Chapter 2 Winter Residency and Site Association in the 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 (MPAs) might be used to help conserve species with high migratory potential. There is evidence that 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 endangered. Here we investigate 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 mature female spurdog over wintered 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 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.

Keywords: Archival tag, Conservation, Migration, Spatial ecology, residency, Marine Protected Areas

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 species of elasmobranch, often associated with critical habitats and important life history stages. Due to 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 displayed 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 there being 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 with low fecundity and a gestation period of up to 24 months (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 spurdog are considered highly vulnerable to over-fishing (Ellis et al. 2008). This vulnerability has been demonstrated in the North East 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 north and south populations, between which there is little mixing (Holden 1965, Holden 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 south western to areas to north eastern areas annually (Vince 1991).

Movements in coastal waters around the UK are largely unknown, however, 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), mature spurdog on the eastern coast of the United States (Carlson et al. 2014) and the eastern coast of British Columbia and Canada (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). 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. 2.1), 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.

Methods

The study site

Loch Etive is situated on the Scottish west coast (see Fig. 2.1). This sea loch is approximately 30km long and has a mean width of 2km. It is separated into two 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 5m deep, separates the lower basin from the ocean (Hsieh et al. 2013) (Fig. 2.2). 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 (Aleynik et al. 2012), and deep water stagnation in the upper basin (Edwards & Edelsten 1977).

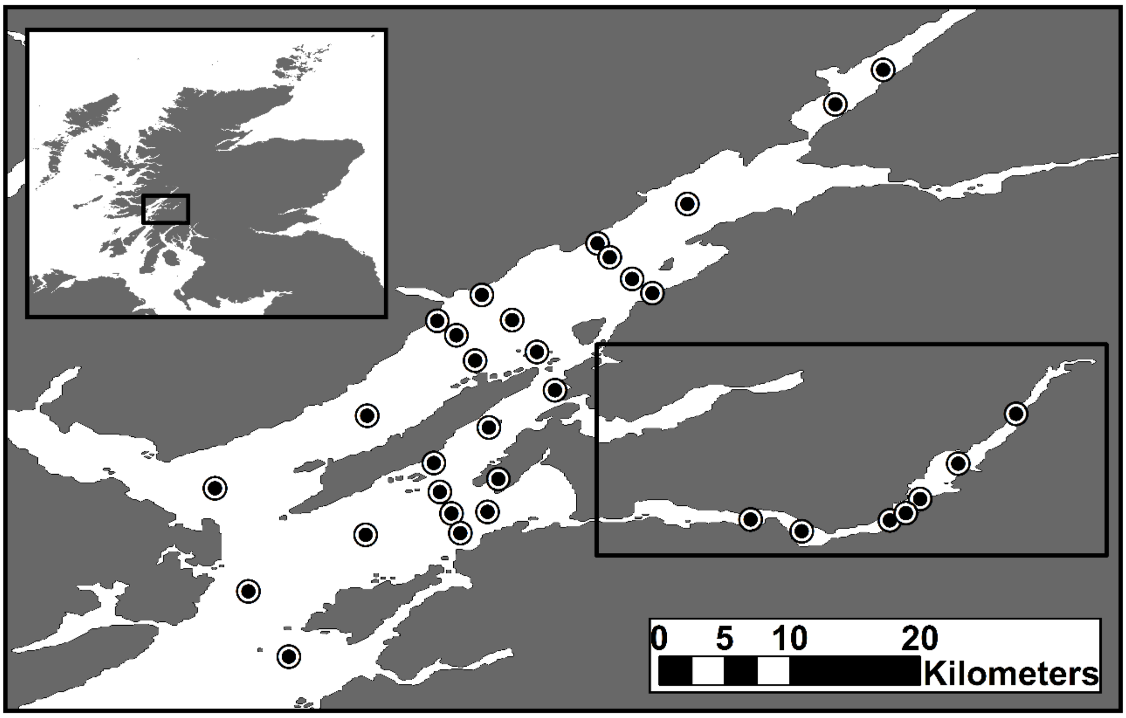

Figure 2.1: The study area Loch Etive on the West coast of Scotland. Loch Etive is shown in the inset by a black frame. Black circles denote the location of environmental monitoring stations recording temperature at depth

Acoustic monitoring stations

Two VEMCO hydrophone recorders (VR2W 69kHz - Vemco-Amirix Systems, Canada) were installed on 20th October 2010 in Loch Etive, before tagging spurdog with acoustic tags (see methods 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 2m 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 two surface marker buoys. Seabed depth was 10 m (A) and 17 m (B) (Fig 2.2) 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 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. 2.2). The receivers were retrieved after a year's deployment on the 4/12/2011 and the data downloaded via the built in Bluetooth connection.

