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Winter residency and site association in the Critically Endangered North East Atlantic spurdog *Squalus acanthias*

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ABSTRACT: Identification and incorporation of residential behaviour into elasmobranch management plans has the potential to substantially increase their effectiveness by identifying sites where marine protected areas might be used to help conserve species with high migratory potential. There is evidence that the spurdog *Squalus acanthias* displays site association in some parts of its global distribution, but this has currently not been shown within the North East Atlantic where it is Critically Endangered. Here we investigated the movements of electronically tagged spurdog within Loch Etive, a sea loch on the west coast of Scotland. Archival data storage tags (DSTs) that recorded depth and temperature revealed that 2 mature female spurdog overwintered within the loch, restricting their movements to the upper basin, and remaining either in the loch or the local vicinity for the rest of the year. This finding was supported by evidence for limited movements from conventional mark–recapture data and from an acoustically tagged individual spurdog. Some of the movements between the loch basins appear to be associated with breeding and parturition events. This high level of site association suggests that spatial protection of the loch would aid the conservation of different age and sex classes of spurdog.

KEY WORDS: Archival tag · Conservation · Migration · Spatial ecology · Residency · Marine protected areas · Spiny dogfish · Loch Etive

INTRODUCTION

Marine protected areas (MPAs) are increasingly used as part of the management strategy to conserve marine biodiversity (Edgar et al. 2007). While there is evidence that MPAs aid the conservation of benthic species (Rogers-Bennett et al. 2002) and may increase fish stocks (Pitchford et al. 2007), their efficacy in the management of migratory species is unclear (Hilborn et al. 2004). While it has been suggested that MPAs should not be used to manage migratory marine species from a fisheries point of view (Botsford et al. 2003), there is emerging evidence that small-scale spatial management may indeed benefit some species (Moland et al. 2013, Rogers et al. 2014).

Many species of elasmobranch are highly mobile (Templeman 1976, Gauld 1982, Grubbs et al. 2007, Gore et al. 2008, Mucientes et al. 2009) and display complex temporal and spatial movement patterns (Hyrenbach et al. 2000). However, site association is being increasingly recognised for many elasmobranchs, often associated with critical habitats and important life history stages. Because of this, MPAs are now considered a key management tool to aid elasmobranch conservation (Stevens 2002, Barker & Schluessel 2005, Heupel & Simpfendorfer 2005), being particularly effective for species that display site association behaviour permanently, seasonally or for part of their life cycle (Bonfil 1999, Garla et al. 2006, Neat et al. 2014). The most common associations dis-

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played by elasmobranchs are either female natal philopatry, where adult females return to their original pupping/nursery areas to parturate (Pratt & Carrier 2001, Feldheim et al. 2002, Jorgensen et al. 2010), or the residency of juveniles within nursery areas (Heupel & Hueter 2001, Feldheim et al. 2002, Garla et al. 2006, Grubbs et al. 2007). The identification of these areas and behaviours should be a priority for the management of elasmobranchs because they provide an opportunity to effectively use MPAs in order to protect critical life history stages within a population. MPAs designed on the basis of such behaviours would only protect specific life stages, and it has been suggested that to effectively conserve elasmobranch populations, it is important to protect all age classes (Bonfil 1999, Kinney & Simpfendorfer 2009). There are examples where area protection can potentially protect most life history stages of an elasmobranch population, e.g. the common skate (Neat et al. 2014). These cases highlight that effective management relies on suitable prior knowledge on the movement behaviour of the different life stages within a species.

Spurdog *Squalus acanthias* are distributed worldwide throughout temperate continental shelf seas (Camhi et al. 2009). They are a slow-growing, late-maturing species, reaching a global maximum size of around 160 cm (Campagno 1984), but only 120 cm in the NE Atlantic (Hammond & Ellis 2005). This species has low fecundity and a gestation period of up to 24 mo (Ellis et al. 2008). These K-strategy life history traits, along with this species' high susceptibility to fishing gear (McCully et al. 2013) and tendency to segregate into sub-populations based on age and sex (Alonso et al. 2002), mean that spurdog are considered highly vulnerable to overfishing (Ellis et al. 2008). This vulnerability has been demonstrated in the NE Atlantic, where spurdog biomass has declined by 95 % (Fordham et al. 2006) due to commercial fishing since the 1930s (Vince 1991). Spatial management of the remaining NE Atlantic population is hampered because spurdog are generally considered a highly mobile species (Templeman 1976, 1984, Gauld & Macdonald 1982, McFarlane & King 2003), and this population is thought to be a single, large, stock unit, undertaking large-scale seasonal movements (Aasen 1964, Gauld & Macdonald 1982, Vince 1991).

The spatial ecology of spurdog in the NE Atlantic has mostly been informed by mark and recapture studies in offshore areas (Aasen 1964, Holden 1965, Hjertenes 1980, Gauld & Macdonald 1982, Vince 1991). It has been suggested that the UK stock of spurdog is split into northern and southern populations, between which little mixing occurs (Holden 1965, 1967). A more recent study has disputed this suggestion (Vince 1991), indicating a single large migratory stock of spurdog within the UK, with a high national dispersal of juvenile and maturing animals. On this basis, the NE Atlantic population of spurdog is assessed as one stock (Pawson & Ellis 2005). Females appear to aggregate in the eastern Celtic Sea in order to parturate during winter and spring (Pawson 1995). Annual cyclic migrations have been shown, with the regional population on the east coast of the UK making an annual north–south migration (Hjertenes 1980, Gauld & Macdonald 1982). Sex-specific movements have also been shown in the UK, with mature males making return migrations between southwestern and northeastern areas annually (Vince 1991).

Movements in coastal waters around the UK are largely unknown, although research on other populations has shown that some subunits within a spurdog population do not undertake large migrations, but rather maintain a level of site association, often within large (several 100 km^2) coastal areas (Templeman 1984, Ketchen 1986, McFarlane & King 2003, Campana et al. 2009, Carlson et al. 2014). Site association has been shown for both immature spurdog of both sexes and mature males in Newfoundland waters (Templeman 1984, Campana et al. 2009), and for mature spurdog on the eastern coast of the US (Carlson et al. 2014) and the coastal waters of British Columbia (McFarlane & King 2003). In all regions, sub-populations appear to limit their home range to the coastal shelf and partially enclosed water bodies. On the other hand, offshore units appear to be highly migratory (Ketchen 1986, McFarlane & King 2003), with some spurdog undertaking trans-Atlantic (Templeman 1976) and trans-Pacific (McFarlane & King 2003) migrations. It has been suggested that migrations may be related to reproductive cycles, with breeding individuals moving offshore to large breeding aggregations, while non-breeding spurdog display more localised movements (Carlson et al. 2014).

Here we report findings of an archival data storage tagging (DST) study focusing on the movement of coastal spurdog tagged within a Scottish sea loch (Loch Etive, Fig. 1), with particular emphasis on site association. Loch Etive, a partially enclosed water body on the west coast of Scotland, was chosen as a site due to the existence of a local ongoing angler-led tagging programme. Data from the conventional mark–recapture study and an active acoustic monitoring study were used to support the findings from the DSTs.

