawning season (April to June) and inshore tagged *D. labrax* scheduled to detach in August–September, to identify potential inshore feeding and nursery site fidelity post-spawning migration. Detachment of the tag from the fish at the designated time is achieved *via* the detonation of a small charge of

Quikburst powder (www.quickburst.net), supplied by the tag manufacturer, in the nose-cone burn chamber of the tag.

The SeaTag-GEO was programmed to release from the fish if the temperature or light levels were below manufacturers pre-set thresholds for an extended period of time, which would indicate a dead or dying fish. To reduce the potential for biofouling on tag surfaces, tags were treated with a light coat of marine-grade varnish, as per the tag manufacturer's instructions. Once detached, the archived data were transmitted from the tag *via* the ARGOS satellite network. Data were transmitted in packets which contained daily summaries of recorded environmental data. In cases where PSATs were physically recovered however, more accurate tracks could be constructed from the higher resolution raw archived environmental data downloaded.

The data recorded by SeaTag-GEO tags included daylight length (resolution of ±2 s), time of noon (resolution of ±1 s); mean water temperature (resolution of ±0·002∘ C) and readings from a 3-axis internal magnetometer with a 60 nT reporting resolution which archived readings from the Earth's magnetosphere. Ambient seawater temperature readings were recorded from an inbuilt thermometer, while the corresponding satellite observed sea-surface temperatures were provided by Collecte Localisation Satellites (CLS) through the use of the ARGOS satellite network.

The level of light intensity was calculated as the time of noon, the point halfway between light levels rising above the threshold of 1·4 Lux in the morning and decreasing below 1·4 Lux in the evening. Tag accuracy for the calculation of longitude was to within ±0·5∘, equating to a distance of *c*. 55 km (30 nautical miles) at the equator. The degree of confidence in the longitude calculation varied with day length, with longer days having a higher degree of accuracy. Magnetic-field values typically increase with increasing distance from the equator, with the exception of areas of magnetic anomalies such as areas of volcanic rocks. In addition, tags in the vicinity of large metallic structures may report erroneous values due to compromised magnetic-field readings. Readings of magnetic-field intensity were recorded every 4 min and daily tag latitude was calculated using the mean of the 80% most closely correlated magnetic field values within the 24 h period to improve accuracy (Desert Star Systems, 2016). The predicted mean accuracy of this method is to within *c*. 72 km (39 nautical miles).

Daily minimum, maximum and average water temperatures were recorded by the PSATs. A total of three sea-surface temperature (SST) observations were used in aiding geolocation. Skin SST refers to satellite observed water temperatures in the upper few mm of water at the sea surface. Foundation SST corresponds to the temperature at an indeterminate depth where diurnal variations no longer affect daily temperatures. Between these two layers is the sub-skin SST where modelled values based on wind minimizing the temperature gradient between skin and foundation SST were calculated. Due to the assumed behaviour of the *D. labrax* swimming below the skin and sub-skin layers, foundation SST was used in this study, typically corresponding with the average daily temperatures recorded on the PSAT. A bias compensation between PSAT recorded temperature and foundation SST was conducted based on the ARGOS detected location of tag detachment.

Collecte Localisation Satellites (CLS; www.cls.fr) undertook Track+Loc processing of transmitted archived data to construct estimate migratory tracks. The aim of track construction was to estimate a daily location for each fish based on a combination of magnetic-field readings, light levels and water temperature data. This was achieved through the use of a space–state model which worked off the principle that the daily location is the unknown state of a dynamic system governed by a random-walk model. Therefore, the sequence of the daily state follows a Markovian process (Stehfest *et al.*, 2014) whereby the probability of a fish being at a location at a certain time-step is determined by its estimated location at the previous time-step. The probability of the current unknown location is then updated according to the current observation likelihood through the magnetic field, light intensity and water temperature data. The state–space model that was used to calculate geolocation operates using a grid filter dividing the map into a resolution of 0·1° × 0·1° grid cells. The grid filter (Neilsen *et al.*, 2014) is based on a recursive Bayesian estimation technique similar to Kalman filtering. The initial step of the model undertakes the solving of the advection–diffusion equation at each time-step to estimate the 2D probability of the animal's presence within the grids. The archived environmental data stored on each tag were then used to calculate and update position. The model assessed each of the environmental variable measurements (light intensity, magnetic field strength, water temperature) and then weighted them whereby the most reliable variable (the one with the least variance) was designated the greatest weight within the model. These combined steps were averaged over 24 h to estimate the daily geolocation of the fish. Tracks were constructed between daily estimated geolocations in chronological order using known opportunistic ARGOS transmitted locations (coordinates of tag deployment and detachment) as anchor points. The confidence intervals for daily locations were produced based on the semi-minor and semi-major error covariance matrix of the daily distribution.. Therefore, PSATs which transmitted a higher proportion of archived data resulted in a higher degree of accuracy regarding track estimation. A comprehensive description of method of track construction can be found in Biais *et al*. (2017).