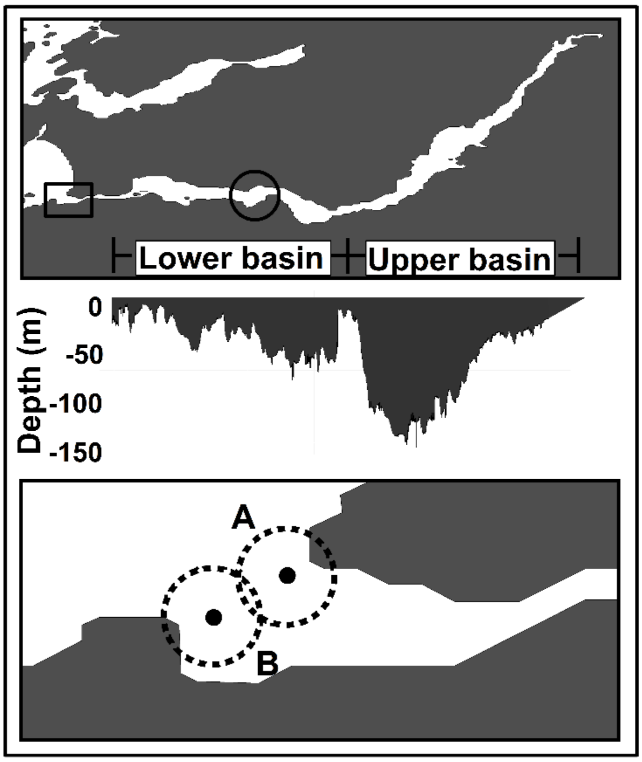

Figure 2.2.2: Upper and lower basins of Loch Etive (upper panel); bathymetric profile shown to longitudinal scale; tagging and acoustic receiver unit deployment sites (lower panel). Upper panel: Black square indicates acoustic receiver unit deployment site, and black circle the tagging (both acoustic and DST) site. Lower panel: acoustic stations A & B, minimum detection range shown by black dashed line (minimum range recorded in flow tidal state)

Tagging

All spurdog were all caught using individual baited hook and line in Loch Etive (Fig. 2. 2).

Data Storage Tags

Ten spurdog were tagged and measured on the 25th and 26th October 2010 (eight female and two males). Pre-started tags (Star Oddi centi-TD) were fitted externally, anchored through the base of the dorsal fin using two stainless steel pins permitting easy removal. Each tag was marked with a specific ID number and set to record depth and temperature every five (n=5) or ten (n=5) minutes. 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 United Kingdom Home Office.

Mark recapture

Tag and release data were collected by the Scottish Shark Tagging Program (SSTP) from 2007 - 2013. During this time 164 spurdog were opportunistically tagged and released by volunteer anglers in Loch Etive and the Firth of Lorn (Fig. 2.1). 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 - cm), girth (around the central thorax, in front of the first dorsal fin and behind the pectoral fins - cm), sex and weight (kg) were recorded. Recaptures were opportunistically reported by anglers.

Acoustic

A total of twelve spurdog were tagged on 25th and 26th of October 2010 (seven female, five male). 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 then placed with their ventral surface exposed in a grooved work bench. Total length and girth were measured (as with mark and 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. 2.2).

Data Analysis

Data storage tags

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 if 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 was made available from several separate studies: 1) Loch Etive mouth continual monitoring. Two 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 minutes; 2) Temperature at depth profiles for Loch Etive were provided by two studies running in Loch Etive by Hsieh et al. (2013) and Friedrich et al. (2014); 3) Temperature at depth profiles were recorded by Marine Scotland in the Firth of Lorn in December 2010, March 2011, both partial coverage and May 2011, full coverage (Fig. 2.1 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. 2.5 and corresponding Table 2.2 for an example). A two round filtering process (appendix 1) using MSE values was used to place the spurdog in one of three areas, the upper or lower basins of Loch Etive, or the Firth of Lorn (Fig. 2.6). The boundary for each area was designated as the shallow water sill that physically separates the two basins and the adjoining oceanic water body (Fig. 2.2).