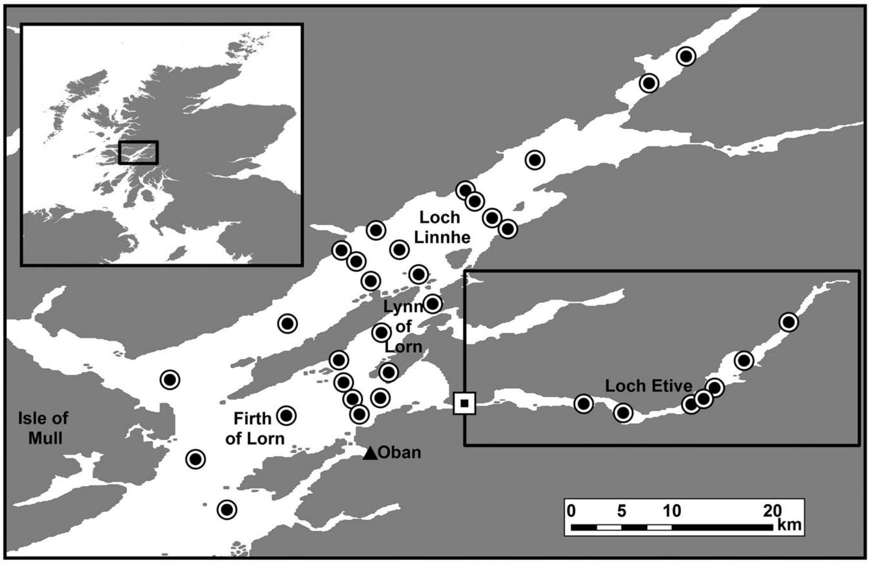

Fig. 1. Study area on the west coast of Scotland. Loch Etive is shown by a black frame in the main figure. Black circles denote the location of environmental monitoring stations recording temperature at depth profiles throughout Loch Etive, the Firth of Lorn, the Lynn of Lorn and Loch Linnhe. The black and white square denotes the continuous temperature recording stations at the mouth of Loch Etive

MATERIALS AND METHODS

Study site

Loch Etive is situated on the Scottish west coast (see Fig. 1). This sea loch is approximately 30 km long and has a mean width of 2 km. It is separated into 2 basins, an upper (inland) basin with a maximum depth of 145 m, and an outer (seaward) basin with a maximum depth of 70 m; these basins are separated by a 13 m sill. A second sill, approximately 5 m deep, separates the lower basin from the ocean (Hsieh et al. 2013; Fig. 2). This bathymetric profile affects water flow within the loch, causing a tidal water fall (the Falls of Lora) at the mouth of Loch Etive with a peak flow rate of 8 knots (Wilding et al. 2005), and deep water stagnation in the upper basin (Edwards & Edelsten 1977). Loch Etive opens into the water system of the Firth of Lorn, Loch Linnhe and the Lynn of Lorne; for simplicity, this area will be referred to as the Firth of Lorn throughout the rest of the text.

Acoustic monitoring stations

Two VEMCO hydrophone recorders (VR2W 69kHz, Vemco-Amirix Systems) were installed on 20 October 2010 in Loch Etive, before tagging spurdog with acoustic tags (see the section on tagging below). The receiver units were each moored approximately 5 m above the substrate, ballasted with 15 kg weight and with a small buoy placed 2 m above them on the mooring line to hold them upright. The mooring line from each unit went to the surface where it was marked with 2 surface marker buoys. Seabed depth was 10 m (Stn A) and 17 m (Stn B) (Fig. 2) below chart datum. An unattached reference transmitter was used to test the range of the installed recording units at seabed level, mid-water and at the surface during tidal flow and slack water to ensure that they covered the width

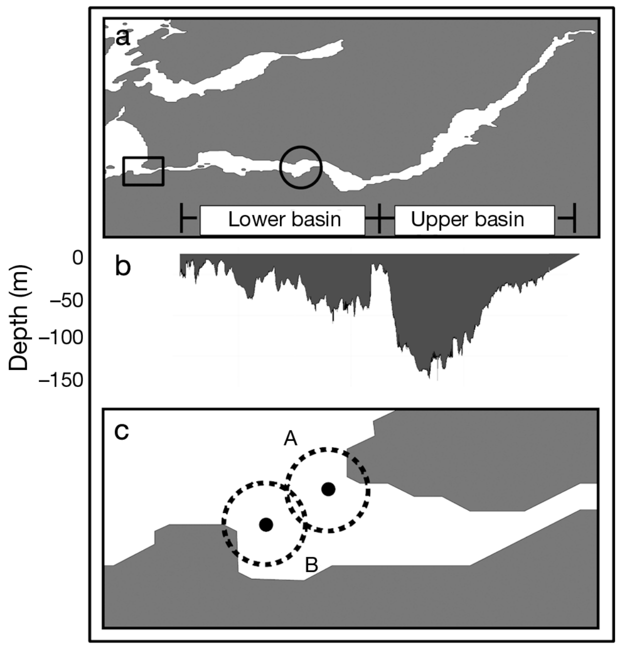

Fig. 2. (a) Upper and lower basins of Loch Etive, Scotland. Black rectangle indicates acoustic receiver unit deployment site (shown in c), and black circle shows the tagging site (for both acoustic and data storage tags). (b) Bathymetric profile. (c) Tagging and acoustic receiver unit deployment sites (acoustic stations A and B); minimum detection range is shown by black dashed line (minimum range recorded in flow tidal state)

of the entrance. Minimum range of each receiver was during tidal flow when it was reduced to approximately 150 m. Recorders were placed so that ranges overlapped (Fig. 2). The receivers were retrieved after 1 yr of deployment on 4 December 2011 and the data downloaded via the built-in Bluetooth connection.

Tagging

All spurdog were caught using individual baited hook and line in Loch Etive (Fig. 1).

Data storage tags (DSTs). Ten spurdog were tagged and measured on 25 and 26 October 2010 (8 females and 2 males). Pre-started tags (Star Oddi centi-TD) were fitted externally, anchored through the base of the dorsal fin using 2 stainless steel pins permitting easy removal. Each tag was marked with a specific ID number and set to record depth and temperature every 5 (n = 5) or 10 (n = 5) min. Spurdog were released at their capture site within Loch Etive. Tags were marked with contact details and notice of a £50 reward for return. All restricted tagging procedures were carried out under a personal licence authorised by the UK Home Office.

Mark–recapture. Tag and release data were collected by the Scottish Shark Tagging Programme (SSTP) from 2007 to 2013. During this time, 164 spurdog were opportunistically tagged and released by volunteer anglers in Loch Etive and the Firth of Lorn (Fig. 1). Floy dart tags were inserted into the dorsal musculature at the base of the first dorsal fin. Total length (TL: snout to the tip of the terminal dorsal lobe on the tail fin, in cm), girth (around the central thorax, in front of the first dorsal fin and behind the pectoral fins, in cm), sex and weight (kg) were recorded. Recaptures were opportunistically reported by anglers.