RESULTS

TAG SUCCESS RATE

Twelve PSAT tags were deployed with all fish swimming away strongly post-tagging. Data were obtained for five tagged sea bass (41.6%). Of the tags which reported data, three were from *D. labrax* tagged in inshore Irish waters (145143, 145144 and 145152) and two were from specimens tagged offshore in the eastern Celtic Sea (145137 and 145142). In addition to the five tags which reported information, Tag 145148 was recovered and returned for analyses from the western coast of Britain but had recorded no data. Tag 145141 detached 1 day post-release and floated north to the southern coast of Scotland. Of the five tags which returned data, Tag 145137 was also recovered from the western coast of Britain and data were successfully downloaded. All other tags failed to communicate with the ARGOS satellite network. The detachment dates, transmitted by ARGOS, showed that of the five tags which transmitted data, three tags detached later than the user-defined settings, while the remaining two detached prior to their scheduled time (range of -96 to +76 days; mean = 62.6; S.D. = 28; Table II). Tag retention duration on specimens varied from 38 to 256 days (mean = 150.4, S.D. = 79.1). The percentage ratio of PSAT mass to fish body mass varied between 1.11% and 3.22% (S.D. = 0.58). There was no correlation between tag retention duration and specimen size (Pearson correlation = 0.239, $n = 6$, $P > 0.05$).

The number of messages received from each tag ranged between 35 and 1199 (mean = 295.8; S.D. = 452.3). Each message received contained a reading of the magnetic field strength, the time of noon, day duration (measured in seconds), observed water temperature and tag status information

Table II. Retention periods for pop-up satellite tags (PSAT) mounted to *Dicentrarchus labrax* successfully transmitting data

PSAT ID	Pre-defined detachment date	ARGOS transmitted detach date	Difference (+/- days)	No. of days of tag retention	No. of messages received	Period of data archiving	Estimated total tack length (km)	Estimated mean distance per day (km/day^{-1})	Estimated maximum linear distance from release location (km)
145137	27/05/2016	11/08/2016	+76	256	35	26/11/15 to 11/08/16	884	3.45	157
145142	26/06/2016	12/06/2016	-14	87	1199	17/03/16 to 12/06/16	674	7.7	89
145143	12/06/2016	28/07/2016	+52	163	123	16/02/16 to 28/07/16	923	5.56	321
145144	31/08/2016	27/05/2016	-96	38	59	19/04/16 to 27/05/16	484	12.7	211
145152	30/08/2016	13/11/2016	+75	208	63	19/04/16 to 13/11/16	1020	4.9	180

INTERPOLATED HORIZONTAL MOVEMENTS

Owing in part to the low numbers of data packets received from the PSATs, some tag tracks were found to have large (50 and 95%) confidence areas. Nonetheless, modelled tracks for inshore tagged specimens suggested periods of migration offshore, corresponding to previously observed spawning periods (Pickett & Pawson, 1994). Both offshore tagged specimens showed distinct track patterns. Fish 145137 [Fig. 2(a)] moved in a south-westerly direction during January and February, out of the Bristol Channel and into the open waters of the Celtic Sea. This fish then returned towards the Bristol Channel during March and April before moving up into the Irish Sea, crossing St. Georges Channel during May, to approach the west coast of Wales. The specimen was then estimated to have changed direction, moving south during June to August, before the late detachment of the tag (76 days beyond the user-defined detachment date) while the fish was off the south-west Welsh coastline. The mean distance day−1, based on the estimated track, covered by this *D. labrax* was 3·74 km day−1 which was the slowest mean daily rate of movement recorded during this study.

Sufficient data from fish 145142 were received to produce an accurate track with a relatively low degree of error [Fig. 2, (b)]. This fish, tagged and released in March 2016, travelled in an anti-clockwise loop in the Bristol Channel before travelling in a south-westerly direction into the eastern Celtic Sea during April and May. The specimen then changed direction, heading south–south-east and approached the north coast of Cornwall, U.K. where it remained, most probably in inshore waters, during May and June prior to tag release (which occurred 14 days before the pre-defined detachment date). While fish 145142 was estimated to have travelled approximately 647 km, the maximum linear distance that this fish travelled from its release site was estimated to be 89 km.