For those months when no environmental temperature at depth data was 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 (Fig. 2.4).

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

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 if 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 tag

In total, 3 of the 10 spurdog tagged with DSTs were recaptured, all within Loch Etive. One after only seven days of deployment; data from this tag was not used in further analysis. The remaining two tags (numbers 5159 and 5162) were recovered after a full year (Table 2.1), although due to memory constraints both had data only between 26th October 2010 and 25th August 2011 (303 days). The size of both females is compatible with early stage maturity. Both spurdog showed a move to deeper water in February returning to shallower water in April (Fig. 2.3), although maximum depths recorded by all returned tags were within the depth range of Loch Etive.

Both tags recorded temperature ranges between 6.3–15.2^{o}C, with most recordings being between 10-11^{o}C (Fig. 2.3); they were present at depths between 0 to 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 2.1: Spurdog recaptured within Loch Etive from both the Scottish Shark Tagging Programmes mark recapture programme and the Data Storage Tag study in this project. Data in bold relates to fish tagged with DSTs. Recapture data (other than location) is missing for fish 5935.

Tag.	Sex	Tagged	Recaptured	Weight	Total	Days
368	F	15/11/2009	13/11/2010	1.9	76	363
1542	F	14/11/2009	04/12/2009	2.5	81	20
1806	F	05/09/2010	29/05/2011	2.6	84	266
1809	F	04/04/2010	21/11/2010	4.3	-	231
1816	F	05/09/2010	28/01/2012	4.3	100	510
2004	F	10/07/2010	25/09/2010	4.2		77
5162	**F**	**26/10/2010**	**08/11/2011**	**2.36**	**82.5**	**378**
5935	F	14/01/2012	-	-	-	-
5159	**F**	**26/10/2010**	**16/10/2011**	**2.7**	**71**	**355**
7288	F	21/06/2011	08/01/2012	5.2	102	201
27926	F	05/07/2008	09/11/2009	6.8	-	492
27987	F	17/01/2009	01/05/2009	4.5	-	104
27996	F	09/02/2008	23/10/2010	3.2	79	987
7424	F	04/08/2012	02/12/2012	4.1	91	120
5171	**F**	**26/10/2010**	**2/11/2010**	**1.34**	**64**	**7**