Acoustic. Twelve spurdog were tagged on 25 and 26 October 2010 (7 females, 5 males). Once landed, health was assessed by checking for visual wounds, surface parasite load or any malformations. Two spurdog were rejected due to heavy parasite load and large skin lesions. Healthy spurdog were placed in an anaesthetising tank dosed with MS-222 anaesthetic (1 g in 10 l). Once anaesthetised, the spurdog were weighed and then placed with their ventral surface exposed in a grooved work bench. Total length and girth were measured (as described in the mark–recapture methods). A small slit, approximately 1 cm long, was made along the ventral surface in the abdominal wall approximately halfway between the pectoral and anal fins. A pre-started transmitter tag (VEMCO V13) was inserted into the peritoneal cavity through the opening which was then closed with monofilament suture through the muscle and skin layer. Once the procedure was complete, the spurdog were placed in a recovery tank of clean seawater until they started moving. They were then placed over the side of the vessel and held head into current to force ventilate until they were able to swim. All spurdog were released at their capture point within Loch Etive (Fig. 2).

Data analysis

DSTs. Standard methods of geolocation include the use of tidal cycles (Metcalfe & Arnold 1997, Hunter et al. 2003) and/or a combination of light and sea surface temperature (Sims et al. 2003, Teo et al. 2004). Due to the large vertical range displayed by the spurdog and the lack of light records, it was not possible to implement these methods on data from this study. In order to determine whether tagged spurdog were present in Loch Etive, temperatures recorded by the tags were compared against environmental temperatures. Environmental temperature data for the time period of tag deployment for the area were made available from several separate studies: (1) Loch Etive mouth continual monitoring, whereby 2 static temperature loggers at 10 m depth at the mouth of Loch Etive run by the Scottish Association of Marine Science (SAMS) continually recorded temperature every 12 min; (2) temperature at depth profiles for Loch Etive, provided by 2 studies running in Loch Etive by Hsieh et al. (2013) and Friedrich et al. (2014); and (3) temperature at depth profiles, recorded by Marine Scotland in the Firth of Lorn in December 2010, March 2011, both partial coverage, and May 2011, full coverage (Fig. 1 shows the full area covered by recording stations). Comparisons between temperature at depth profiles from the tags and environmental values were made using a mean squared error (MSE) process, fully described in Appendix 1, to determine how closely spurdog records matched water temperatures (see Fig. 6 and corresponding Table 2 for an example). A 2-round filtering process (Appendix 1) using MSE values was used to place the spurdog in 1 of 3 areas, the upper or lower basins of Loch Etive, or the Firth of Lorn (see Fig. 5). The boundary for each area was designated as the shallow water sill that physically separates the 2 basins and the adjoining oceanic water body (Fig. 2).

For those months when no environmental temperature at depth data were available, environmental temperature data from constant depth recorders at the mouth of Loch Etive (11 m) were compared against tag temperatures from the same depth range (9–13 m, allowing for tidal variation) to place the spurdog inside or outside this area (see Fig. 4).

Mark–recapture data. Limited recapture data prevented statistical analysis, but presence of males and females each month was looked at as well as size class of each sex throughout the year. Movements between initial mark event and subsequent recapture event were also investigated.

Acoustic tags. Data from hydrophones were used to show when tagged spurdog were within receiving range (date and time). Presence times were matched against local tidal data for Loch Etive to see whether first and last detections (i.e. the spurdog entering and leaving the hydrophones' range) coincided with the loch's flood and ebb states of tide.

RESULTS

Data storage tags

In total, 3 of the 10 spurdog tagged with DSTs were recaptured, all within Loch Etive. One tag was retrieved after only 7 d of deployment; data from this tag were not used in further analysis. The remaining 2 tags (numbers 5159 and 5162) were recovered after a full year (Table 1), although due to memory constraints both had data only between 26 October 2010 and 25 August 2011 (303 d). The size of both females was compatible with early-stage maturity. Both spurdog showed a move to deeper water in February, returning to shallower water in April (Fig. 3), although maximum depths recorded by all returned tags were within the depth range of Loch Etive.

Both tags recorded temperature ranges between 6.3 and 15.2°C, with most recordings being between 10 and 11°C (Fig. 3); they were present at depths between 0 and 150 m throughout the year. Spurdog 5162 showed less temperature variation than 5159, especially between October and April; the depth profile mirrors this, with 5162 showing less vertical movement than 5159.

Table 1. Spurdog *Squalus acanthias* recaptured within Loch Etive from both the Scottish Shark Tagging Programme's mark–recapture programme and the data storage tag (DST) study in this project. All individuals were female. Data in **bold** relate to fish tagged with DSTs. Recapture data (other than location) are missing for fish 5935. TL: total length. Dates are given as dd/mm/yyyy

Tag. no.	Tagging date	Recapture date	Weight (kg)	TL (cm) at tagging	Days at liberty
368	15/11/2009	13/11/2010	1.9	76	363
1542	14/11/2009	04/12/2009	2.5	81	20
1806	05/09/2010	29/05/2011	2.6	84	266
1809	04/04/2010	21/11/2010	4.3	–	231
1816	05/09/2010	28/01/2012	4.3	100	510
2004	10/07/2010	25/09/2010	4.2		77
5162	**26/10/2010**	**08/11/2011**	**2.36**	**82.5**	**378**
5935	14/01/2012	–	–	–	–
5159	**26/10/2010**	**16/10/2011**	**2.7**	**71**	**355**
7288	21/06/2011	08/01/2012	5.2	102	201
27926	05/07/2008	09/11/2009	6.8	–	492
27987	17/01/2009	01/05/2009	4.5	–	104
27996	09/02/2008	23/10/2010	3.2	79	987
7424	04/08/2012	02/12/2012	4.1	91	120
5171	**26/10/2010**	**02/11/2010**	**1.34**	**64**	**7**

Tag temperature compared to water temperature at the mouth of Loch Etive

From deployment until early December, temperatures recorded at 9–13 m by tag 5159 (hereafter referred to as 'tag temperatures') were all within the temperature range of Loch Etive (Fig. 4). From 6 December 2010 until 27 January 2011, many tag temperatures were outside the range of the mouth of Loch Etive. Throughout February and March, there were only sporadic tag temperatures within the same depth range as the temperature loggers at the mouth of Loch Etive (9–13 m). The few tag temperatures recorded in April were all below the temperature range of Loch Etive until 21 April 2011; at this point, tag temperatures increased into the range of the loch. For the rest of the tag record (end date 25 August 2011), temperatures recorded by the tag at 9–13 m were mostly within the temperature range of the mouth of Loch Etive.

From deployment until the end of November, there were very few temperatures from 5162 at the necessary depth for comparison with the fixed temperature loggers. From the end of November until the beginning of January, tag temperatures were similar to the temperature range at the mouth of Loch Etive. From the beginning of January until April, there were very few tag temperature records between 9 and 13 m depth. From 25 April 2011 onward, tag temperatures were back in the range of the mouth of Loch Etive, and remained there for the rest of the record (until 25 August 2011).