The estimated tracks for the specimens released from the inshore site had large associated areas when bound by 50 and 95% confidence estimates. Data for fish 145144 [Fig. 2(d)] and

145152

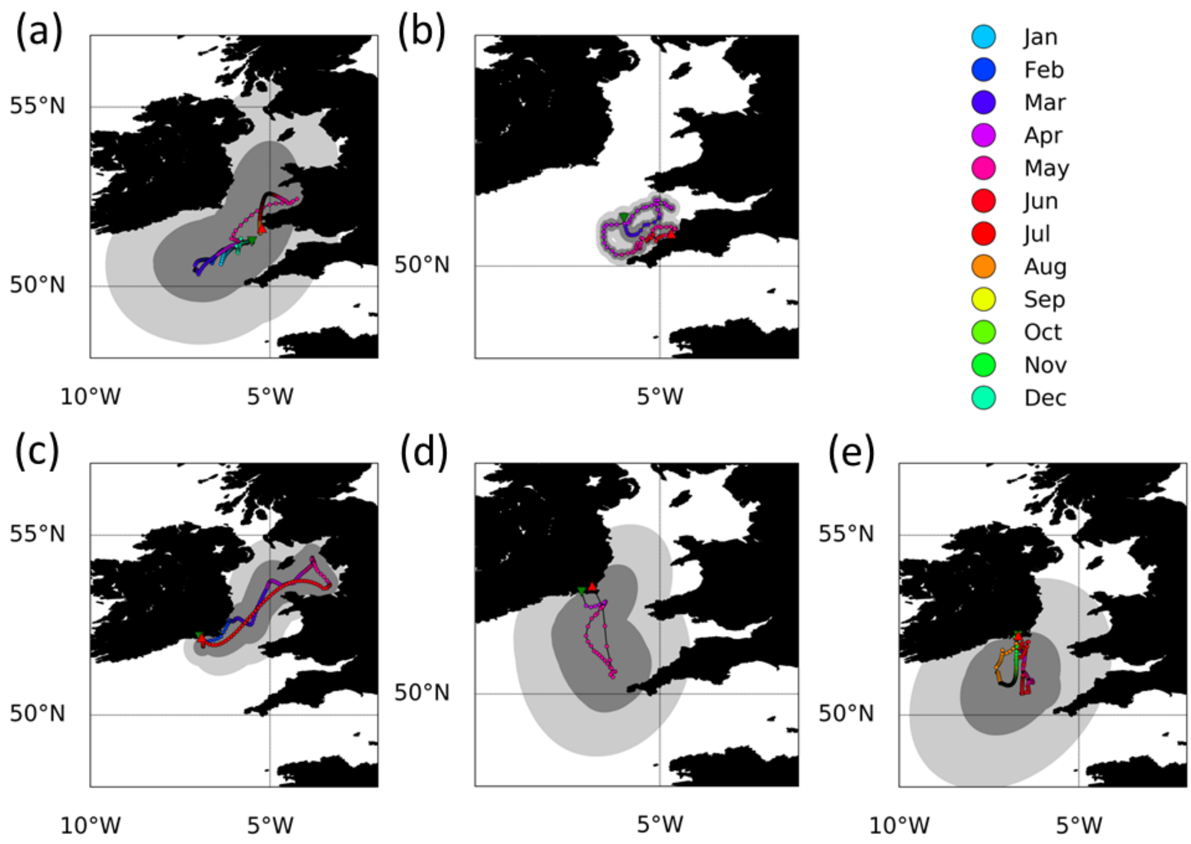

Fig. 2. Interpolated migration tracks of fish GEO pop-up satellite tag (PSAT) numbers (a) 145137, (b) 145142, (c) 145143, (d) 145144 and (e) 145152. ▼, initial release location; ▲, location of tag detachment. Confidence intervals on location data: ■, 50%; ■, 95%.

[Fig. 2(e)] suggest that they both migrated offshore during the assumed peak spawning period (May), returning towards inshore waters during the same month. The tag for fish 145144 detached prematurely (96 days before the pre-defined detachment date), 38 days post release on 27 May 2016.

Fish 145144 was estimated to have had the highest mean rate of movement, travelling 12·7 km day^{-1} on average based on the estimated track length. Fish 145152 retained its tag until the 13 November 2016, a tag retention period of 208 days (75 days after the user-defined release date).

This fish moved north towards the southern Irish coast during June, towards its release location. This fish migrated south into offshore waters during August, before travelling north towards its tagging location during November. It also recorded the highest estimated track length at 1020 km while travelling approximately 180 km linear distance from its release location.

The interpolated tracks of fish 145144 and 145152 display similar characteristics relating to migration direction and timing, showing that they travelled to within *c*. 40 km of each other at the southernmost point of their migrations, returning to the same approximate area of coastline afterwards. When taking the offshore tagged fish (145137 and 145142) into account also, it was found the tracks of all four *D. labrax* were within 240 km2 of each other within the eastern Celtic Sea during the mid-April to mid-May period.