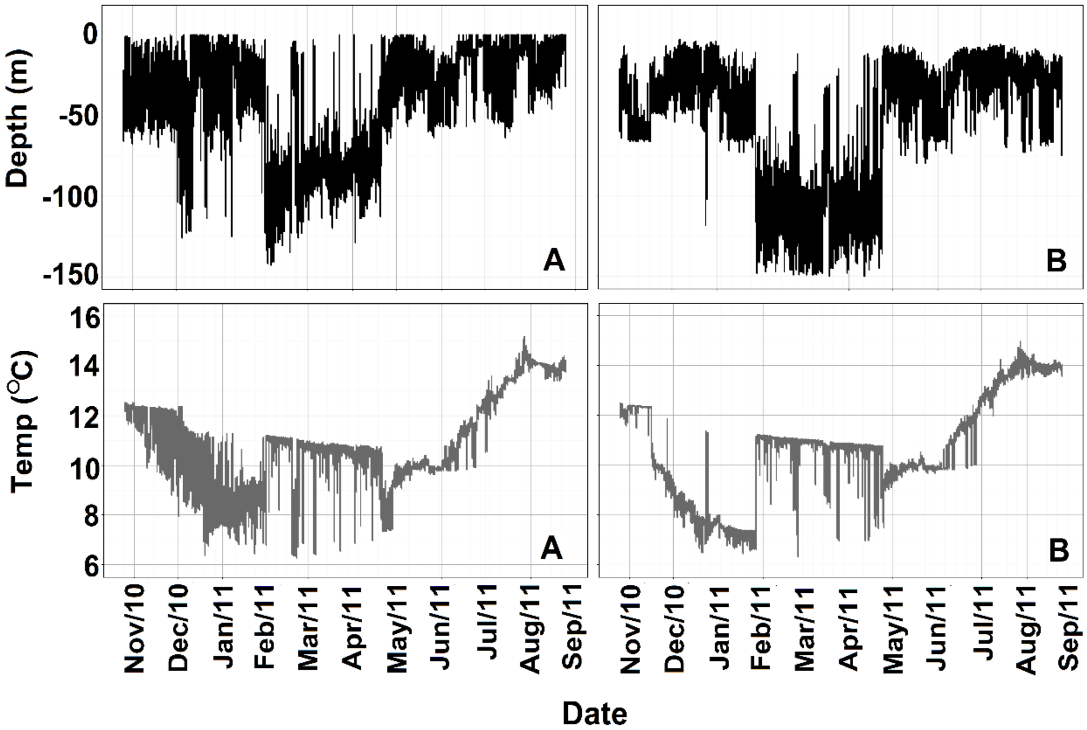

Figure 2.2.3: Separate depth and temperature plots from data recorded by DSTs 5159 (A) and 5162 (B) between 25th and 26th October 2010 (deployment) and 25th August 2011; each variable was recorded at 5 minute intervals

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. 2. 4). From 6th December 2010 until the 27th January 2011 there were many tag temperatures 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 21st April 2011, at this point, tag temperatures increased into the range of the loch. For the rest of the tag record (end date 25th August 2011) temperatures recorded by the tag at 9-13 m were mostly within the temperature range of the mouth of Loch Etive.

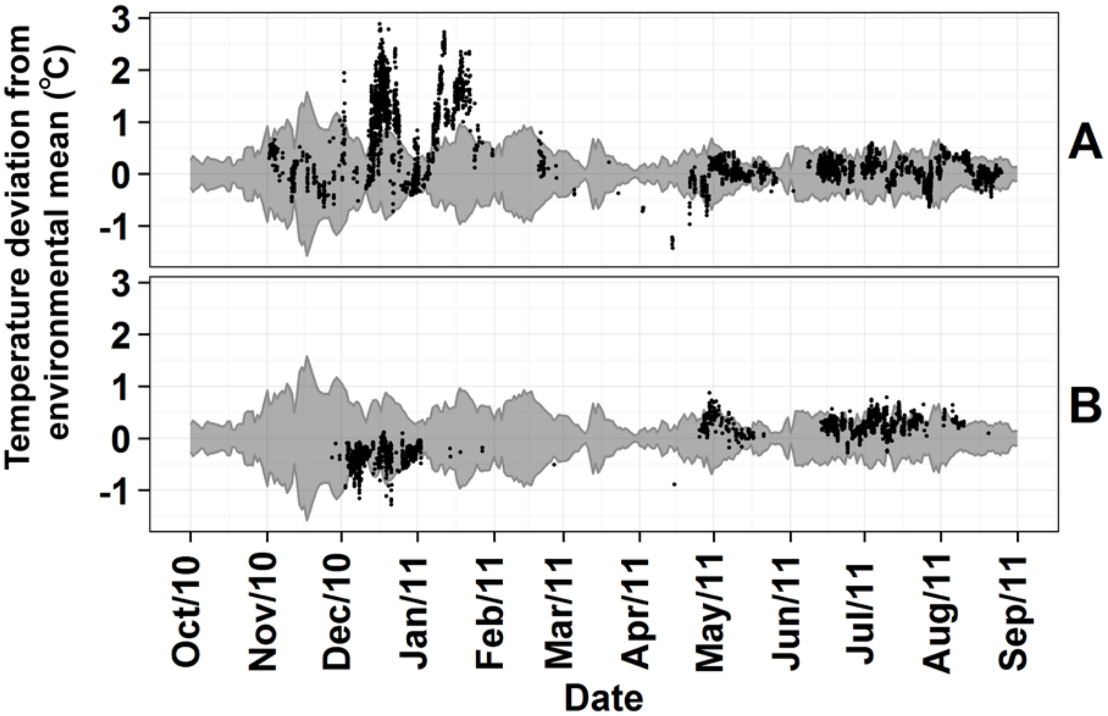

Figure 2.2.4: Deviation of spurdog tag temperature data from the mean environmental temperature at the mouth of Loch Etive. The grey ribbon on the lower half of each panel shows the environmental temperature variation around the mean temperature between 9-13m depth. Black points in the lower panel show the deviation of spurdog 5159 (A) and 5162 (B) tag data within the same depth range from the environmental mean.

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 9–13 m depth. From 25th April 2011 tag temperatures were back in the range of the mouth of Loch Etive, and remained there for the rest of the record (25th August 2011).