Comparison of temperature depth profiles

Filtered MSE values (Fig. 5) show that spurdog 5159 made extensive use of the lower basin of

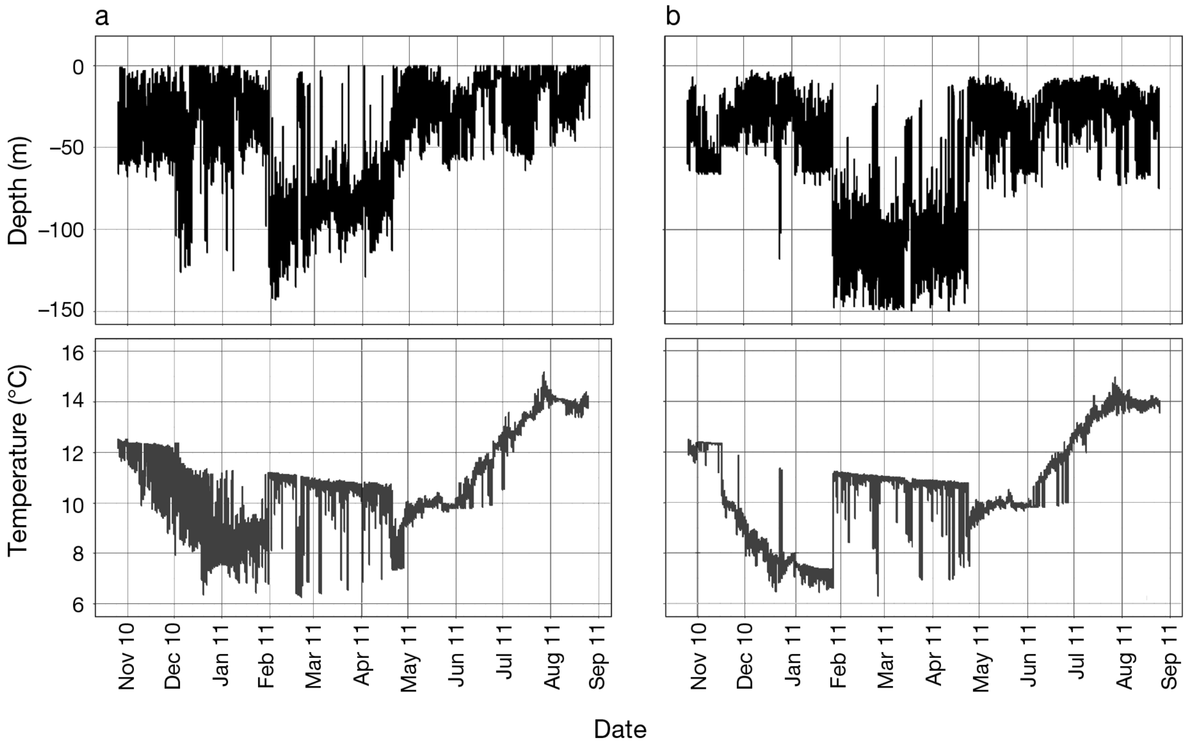

Fig. 3. Separate depth and temperature plots from data recorded by spurdog *Squalus acanthias* data storage tags (a) 5159 and (b) 5162 between 25–26 October 2010 (deployment) and 25 August 2011; each variable was recorded at 5 min intervals

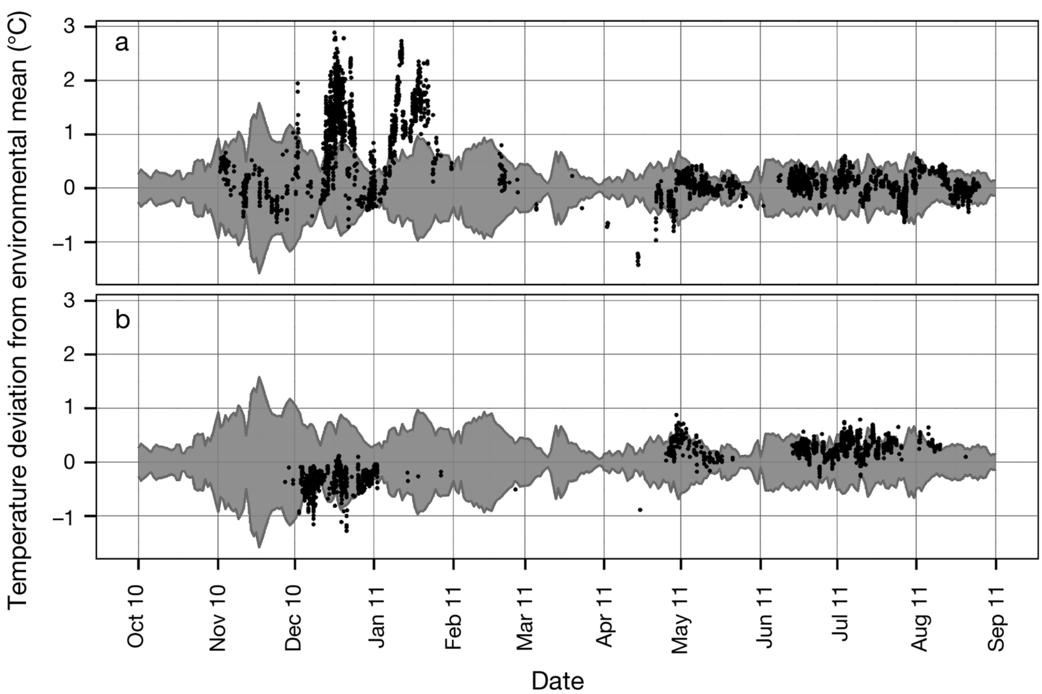

Fig. 4. Deviation of spurdog *Squalus acanthias* tag temperature data from the mean environmental temperature at the mouth of Loch Etive. The grey ribbon in each panel shows the environmental temperature variation around the mean temperature between 9 and 13 m depth. Black points show the deviation of spurdog (a) 5159 and (b) 5162 tag data within the same depth range from the environmental mean

Loch Etive throughout November with just 3 consecutive days spent in the Firth of Lorn. During December, 5159 started to make use of the upper basin, splitting its time equally between upper and lower basins after starting the month in the Firth of Lorn. In the first half of January, 5159 travelled between all 3 areas before moving to the upper basin on 13 January, where it remained exclusively for the rest of the month and all of February and March. In April, the spurdog remained in the upper basin until 21 April, when it moved through the lower basin over 7 d and out into the Firth of Lorn on 29 April (Figs. 5 & 6, Table 2). For much of May, 5159 remained in the Firth of Lorn, with occasional use of the lower basin. In June it made equal use of the Firth of Lorn and the lower Loch Etive basin.

Spurdog 5162 was present in the lower basin in November before moving to the Firth of Lorn on 16 November (Fig. 5). On 5 December, it moved back into the lower basin, where it spent most of the month with occasional use of the upper basin on 24 and 25 December. During January, spurdog 5162 remained in the lower basin until 28 January, when it moved into the upper basin. Area use was restricted exclusively to the upper basin over February and March. It remained in the upper basin until 24 April, when it moved into the lower basin for 1 d before moving into the Firth of Lorn on 26 April (Figs. 5 & 6, Table 2). During May, 5162 remained mostly in the Firth of Lorn, with occasional use of the lower basin over 4 individual days.