In contrast to the estimated tracks from the other *D. labrax* released from inshore waters, data obtained from fish 145143, tagged and released approximately 20 km to the west of both fish 145144 and 145152, showed the *D. labrax* travelling within Irish inshore waters in February and March, migrating around Carnsore Point (south-easternmost point of the Irish mainland) and heading north into the Irish Sea along the eastern Irish coast [Fig. 2(c)]. This specimen then moved offshore and travelled in a north-easterly direction, crossing the Irish Sea and passing to the south of the Isle of Man during the months of April–May, travelling an estimated linear distance of 321 km from its release location. This *D. labrax* subsequently returned to the southern Irish coast again during June, after which the PSAT detached, having been retained for 163 days (52 days beyond the pre-defined tag detachment setting).

WATER TEMPERATURE

Tag-recorded temperatures were used in conjunction with foundation SST to further refine geo-location. Due to the different deployment times of the PSAT tags and the failure of some tags to record and transmit data, the results for temperature data are widely dispersed, though the majority of data recorded were for the assumed period associated with peak spawning in April, May and June with a mean of 28·3 temperature recordings for each of these months (Table III). The month with the warmest mean water temperature recorded by the tags was August 2016 (18·0∘ C) though these data were based on a low number of recordings (*n*=7) from a single *D. labrax*. The month with the lowest mean temperature recorded was February (7·6∘ C), which was also found to have the most variable water temperatures (S.D.±1·39). When mean daily tag-recorded temperature readings were restricted to the assumed peak spawning period (April–June), it was found that water temperature ranged between 7·3∘ C to 18·0∘ C. The mean daily water temperature did not fall below the 8·5∘ C threshold after 11 April 2016.

Low water temperatures (6·5∘ C) were recorded by fish 145143 [Fig. 3(c)] in February during the initial days post-release when the specimen was estimated to still be at the inshore location in which it was released. The tag recorded water temperature values remained between 6·3 and 7·9∘ C during the time that this fish was in Irish inshore waters (February–mid-March) and did not increase above 8·5∘ C until mid-April, when the specimen appeared to be travelling in a north-westerly direction across the Irish Sea. Data for fish 145137 [Fig. 3(a)] and 145142 [Fig. 3(b)] show close correlation between tag-recorded temperature data and satellite observed sea surface temperature (SST), though there were large gaps in temperature data for the fish 145137. Tag recorded water temperature was higher than satellite SST in all but one reading for fish 145144 [Fig. 3(d)]. All specimens, with the exception of fish 145152 [Fig. 3(e)], showed an increase in water temperatures from March onwards. There was significantly higher tag recorded temperatures compared with satellite observed SST values found in fish 145137 (paired *t*-test, t_{19} = 5·68, P < 0·001), 145144 (paired t-test, t_{20} = 8·54, P < 0·001) and 145152 (paired *t*-test, t_{43} = 9·7, P < 0·001) while no significant differences were observed in fish 145142 (paired *t*-test, t_{80} = 0·38, P > 0·05) and 145143 (paired *t*-test, t_{66} = −0·79, P > 0·05).

Table III. Mean monthly water temperatures recorded by *Dicentrarchus labrax* specimens tagged with pop-up satellite tags (PSAT)

Date		**No. of temperature recordings**	**Temperature (°C; mean ± S.D.)**
2015	November	1	14.4 ± 0
	December	5	12.14 ± 0.08
2016	January	1	11.3 ± 0
	February	13	7.6 ± 1.39
	March	25	8.4 ± 0.78
	April	29	9.4 ± 0.87
	May	31	12.3 ± 1.10
	June	17	15.2 ± 1.22
	July	9	15.9 ± 1.24
	August	7	17.0 ± 1.12

DISCUSSION

This study presents the application of pop-off satellite tags on *D. labrax* for migration studies. Acknowledging the low sample size and the degree of uncertainty in respect of track estimation, these results indicate that the use of PSATs as a tool for tracking *D. labrax* in oceanic waters provides a clearer understanding of annual migrations. The timing of the offshore tracks obtained coincided with the assumed peak spawning period between April and June, while the distances undertaken indicate extensive migration to offshore waters during this time. Increasing the number of successful tracks should allow for a more positive identification of putative spawning aggregation areas in the Celtic Sea.