Comparison of temperature depth profiles

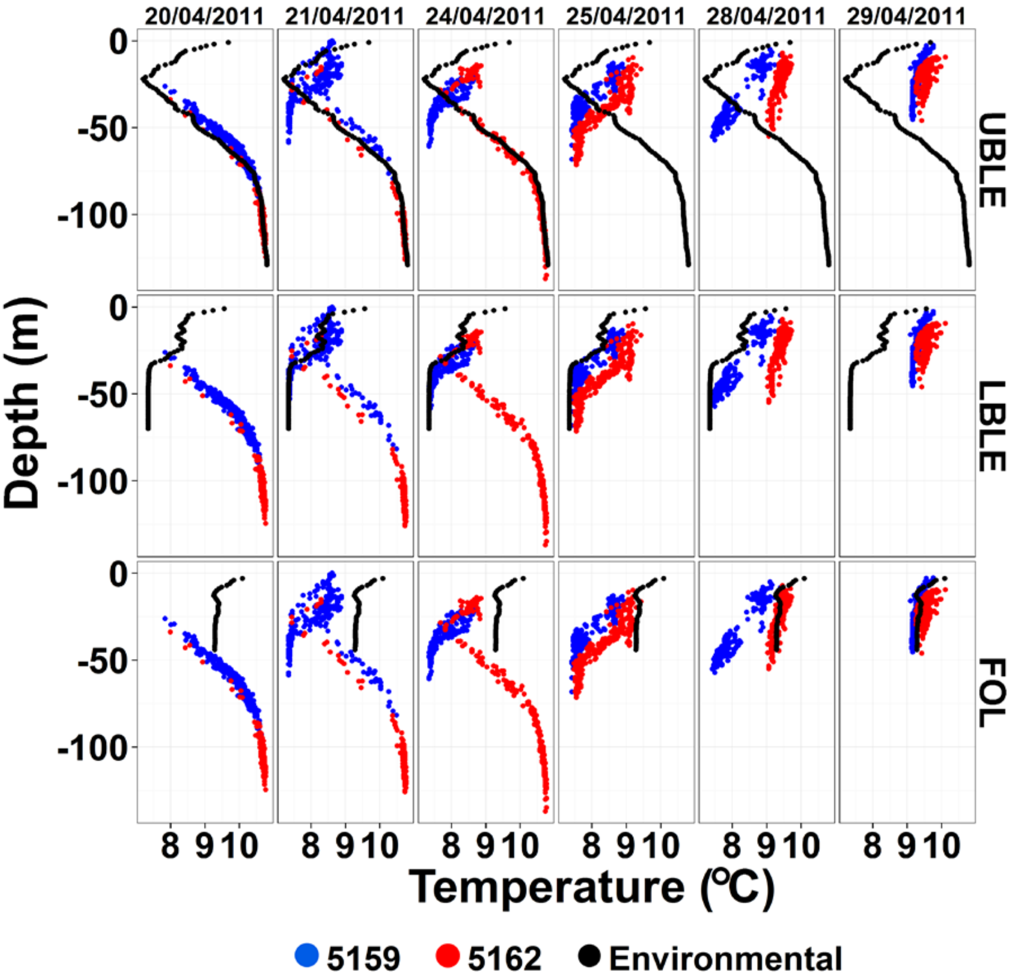

Figure 2.5: Temperature at depth data from both tags plotted against environmental data from the upper basin (UBLE) the lower basin (LBLE) of Loch Etive and the Firth of Lorn (FOL). Spurdog 5159 is represented by blue points, 5162 by red points and environmental temperature by black points. Data is shown from the event in April where both spurdog exited the upper basin after nearly 3 months residency, moved through the lower loch and exited into the Firth of Lorn. Table 2.2 shows corresponding Mean Squared Error values for each day per tag

Table 2.2: Mean Squared Error values corresponding to comparisons between spurdog tag and environmental temperature at depth data after first round of filtering as described in appendix 1. Data visualised in Fig. 2. 5

	5159			5162		
	Upper	Lower	Firth of	Upper	Lower	Firth of
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