Over June, July and August, it was impossible to place the spurdog in one of the 3 habitats, as there were no temperature depth profiles for this time period. However, the temperatures recorded by both tags between 9 and 13 m depth were within the temperature range recorded at the mouth of Loch Etive, suggesting that both tags remained in the vicinity. MSE values from day to day tag temperatures suggest that both 5159 and 5162 did not use the upper basin over June, July or August.

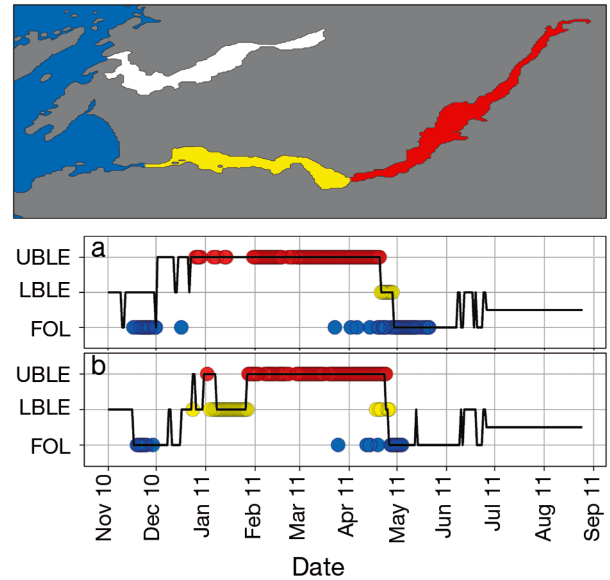

Fig. 5. Presence of spurdog *Squalus acanthias* (a) 5159 and (b) 5162 in the upper basin of Loch Etive (UBLE, red), the lower basin of Loch Etive (LBLE, yellow) or the Firth of Lorn (FOL, blue). Presence is based on the mean squared error values between environmental temperature at depth records and spurdog temperature values at a corresponding depth after the first filtering process (coloured points) and second round filtering (thick black line) as described in Appendix 1. Where the line runs between 2 areas there is a 50/50 chance that the spurdog was in either

Mark–recapture

A total of 164 spurdog were tagged in Loch Etive (31 males: mean length = 73.8 cm, range 51–110 cm; 133 females: mean length = 84.5 cm, range 78–110 cm;

Table 2. Mean squared error values corresponding to comparisons between spurdog *Squalus acanthias* tag and environmental temperature at depth data after the first round of filtering as described in Appendix 1. These data are visualised in Fig. 6. Dates are given as dd/mm/yyyy. NAs refer to 24 h periods when no environmental temperature data were available to compare to tag temperatures

Date	Tag no. 5159			Tag no. 5162		
	Upper basin	Lower basin	Firth of Lorn	Upper basin	Lower basin	Firth of Lorn
20/04/2011	0.0412	1.9406	0.0663	0.0013	0.0028	NA
21/04/2011	0.7557	0.1611	0.6400	0.0089	0.0891	0.4544
24/04/2011	0.7352	0.0521	0.2079	0.1928	0.2238	1.2700
25/04/2011	0.8765	0.0693	0.3011	1.7812	NA	NA
28/04/2011	0.9525	0.0953	0.3041	2.5649	0.9554	0.0145
29/04/2011	1.6262	1.3310	0.0170	3.2681	0.8462	0.0305

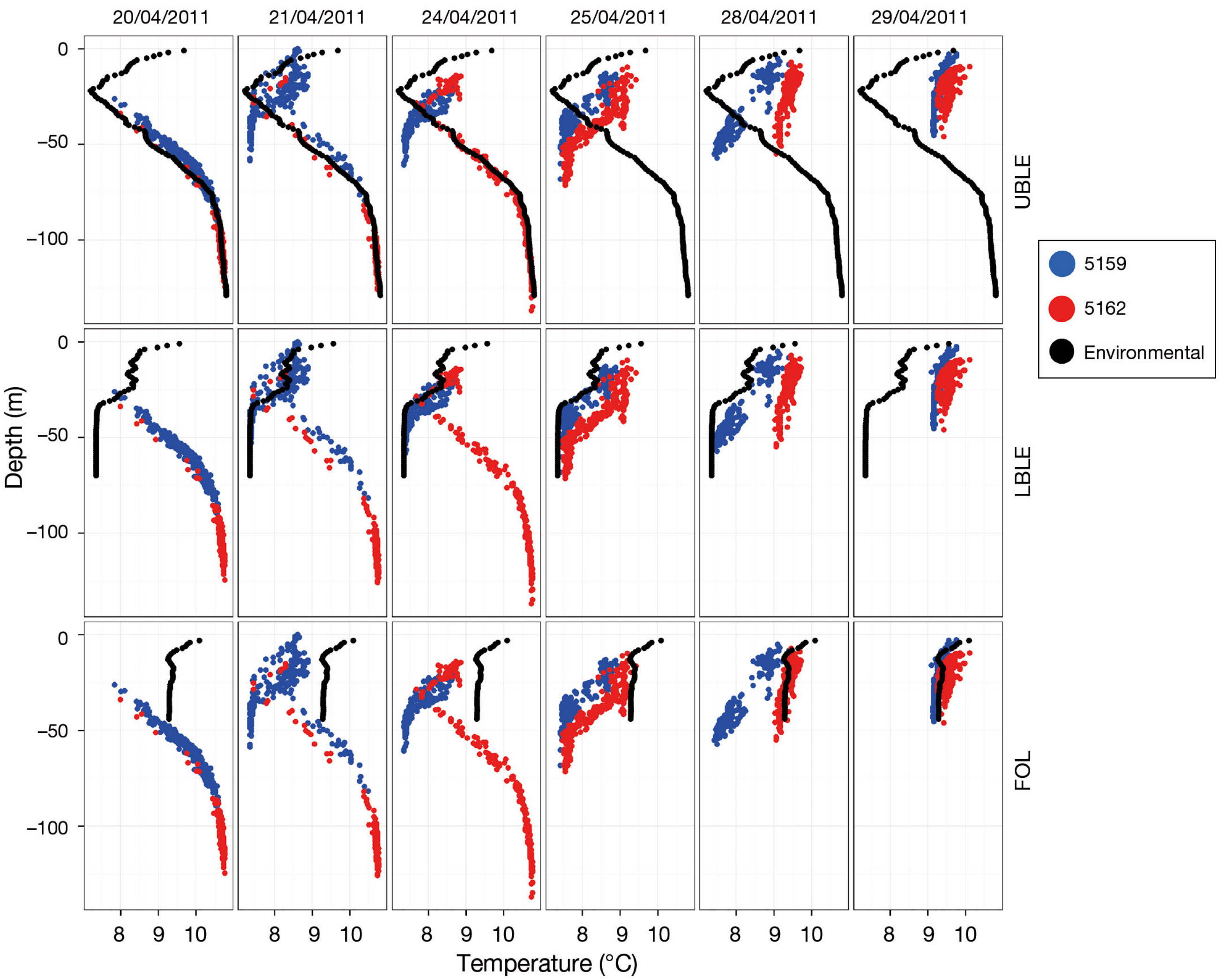

Fig. 6. Temperature at depth data from both spurdog *Squalus acanthias* tags plotted against environmental data from the upper basin (UBLE) the lower basin (LBLE) of Loch Etive and the Firth of Lorn (FOL), Scotland. Spurdog 5159 is represented by blue points, 5162 by red points and environmental temperature by black points. Data are shown from the event in April where both spurdog exited the upper basin after nearly 3 mo of residency, moved through the lower loch and exited into the Firth of Lorn. Table 2 shows corresponding mean squared error values for each day per tag