To date, there have been few studies in which small fish species (<100 cm) have been tagged with PSATs (Graves *et al.*, 2009; Lacroix, 2013; Amilhat *et al.*, 2016; Rodgveller *et al.*, 2017). The SeaTag-GEO PSAT, used in this study, has also previously been used on sable-fish *Anoplopoma fimbria* (Pallas 1814), a similar sized fish to *D. labrax*, where a tag reporting rate of 47 to 58% (Echave, 2016) was similar to that recorded here. While Graves *et al.* (2009) reported the successful transmission of data from nine out of 10 PSATs mounted to striped bass *Morone saxatilis* (Walbaum 1792), the retention period for these tags was only 30 days. Though *D. labrax* are a robust species, capable of tolerating low salinities and a wide range of temperatures (Pickett & Pawson, 1994), the effect on swimming speed and the resulting fatigue from bearing an externally attached tag could be significant. Such effects have been observed previously in other species such as Atlantic cod *Gadus morhua* L. 1758 and European plaice *Pleuronectes platessa* L. 1758 (Arnold & Holford, 1978; Jepsen *et al.*, 2015 respectively) though a previous study on adult Atlantic salmon *Salmo salar* L. 1758 found no difference in swimming endurance with small or large external tags attached (Bridger & Booth, 2003). The minimal float diameter and weight of the SeaTag-GEO PSAT however, may have limited the

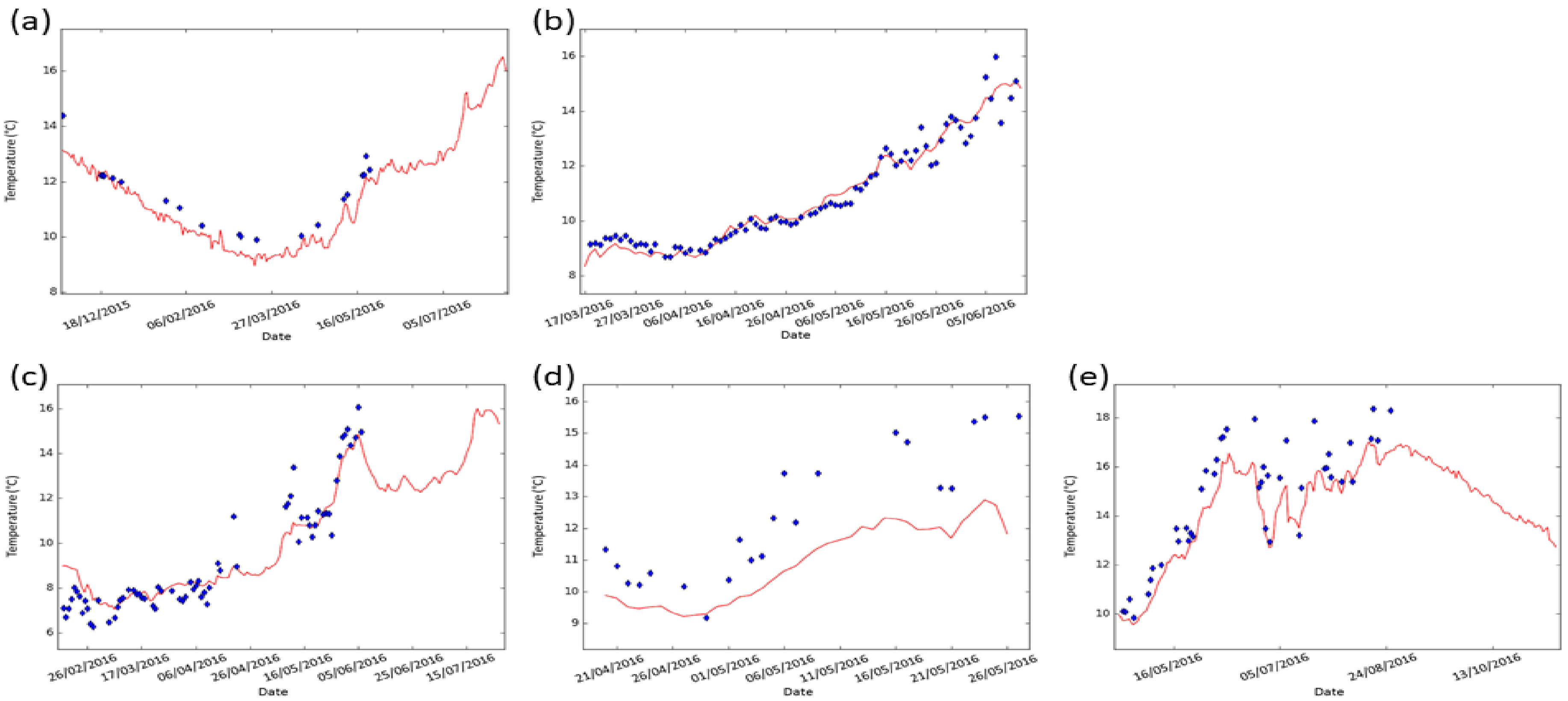

Fig. 3. Tag recorded temperature (♦) and satellite observed (______) sea-surface temperatures for corresponding positions of tag numbers (a) 145137, (b) 145142, (c) 145143, (d) 145144 and (e) 145152

drag effect of the externally mounted tag (Desert Star Systems, 2016). The considerable distances and mean daily rate of movements recorded in the *D. labrax* in this study however, suggest that the presence of the PSAT did not adversely affect the migratory ability of the tagged specimens. A similar conclusion was also reached by Hedger *et al.* (2016) who fitted PSATs to Atlantic salmon *Salmo salar* L. 1758, noting however that PSAT tagged specimens did display reduced diving behaviour and a smaller increase in body mass than other salmon that had been tagged with internal DST and acoustic tags.