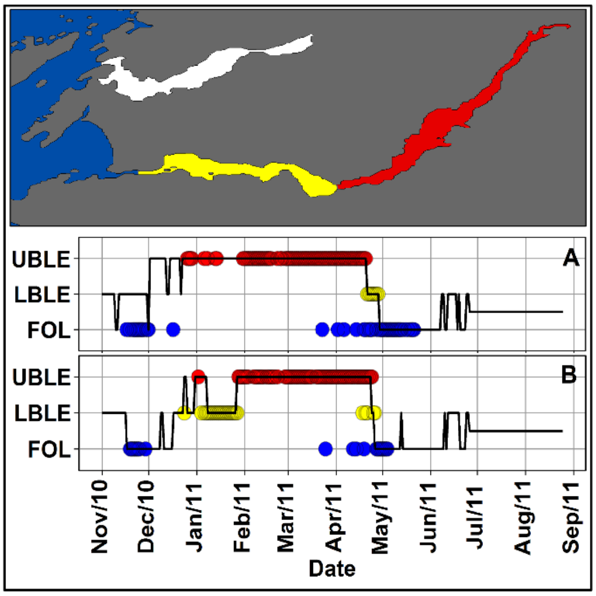

Figure 2.2.5: Presence of spurdog 5159 (A) and 5162 (B) in the upper basin of Loch Etive UBLE - red), the lower basin of Loch Etive (LBLE - yellow) or the Firth of Lorn (FOL - blue). Presence is based on the Mean Squared Error (MSE) values between environmental temperature at depth records and spurdog temperature values at a corresponding depth after the first filtering process (coloured points) and second round filtering (thick black line line) as described in appendix 1. Where the line runs between two areas there is a 50/50 chance that the spurdog was in either

Filtered MSE values (Fig. 2.6) show that spurdog 5159 made extensive use of the lower basin of Loch Etive throughout November with just three 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 three areas before moving to the upper basin on the 13th, 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 the 21st April when it moved through the lower basin over 7 days and out into the Firth of Lorn on the 29th (Fig. 2.5). 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 the 16th November (Fig. 2.5). On the 5th December, it moved back into the lower basin where it spent most of the month with occasional use of the upper basin on the 24th and 25th. During January spurdog 5162 remained in the lower basin until the 28th, 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 April 24th, when it moved into the lower basin for one day

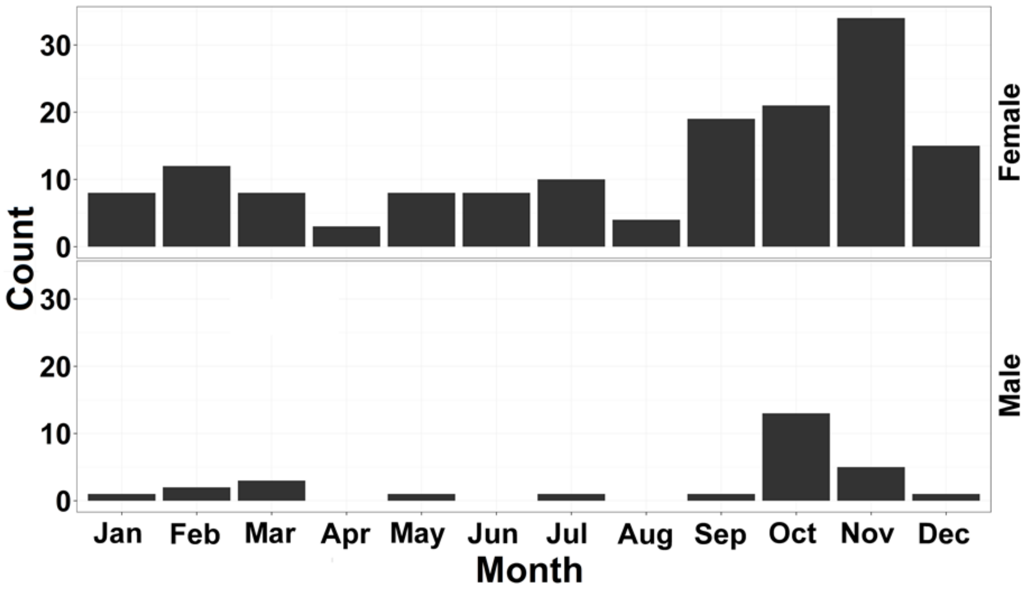

Figure 2.2.6: Spurdog count per month in Loch Etive, split into female and male from the mark and recapture study

before moving into the Firth of Lorn on the 26th (Fig. 2.5). 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 three habitats as there were no temperature depth profiles for this time period. However, the temperatures recorded by both tags between 9-13m deep were within the temperature range recorded at the mouth of Loch Etive, suggesting 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.