Fig. 7). Females were caught in the loch every month of the year, while males were caught in lower numbers throughout the year except in April, June and August, when no males were recorded. There were 15 recaptures (8% of total number), all of which were females (10.5% of total females tagged; Table 1). Thirteen recaptures were made in Loch Etive, 11 of which were originally tagged within the loch, and 2 in the adjoining water body, the Firth of the Lorn, less than 1 km away. Two spurdog tagged at this location in the Firth of Lorn were subsequently recaptured in Loch Etive. Recapture data were unsuitable for standard mark–recapture analysis due to insufficient numbers of recaptures (n = 15) and the large uncertainty in sampling effort.

Acoustic tags

Data were only recorded for one female (66.5 cm long and weighing 1.34 kg). She was recorded by the receiver at Stn A over 3 consecutive days from 5 to 7 November 2010, then again for 2 consecutive days from 10 to 11 November 2010. The same individual was also recorded by the same receiver for 26 min on 2 April 2011.

DISCUSSION

By combining the data from the DSTs with environmental temperature at depth data, we were able

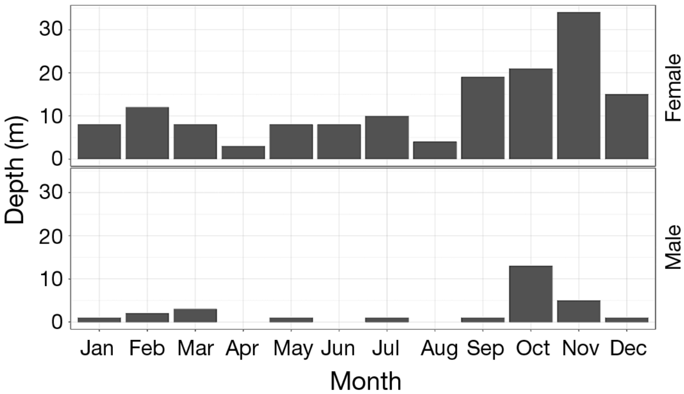

Fig. 7. Spurdog *Squalus acanthias* count per month in Loch Etive, Scotland, split into females and males from the mark and recapture study

define the movements between the upper and lower basin of Loch Etive and the Firth of Lorn. From this, we could see that 2 small mature females remained either in Loch Etive or the local area over a 10 mo period. This is highly suggestive of a residential component of spurdog in Loch Etive. The exclusive use of the upper basin over winter, an area of approximately 17 km^2, by both females is particularly unusual due to the small size of the area that both spurdog used exclusively for almost 3 mo.

Residential behaviour is previously unrecorded in NE Atlantic spurdog, traditionally thought to be highly migratory, and undertaking large-scale migrations as shown by previous tagging studies (Hjertenes 1980, Vince 1991, Henderson et al. 2002). Spurdog populations in other coastal regions do fragment into residential and migratory components (Ketchen 1986, McFarlane & King 2003, Campana et al. 2009, Carlson et al. 2014). 'Residency' in these studies usually refers to spurdog that remain on the continental shelf (Carlson et al. 2014) and do not cross national boundaries (i.e. Campana et al. 2009). There are some cases where residential units of spurdog are associated with partially enclosed water bodies, such as the Strait of Georgia in British Columbia (McFarlane & King 2003). This area, 6800 km^2, is significantly larger than Loch Etive (30 km^2), highlighting Loch Etive as a unique case of site residency in spurdog.

The timing of both female spurdog (tags 5159 and 5162) exiting the upper basin to move through the lower basin and out into the Firth of Lorn in April is separated by only 5 d, which suggests they are responding to either a biological or an environmental cue. Drivers behind spurdog migrations are generally thought to be related to either breeding cycles (Hanchet 1988, Henderson et al. 2002, Carlson et al. 2014) or environmental variables (Garrison 2000, Shepherd et al. 2002). Temperature has been shown to affect the dispersal of spurdog (Shepherd et al. 2002) and in the NW Atlantic is thought to cue their annual offshore/inshore migrations, when falling coastal water temperatures trigger a move to offshore habitats (Garrison 2000). The move into the deeper water of the upper basin during falling temperatures in the lower basin suggests that the spurdog were seeking out a habitat with preferred temperatures. The stagnation of water in the upper basin produces a different thermal environment to that of surrounding water bodies (Edwards & Edelsten 1977), creating a thermal niche spurdog may utilise over winter. The movement out of the upper basin corresponds to warming recorded by the monitoring station at the mouth of the loch. Both spurdog spent only a few days in the cooler waters of the lower basin before moving to the warmer waters of the Firth of Lorn.

These observations suggest thermal considerations may play an important role in the movement of spurdog within the Loch Etive area as both spurdog appeared to move in order to remain in a temperature range of 10–11°C where possible, similar to temperature preferences shown for spurdog in other regions (Shepherd et al. 2002) in the NW Atlantic. The Strait of Georgia, like Loch Etive, has a series of silled basins which causes water stagnation (Johannessen et al. 2014). The temperatures in these basins remain warmer than surface waters during winter months (Masson & Cummins 2007), creating a potential thermal refuge. This suggests that temperature may be a significant driver in spurdog migration, and areas that provide suitable thermal environments year round promote residential behaviour.

Spurdog in the NE Atlantic parturate offshore (Pawson 1995), suggesting that offshore migrations may occur in response to breeding cycles. Extrapolating from this, residential behaviour displayed by some adult spurdog may be related to non-breeding individuals, while breeding individuals migrate offshore (Carlson et al. 2014). This would imply that resident mature spurdog in Loch Etive are non-breeding; however, there is evidence of parturition and breeding in this area. During October/November 2010 and 2011, small spurdog (19–30 cm TL) with clearly visible throat scars from the attached yolk sac were observed in the loch, suggesting a maximum age of approximately 8 wk (Castro 1993, Sulikowski et al. 2012). Other signs of breeding were also observed in Loch Etive during April 2011, when mature males with swollen red claspers (Heupel et al. 1999) and females with a swollen red cloaca were both present.

The timing of these events coincides with movements in and out of the loch in November and April shown by both DSTs and are supported by the acoustic data. This suggests that some spurdog in Loch Etive move between the 3 areas in response to their reproductive cycle, and it is not solely non-breeding individuals that remain resident in the area.