While the comparative size of PSATs may appear too large for small fish species, the successful tagging of *S. salar* kelts as small as 52 cm with PSATs by LaCroix (2013) shows that smaller fishes are capable of accommodating these tags. Additionally, previous studies on *S. salar* (Thorstad *et al.*, 2000), chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Gray & Haynes, 1979) and lemon sharks *Negaprion brevirostris* (Poey 1868) (Sundström & Gruber, 2002) have also found that the attachment of a large external biotelemetry tags to the fish did not result in any appreciable effects on the swimming endurance of the specimens. The effects of PSAT hydrodynamic drag, tag mass in water, likeliness of fouling and method of tag attachment may now be more important to the suitability of fish for PSAT tagging than the physical burden of having to carry the tag itself, often referred to as the 2% rule, where the mass of the tag in air should not be more than 2% of the mass of the fish (Smircich & Kelly, 2014). Traditionally, PSATs were used predominately on large pelagic or elasmobranch species where this ratio was not a concern due to the large body mass of the tagged specimens.

A number of factors may be attributable to the observed reporting rate of the PSATs in this study. While the failure of the PSAT hardware or software may have resulted in the failure of some tags to report, such conclusions are difficult to substantiate. Physical damage to tags may have prevented archived data from being successfully transmitted from non-reporting tags (Hays *et al.*, 2007; Abascal *et al.*, 2016). It may also be possible that some tags had become trapped underwater or retained by commercial fishers and therefore unable to transmit data (Bridger & Booth, 2003; Hays *et al.,* 2007; Jepsen *et al.,* 2015). User error may also have resulted in the burn chamber, storing the powder to allow the detachment of the tag from the fish, becoming infiltrated with water, thus preventing release of the tag from the bridle system. User error in the tag configuration process may also have resulted in some tags not being correctly set up to record data when deployed, potentially explaining the lack of data on the recovered tag 145148. Design flaws with the bridle system itself may also have contributed towards the low reporting level of the PSATs with an angler in the south-east of Ireland reporting the recapture of specimen 145151 after 435 days post-release with the fish showing no evidence of the PSAT bridle, suggesting that the bridle system may need to be re-examined and optimized for use in future research.

Although all fish appeared to swim away strongly post-release, it is not known the extent to which fitting a PSAT to a *D. labrax* effects subsequent survival and performance. The catching of specimens for tagging, whether through seine net, commercial trawl or angling and the subsequent handling of the fish by taggers, could have contributed to physiological stress responses such as build-up of lactic acid. The additional handling and tagging process might further exacerbate these physiological responses, thereby increasing negative effects on fish health after the post-release period, as has been observed previously for PSAT tagged white marlin *Negaprion brevirostris* (Poey 1860) (Horodysky & Graves, 2004). Additionally, the small incisions for the mounting of the PSAT bridle (Echave, 2016) may also be another source of post-tagging infection. Despite these potential risks, it does appear that *D. labrax* are capable of swimming long distances and for a considerable time while carrying these externally mounted tags.

The 50 and 95% confidence areas associated with track estimations for tags 145137, 145143, 145144 and 145152 may be due to the presence of magnetic anomalies within the study area, thus affecting data collected by the tags magnetometers. Typically, the geolocation of PSATs temporally and spatially is calculated based on archived luminosity and temperature data. The addition of a magnetometer within the SeaTag-GEO should therefore have resulted in a more accurate track prediction. However, a line of iron-rich rock bodies, stretching from the southern coast of Co.Wexford, Ireland to the northern Anglesey coast in Wales, U.K. (Wonik *et al.*, 2001), in addition to the presence of sunken shipwrecks in the vicinity of the release area, particularly for inshore tagged specimens (Brady *et al.*, 2012), may have reduced the effectiveness of the magnetometer thereby reducing estimated track accuracy (Desert Star Systems, 2016). The future use of PSATs on fish likely to migrate within this specified area should take these factors into account, perhaps employing the use of light and temperature only based tags for geolocation as a potentially more reliable alternative.