Mark Recapture

A total of 164 spurdog were tagged in Loch Etive, with 31 males (mean length = 73.8 cm; range 51 – 110 cm) and 133 females (mean length = 84.5 cm; range 78 – 110 cm) (Fig. 2.7). 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 female (10.5% of total females tagged) (Table 2.1). Thirteen recaptures were in Loch Etive, 11 of which were originally tagged within the loch, and two in the adjoining water body, the Firth of the Lorn less than 1km away. Two spurdog tagged at this location in the Firth of Lorn were subsequently recaptured in Loch Etive. Recapture data was unsuitable for standard mark recapture analysis due to insufficient numbers of recaptures (n=15) and the large uncertainty in sampling effort.

Acoustic

Data was only recorded for one female (66.5 cm long and weighing 1.34 kg). She was recorded by receiver A over three consecutive days from the 5th until the 7th of November 2010, then again for two consecutive days from the 10th and 11th of November 2010. The same individual was also recorded by receiver A for 26 minutes on 2nd April 2011.

Discussion

By combining the data from the DSTs with environmental temperature at depth data, we were able define the movements between the upper and lower basin of Loch Etive and the Firth of Lorn. From this, we could see that two small mature females remained either in Loch Etive or the local area over a 10 month 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 approximately 17 km^2, by both females is particularly unusual due to the small size of the area both spurdog used exclusively for almost three months.

Residential behaviour is previously unrecorded in NE Atlantic spurdog, traditionally thought to be highly migratory, undertaking large scale migrations as shown by previous tagging studies (Hjertenes 1980, Vince 1991, Henderson et al. 2002a). 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 (e.g. 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 Etive as a very 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 days, 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. 2002b, 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 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 moved through the cooler lower basin and out into the Firth of Lorn within a few days. These observations suggest that thermal considerations play an important role in the movement of spurdog within the Loch Etive area as both spurdog appear to move in order to remain in a temperature range of 10-11^{o}C where possible, similar to temperature preferences for spurdog shown by Shepherd et al. (2002) in the NW Atlantic. The Strait of Georgia, BC, like Loch Etive, has a series of silled basins which causes water stagnation (Johannessen et al. 2014). The temperatures in these basins remains 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 are known to parturate offshore (Pawson 1995) suggesting 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, breeding individuals migrating offshore (Carlson et al. 2014). This would imply 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 – 30cm TL) with clearly visible throat scars from the attached yolk sac were observed in the loch, suggesting a maximum age of approximately 8 weeks (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 three 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 is an isolated population of spurdog as 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, Sulikowski et al. 2010), suggesting 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 Loch Etive is used as a nursery area, however, it is unusual for mature individuals to remain in nursery areas (Heupel & Hueter 2001, Grubbs et al. 2007). Mark and recapture data suggests 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, effectively creating the ideal situation for an effective MPA (Bonfil 1999). This study highlights that, in some cases, area protection as part of a larger management plan may benefit some traditionally highly migratory species, providing sufficient research is undertaken to show strong site association to small geographic areas.

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Appendix 1

Filtering process for Mean Square Error values obtained from comparing environmental temperature depth records to corresponding depth temperatures from tags.

Environmental records were placed within one of the three geographical areas; the upper or lower basin of Loch Etive and the Firth of Lorn (Fig. 2. 2). Tag records were binned into 1m depth ranges to match the 1m depth intervals recorded by the environmental monitoring stations. Mean Squared Error (MSE) values were obtained for each 24 hour period by comparing all spurdog temperature records against environmental records at the same depth range (see Fig. 2.5 and corresponding Table 2.2 for an example). The MSE values then went through two rounds of filtering to ascertain presence in one of the three areas.

1) First round:

MSE values obtained from a 24hr period where there was only a 5 m or less 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 weeks 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 or higher to this were removed. Remaining MSE values were deemed to denote presence in the locations for that 24hr period. There were 24hr periods where there were two potential locations base don MSE values and other 24hr periods where, due to a lack of environmental data, there was no location assigned. Due to this, it was necessary to undertake a second round of filtering removed instances where MSE values predated presence in more than one location.

2) Second round:

The MSE values for tag temperature records for corresponding 24hr 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 24hr period. The MSE value per tag was obtained for each 24hr period against the following 24hr period, then with a 24hr, 48hr, 72hr and 96hr gap which showed if 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 one area remained, the comparisons between the two tags and the preceding/proceeding 24hr 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 was 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 no recording and we could assign the most likely location (Fig 2.6).

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