It is unlikely that Loch Etive harbours an isolated population of spurdog, as the comparatively low numbers of males recorded by the mark recapture programme suggest they move into the area to breed. In other areas where residency is thought to occur, tagging shows some individuals moving from the residential area to other regions (McFarlane & King 2003), suggesting that these areas are not isolated. Low numbers of large mature females in the loch also suggest they only make sporadic use of the area, most likely in relation to their reproductive cycle, using the loch to breed and parturate. The presence of neonates suggests that Loch Etive is used as a nursery area, although it is unusual for mature individuals to remain in nursery areas (Heupel & Hueter 2001, Grubbs et al. 2007). Mark and recapture data suggest that there are small mature spurdog of both sexes in Loch Etive all year round. This does not discount Loch Etive as a potential nursery, as some species of smaller shark use depth distribution to spatially segregate size classes (Bres 1993). This may be the case in Loch Etive, with fish of different sizes separated vertically throughout the water column, potentially reducing cannibalism, which has been recorded in this species (Stenberg 2005). Vertical distribution could also reflect a difference in diet; smaller spurdog are pelagic predators, but after maturity their diet shifts to more demersal and benthic prey (Alonso et al. 2002). The lack of tagging data on juvenile spurdog means their movements between the Loch and Firth of Lorn are largely unknown.

In conclusion, this study has shown that spurdog of all sex and age classes utilise Loch Etive, with some adults exhibiting residential behaviour. This implies that spatial management of the loch would benefit all age and sex classes, creating an ideal situation for an effective MPA (Bonfil 1999). This is proposed with a certain amount of caution as the evidence for this is currently from a relatively small sample size and, ideally, more work in this area on this species is required to clarify wider population movements. This study highlights that, in some cases, area protection as part of a larger management plan may benefit some traditionally highly migratory species, provided sufficient research is undertaken to show strong site association to small geographic areas.

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LITERATURE CITED

Aasen O (1964) The exploitation of the spiny dogfish (*Squalus acanthias* L.) in European waters. Fiskeridir Skr Ser Havunders 13:5–16

Alonso MK, Crespo EA, García NA, Pedraza SN, Mariotti PA, Mora NJ (2002) Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environ Biol Fish 63:193–202

Barker MJ, Schluessel V (2005) Managing global shark fisheries: suggestions for prioritizing management strategies. Aquat Conserv 15:325–347

Bonfil R (1999) Marine protected areas as a shark fisheries management tool. In: Seret B, Sire JY (eds) Proceedings of the 5th Indo-Pacific fish conference, Noumea, New Caledonia, 3–8 November 1997. Societe Francaise d'Ichtyologie, Paris and Institut de Recherche pour le Developpement, Paris, p 217–230

Botsford LW, Micheli F, Hastings A (2003) Principles for the design of marine reserves. Ecol Appl 13:25–31

Bres M (1993) The behaviour of sharks. Rev Fish Biol Fish 3: 133–159

Camhi M, Valenti S, Fordham S, Fowler S, Gibson C (eds) (2009) The conservation status of pelagic sharks and rays. Report of the IUCN Shark Specialist Group pelagic shark red list workshop. IUCN Species Survival Commission Shark Specialist Group, Newbury

Campagno LJV (1984) FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. FAO Fish Synop 125:1–249

Campana S, Joyce W, Kulka DW (2009) Growth and reproduction of spiny dogfish off the eastern coast of Canada, including inference on stock structure. In: Galluci VF, McFarlane GA, Bargmann GG (eds) Biology and management of dogfish sharks. American Fisheries Society, Bethesda, MD, p 195–208

Carlson AE, Hoffmayer ER, Tribuzio CA, Sulikowski JA (2014) The use of satellite tags to redefine movement patterns of spiny dogfish (*Squalus acanthias*) along the U.S. East Coast: implications for fisheries management. PLoS ONE 9:e103384

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the south-eastern coast of the United States. Environ Biol Fish 38:37–48

Edgar GJ, Russ GR, Babcock RC (2007) Marine protected areas. In: Connell S, Gillanders BM (eds) Marine ecology. Oxford University Press, Oxford, p 533–555

Edwards A, Edelsten DJ (1977) Deep water renewal of Loch Etive: a three basin Scottish fjord. Estuar Coast Mar Sci 5: 575–595

Ellis JR, Clarke MW, Cortés E, Heessen HJL, Apostolaki P, Carlson JK, Kulka DW (2008) Management of elasmobranch fisheries in the North Atlantic. In: Payne A, Cotter J, Potter T (eds) Advances in fisheries science: 50 years on from Beverton and Holt. Blackwell, Oxford, p 184–228

Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. Proc R Soc Lond B Biol Sci 269:1655–1661

Fordham SFS, Coelho R, Goldman KJ, Francis M (2006) *Squalus acanthias*. IUCN Red List of Threatened 450 Species. Version 2011.1. www.iucnredlist.org (accessed 07/10/2012)

Friedrich J, Janssen F, Aleynik D, Bange HW and others (2014) Investigating hypoxia in aquatic environments: diverse approaches to addressing a complex phenomenon. Biogeosciences 11:1215–1259

Garla RC, Chapman DD, Wetherbee BM, Shivji M (2006) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. Mar Biol 149:189–199

Garrison LP (2000) Spatial and dietary overlap in the Georges Bank groundfish community. Can J Fish Aquat Sci 57:1679–1691

Gauld JA (1982) The dogfish — an ocean rover. Scott Fish Bull 47:13–16

Gauld JA, Macdonald WS (1982) The results of tagging experiments on spurdogs, *Squalus acanthias* L., around Scotland. ICES CM Doc 1982/H:51. International Council for the Exploration of the Sea, Copenhagen

Gore MA, Rowat D, Hall J, Gell FR, Ormond RF (2008) Transatlantic migration and deep mid-ocean diving by basking shark. Biol Lett 4:395–398

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50: 87–107

Hammond T, Ellis J (2005) Bayesian assessment of Northeast Atlantic spurdog using a stock production model, with prior for intrinsic population growth rate set by demographic methods. J Northwest Atl Fish Sci 35: 299–308

Hanchet S (1988) Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. NZ J Mar Freshw Res 22:537–549

Henderson AC, Flannery K, Dunne J (2002) Growth and reproduction in spiny dogfish *Squalus acanthias* L. (Elasmobranchii: Squalidae), from the west coast of Ireland. Sarsia 87:350–361

Heupel MR, Whittier JM, Bennett MB (1999) Plasma steroid hormone profiles and reproductive biology of the epaulette shark, *Hemiscyllium ocellatum*. J Exp Zool 284: 586–594

Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Sibert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fishes. Kluwer Academic, Dordrecht, p 217–236

Heupel MR, Simpfendorfer CA (2005) Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. Mar Technol Soc J 39:10–18

Hilborn R, Stokes K, Maguire JJ, Smith T and others (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47:197–205

Hjertenes PO (1980) The spurdogs in the North Sea area in the Norwegian fishery and observations on changes in migration pattern. ICES CM Doc 1980/H:60. International Council for the Exploration of the Sea, Copenhagen

Holden MJ (1965) The stocks of spurdogs (*Squalus acanthias* L.) in British waters and their migrations. Fish Invest Ser 2 Vol 24(4). Ministry of Agriculture, Fisheries and Food, London

Holden MJ (1967) Spurdogs. Laboratory Leaflet. New Series. Ministry of Agriculture, Fisheries and Food Fisheries Laboratory, Lowestoft