The estimated tracks of fish tagged in inshore Irish waters (fish 145144 and 145152) suggest behaviour which may be indicative of a spawning migration, with both specimens having been present in the eastern Celtic Sea during the peak spawning period (April to June) before returning towards the southern Irish coast. This finding also suggests that they originated from Irish inshore nurseries and or feeding areas, displaying post-migration site fidelity to the inshore areas where they had been originally released. Evidence of the return migration to relatively discrete inshore locations on an annual basis by adult *D. labrax* has been noted in tag–recapture studies, with some *D. labrax* being recaptured yearly at the same location (Pawson *et al.*, 2007). Owing to the scale of accuracy of the PSATs, it is not possible to be certain that the fish tagged in inshore waters returned to the estuaries in which they were released, though track output does suggest that these fish returned to within *c*. 73 km of the inshore tagging locations. Similarly, the offshore tagged specimens (145137 and 145142), which had been present in the same region in the Celtic Sea as the two aforementioned inshore tagged fish, subsequently migrated eastwards towards inshore areas on the western British coast. As these fish were captured at sea, it is not known whether they originated from a coastal nursery or feeding area on the western coast of the Britain. However, their migration to coastal locations after the presumed spawning period might suggest this (Kelley, 1979; Pawson *et al.*, 1987). Despite the geographically distinct areas where the fish were tagged and released, the interpolated data provided by the PSATs suggest that they may have migrated to the same approximate area in eastern Celtic Sea during the spawning season (Fig. 4).

While it is unlikely that any of these four *D. labrax* migrated south into the Western Approaches or English Channel, preliminary results from *D. labrax* tagged with DSTs in inshore British waters has revealed migration of *D. labrax* from the English Channel into the eastern Celtic Sea, though research is still ongoing (CEFAS, pers. comm.). The interconnectivity between spawning aggregations within these separate areas is unknown, though there is some suggestion that *D. labrax* from the western coast of Britain do enter the English Channel (Kelley, 1979; Pawson *et al.*, 1987).

Fish 145143, tagged in inshore Irish waters on the south Irish coast, appears to have undertaken a substantially different migration to the other tagged specimens in this study. Kelley (1979) reported northward migration of adult *D. labrax* on the west coast of Britain during summer periods (April–September) after having migrated south during winter periods (October–March). Annual demersal-trawl surveys undertaken by the Agri-Food and Biosciences Institute of Northern Ireland (AFBINI) have identified the presence of *D. labrax* at offshore locations in the northern region of the Irish Sea during November, when it is assumed that adult fish are in a pre-spawning stage (Pawson & Pickett, 1996). The migration of this PSAT tagged specimen to the north-west English coast, entering Liverpool Bay before returning to Ireland would be consistent with this. In addition, a Floy tagged specimen released in inshore waters on the south-east coast of Ireland as part of this study in April 2016, was also recovered by an angler in the north-west coast of Britain (Morecambe Bay).

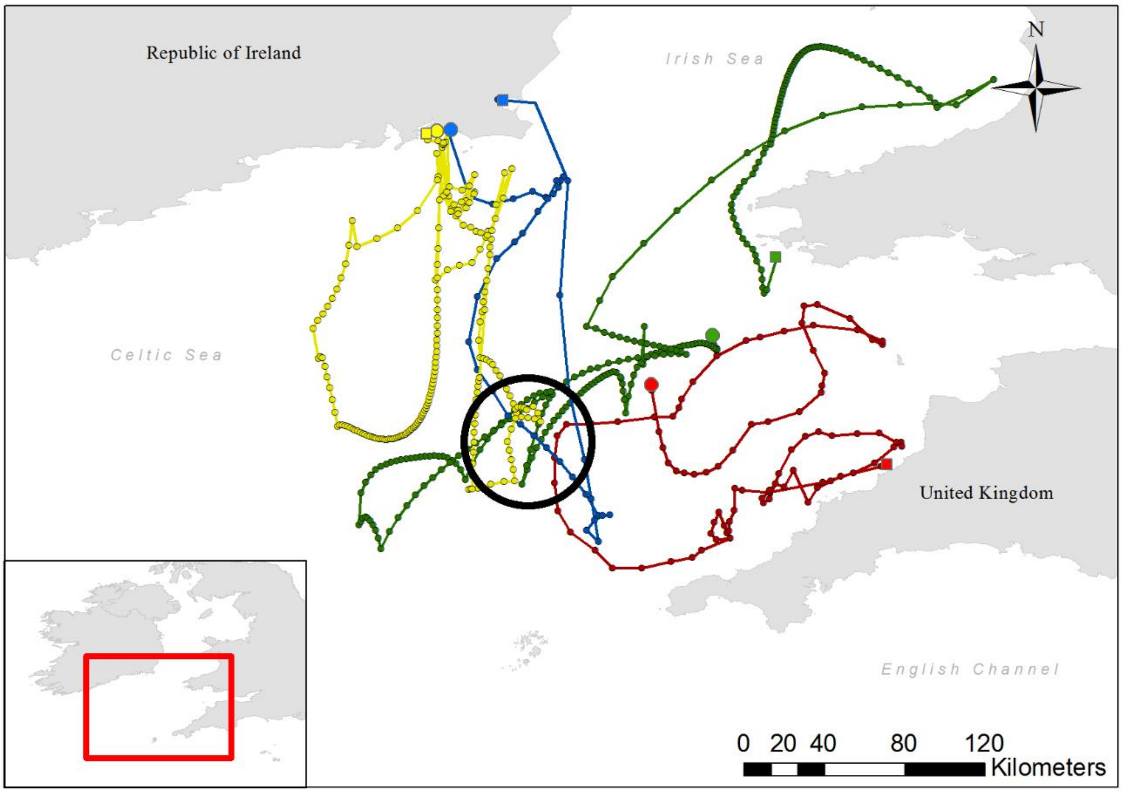

Fig. 4. Interpolated tracks from fish 145137 (______), 145142 (______), 145144 (______) and 145152 (______) showed evidence of an area of possible interaction (O) in the eastern Celtic Sea between April and June. ●,●,●,●, release locations; ■,■,■,■, location of tag detachment.

These migrations are believed to be linked to reproductive behaviour, which has a strong correlation with ambient water temperatures above 8·5∘ C (Pickett & Pawson, 1994). Pawson & Pickett (1996) also suggested that *D. labrax* which remain in warmer offshore waters throughout the winter experience a growth advantage compared with those that stay in shallower, cooler inshore or more northerly waters.

Water temperatures above an 8·5∘ C threshold are believed to be required for *D. labrax* spawning and larval survival (Thompson & Harrop, 1987). Based on mean temperatures recorded by the PSATs in this study, spawning could have occurred anytime from mid-April onwards. The temperature data recorded with the track of fish 145143 is consistent with the southwards–winter and northwards–summer migration pattern. No significant difference was found between tag recorded and satellite observed SST for fishes 142142 and 145143 and this coincides with the high number of packets transmitted for both fish. This finding illustrates the need to have sufficient temperature data to accurately construct migratory routes retrospectively. However, the findings of this study do show that the use of PSATs is a viable method of analysing the correlation of migration duration, timing and potential location of spawning grounds. The primary advantage of this method is that data acquisition can be achieved without the need for physical recovery of the tag. This is an important consideration given the likelihood of negligible recoveries from other tagging methods as a mean of investigating migration. Tracking information is of high importance to fishery managers to ensure effective management of the stock on a short to medium term but also for modelling the potential effects that climate change may have on *D. labrax* distribution and migration in the long term.

Acoustic tagging of *D. labrax* in inshore Irish waters has been used to describe the presence and absence of *D. labrax* from inshore locations on an annual basis (Doyle *et al.,* 2017). However, beyond the coastal region, the movements and behaviours of *D. labrax* in Irish waters remain relatively poorly understood. The findings of this study show that as a method of biotelemetry, the application of PSATs on *D. labrax* will generate tracks of migration and that these can be of long duration and over an extended geographic area. However, this study has revealed a number of specific issues. Selection of tags measuring appropriate variables for the locations where the fish are likely to occur is essential and consideration of possible anomalies such as geomagnetic features which might affect accuracy of geolocation. Additionally, the behaviour and size of the tagged species must be taken into account, with *D. labrax* being a relatively small-sized candidate for PSATs while also spending considerable time swimming and foraging in areas such as weed beds, reefs and wrecks where chances of tag loss may be high (Bridger & Booth, 2003).

The sexually mature adult *D. labrax* tagged in Irish waters migrated from the southern Irish coast to the eastern Celtic Sea and north-west Irish Sea during the assumed peak spawning season between April and June. The extent to which this reflects *D. labrax* populations in general would require further PSAT tracking information. The relationship between the extent of migration, annual variation, water temperature and prey availability could also be inferred from additional interpolated migration tracks. Given the limited number of informative tracks in this study, further tracking research is required to substantiate whether there is an aggregation of *D. labrax* in the eastern Celtic Sea at any time, though particularly during the assumed peak spawning period. However, given the information provided by PSATs and more extensive studies on marine mega fauna and fish species, expansion of PSAT studies will allow for significant advancements in the understanding of the interconnectivity and movements of *D. labrax* in different regions in Europe and potential confirmation of spawning locations and their extent. These data could also provide an insight into the potential effects of climate change, with annual tagging programmes helping to identify potential shifts in the location and duration of migrations with respect to changing environmental conditions.

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