Hsieh YT, Geibert W, Van-Beek P, Stahl H, Aleynik D, Henderson GM (2013) Using the radium quartet (Ra-228, Ra-226, Ra-224, and Ra-223) to estimate water mixing and radium inputs in Loch Etive, Scotland. Limnol Oceanogr 58:1089–1102

Hunter E, Aldridge JN, Metcalfe JD, Arnold GP (2003) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. Mar Biol 142:601–609

Hyrenbach KD, Forney KA, Dayton PK (2000) Marine protected areas and ocean basin management. Aquat Conserv 10:437–458

Johannessen SC, Masson D, Macdonald RW (2014) Oxygen in the deep Strait of Georgia, 1951–2009: the roles of mixing, deep-water renewal, and remineralization of organic carbon. Limnol Oceanogr 59:211–222

Jorgensen SJ, Reeb CA, Chapple TK, Anderson S and others (2010) Philopatry and migration of Pacific white sharks. Proc R Soc Lond B Biol Sci 277:679–688

Ketchen KS (1986) The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. Can Spec Publ Fish Aquat Sci 88:1–78

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53–60

Masson D, Cummins PF (2007) Temperature trends and interannual variability in the Strait of Georgia, British Columbia. Cont Shelf Res 27:634–649

McCully SR, Scott F, Ellis JR, Pilling GM (2013) Productivity and susceptibility analysis: application and suitability for data poor assessment of elasmobranchs in northern European seas. Collect Vol Sci Pap ICCAT 69:1679–1698

McFarlane GA, King JR (2003) Migration patterns of spiny dogfish in the North Pacific Ocean — *Squalus acanthias*. Fish Bull 101:358–367

Metcalfe JD, Arnold GP (1997) Tracking fish with electronic tags. Nature 387:665–666

Moland E, Olsen EM, Knutsen H, Garrigou P and others (2013) Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. Proc R Soc Lond B Biol Sci 280:20122679

Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. Biol Lett 5:156–159

Neat F, Pinto C, Burrett I, Cowie L and others (2014) Site fidelity, survival and conservation options for the threatened flapper skate (*Dipturus cf. intermedia*). Aquat Conserv (in press) doi:10.1002/aqc.2472

Pawson MG (ed) (1995) Biogeographical identification of English Channel fish and shellfish stocks. Fish Res Tech Rep 99. Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, Lowestoft

Pawson MG, Ellis JR (2005) Stock identity of elasmobranchs in the Northeast Atlantic in relation to assessment and management. J Northwest Atl Fish Sci 35:173–193

Pitchford JW, Codling EA, Psarra D (2007) Uncertainty and sustainability in fisheries and the benefit of marine protected areas. Ecol Model 207:286–292

Pratt HL Jr, Carrier JC (2001) A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ Biol Fishes 60: 157–188

Rogers LA, Olsen EM, Knutsen H, Stenseth NC (2014) Habitat effects on population connectivity in a coastal seascape. Mar Ecol Prog Ser 511:153–163

Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ (2002) Using spatially explicit data to evaluate marine protected areas for abalone in southern California. Conserv Biol 16:1308–1317

Shepherd T, Page F, Macdonald B (2002) Length and sex-specific associations between spiny dogfish (*Squalus acanthias*) and hydrographic variables in the Bay of Fundy and Scotian Shelf. Fish Oceanogr 11:78–89

Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser 248:187–196

Stenberg C (2005) Life history of the piked dogfish (*Squalus acanthias* L.) in Swedish waters. J Northwest Atl Fish Sci 35:155–164

Stevens J (2002) The role of protected areas in elasmobranch fisheries management and conservation. Occas Pap IUCN Species Surviv Comm 25:241–242

Sulikowski JA, Prohaska BK, Carlson AE, Cicia AM, Brown CT, Morgan AC (2012) Observations of neonate spiny dogfish, *Squalus acanthias*, in Southern New England: a first account of a potential pupping ground in the Northwestern Atlantic. Fish Res 137:59–62

Templeman W (1976) Transatlantic migrations of spiny dogfish (*Squalus acanthias*). J Fish Res Board Can 33: 2605–2609

Templeman W (1984) Migrations of spiny dogfish, *Squalus acanthias*, and recapture success from tagging in the Newfoundland area, 1963-65. J Northwest Atl Fish Sci 5: 47–53

Teo SLH, Boustany A, Blackwell S, Walli A, Weng KC, Block BA (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar Ecol Prog Ser 283:81–98

Vince MR (1991) Stock identity in spurdog (*Squalus acanthias* L.) around the British Isles. Fish Res 12:341–354

Wilding TA, Hughes DJ, Black KD (2005) The benthic environment of the North and West of Scotland and the Northern and Western Isles: sources of information and overview. Report 1 to METOC. Scottish Association for Marine Science, Oban

Appendix 1. Filtering process for mean squared error values obtained from comparing environmental temperature depth records to corresponding depth temperatures from tags

Environmental records were placed within 1 of the 3 geographical areas; the upper or lower basin of Loch Etive and the Firth of Lorn (Fig. 1). Tag records were binned into 1 m depth ranges to match the 1 m depth intervals recorded by the environmental monitoring stations. Mean squared error (MSE) values were obtained for each 24 h period by comparing all spurdog temperature records against environmental records at the same depth range (see Fig. 6 and corresponding Table 2 for an example). The MSE values then went through 2 rounds of filtering to ascertain presence in 1 of the 3 areas.

(1) First round: MSE values obtained from a 24 h period where there was only a ≤5 m depth overlap were removed, as a 5 m range did not allow accurate comparison of the depth/temperature profile shape from the tag data compared to the environmental data. Any MSE values that were more than 8 wk away from the environmental record were also removed. Threshold values for presence and absence where obtained from the 10% and 90% quartiles of MSE values from visually assigned matching and non-matching spurdog and environmental profiles. The mean MSE was taken between the 90% match and the 10% non-match values. All MSE values equal to or higher than this were removed. Remaining MSE values were deemed to denote presence in the locations for that 24 h period. There were 24 h periods where there were 2 potential locations based on MSE values and other 24 h periods where, due to a lack of environmental data, there was no location assigned. Because of this, it was necessary to undertake a second round of filtering to remove instances where MSE values indicated presence in more than 1 location.

(2) Second round: The MSE values for tag temperature records for corresponding 24 h periods from both tags were obtained; these values were put through the same threshold process as previously described to ascertain whether both spurdog were in the same or different temperature depth habitats over the 24 h period. The MSE value per tag was obtained for each 24 h period against the following 24 h period, then with a 24, 48, 72 and 96 h gap which showed whether the spurdog had changed its temperature depth environment, suggesting a move between the geographical areas. In instances where, after the first round of filtering, MSE values suggested presence in more than 1 area, the comparisons between the 2 tags and the preceding/following 24 h periods from the same tag were used to keep the most likely MSE value. On occasions where there was a discrepancy in location based on the first round of filters and the second round of filters, data were checked visually and location was chosen. Using the second round of filters, the original presence/absence predictions could be extended over the periods when environmental depth temperature profiles were not available due to different depth ranges or lack of recording, and we could assign the most likely location (Fig. 5).

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