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Original Article

Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine

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Understanding the influence of spawning behaviour on the fine-scale distribution of Atlantic cod is essential to the design of effective conservation measures. Laboratory studies suggest that spawning activity occurs primarily at night, yet no field studies have evaluated the influence of diel period on the behaviour of individual wild spawning cod. Using an acoustic telemetry positioning system, the fine-scale movements of spawning cod were observed *in situ* as they returned to the same spawning location over consecutive seasons. The resulting data identify clear gender-based diel patterns in space use and aggregation behaviour among cod on a spawning ground. During the day, females remained aggregated in one small location that varied little within and between years. Males also aggregated during the day, but occupied a much larger adjacent area. At night, individual males sought out separate small territories while females generally remained near their daytime aggregation site, making periodic excursions into the surrounding area. These patterns were surprisingly stable over the 2 years of observation, indicating little interannual variability in spawning behaviour. This study provides an unprecedented examination of the natural spawning behaviour of Atlantic cod, and makes connections between earlier laboratory studies and field observations.

Keywords: acoustic telemetry, Atlantic cod, *Gadus morhua*, Gulf of Maine, spawning behaviour, VEMCO VPS.

Introduction

Atlantic cod (*Gadus morhua*) is one of the most commercially sought after and socio-economically important fish species in the world (Kurlansky, 1998; FAO, 2012). Despite inordinate attention on stock assessment and fishery management, most cod populations have experienced steep declines in abundance with limited success at rebuilding (Lilly *et al.*, 2008). Overfishing has often been cited as the primary culprit (Myers *et al.*, 1996; Shelton *et al.*, 2006), yet it seems unlikely that the blame falls entirely on imperfect stock assessment models or management decisions that are insufficiently precautionary to account for uncertainty. As many have pointed out, environmental variability (e.g. climate change, Atlantic Multidecadal Oscillation, North Atlantic Oscillation) is having an impact on

productivity, growth, and recruitment of many stocks (Rose, 2004; Brander, 2005; Drinkwater, 2005; Koster *et al.*, 2005); as are fluctuations in the populations of predators, competitors, and prey species (Swain and Sinclair, 2000; Trzcinski *et al.* 2006; Ames and Lichter 2013).

Still, it appears that there is some element to the population dynamics of this species that is currently being ignored or misunderstood that causes such widespread failure to prevent stock collapse and achieve recovery. Several papers have recently suggested that ignoring fine-scale population structure is a contributing, if not a leading cause (Svedäng *et al.*, 2010; Lindegren *et al.*, 2013; Zemeckis *et al.*, in press). There is ample evidence that many cod stocks function as metapopulations, containing multiple sub-

populations made up of semi-discrete spawning components (Smedbol and Wroblewski, 2002; Wright *et al.*, 2006; Rose *et al.*, 2011). By managing stocks as a single homogeneous unit, we ignore this fine-scale population structure and risk the serial depletion of unique sub-components, thereby lowering stock productivity (Frank and Brickman, 2000; Smedbol and Stephenson, 2001). The strong spawning site fidelity exhibited by cod suggests that once a semi-discrete spawning component is extirpated, the likelihood of rapid re-colonization is low (Robichaud and Rose, 2001; Skjæraasen *et al.*, 2011). Spawning behaviour is at the heart of a metapopulation; it provides not only the mechanism by which population structure is developed and maintained, it also influences whether lost or depleted components will recover. Understanding the "where", "when", and "how" of spawning helps us manage cod stocks more effectively by providing the necessary information to design conservation measures that prevent the loss or depletion of spawning components (Zemeckis *et al.*, in press).

Our knowledge of individual spawning behaviour comes primarily from observations made in captivity. These studies have shown that Atlantic cod employ a mating system known as a lek, with males forming a dense aggregation at specific sites where they perform courtship displays to attract females (Nordeide and Folstad, 2000). The largest, most dominant males are thought to form an individual display territory that they defend from other males through agonistic interactions (Hutchings *et al.*, 1999). Females remain segregated from males and periodically enter a dominant male's territory when ready to spawn (Brawn, 1961). The presence of the female in its territory causes the male to initiate a courtship routine involving circling bouts, fin displays, and vocalizations (Hutchings *et al.*, 1999). Mating is based on female choice; after successful male courtship, a spawning pair rises off the bottom and releases their gametes during a "ventral mount" (Brawn, 1961; Hutchings *et al.*, 1999; Morgan *et al.*, 1999). There is also evidence for an alternative male reproductive strategy where a sub-dominant (or "sneaker") male follows the mounted pair and fertilizes a portion of the eggs released by the female (Bekkevold *et al.*, 2002; Rowe *et al.*, 2008). Although our ability to observe mating behaviour is restricted by light availability, tank experiments suggest that spawning events occur primarily at night (Brawn, 1961; Kjesbu, 1989; Hutchings *et al.*, 1999; Morgan *et al.*, 1999).

While little is known about the spawning behaviour of cod in the wild, there is ample indirect evidence from field studies supporting the findings of tank experiments. Survey and fishery-dependent observations have shown that wild spawning cod form dense aggregations that are spatially and temporally predictable (Nordeide, 1998; Marteinsdóttir *et al.*, 2000; Vitale *et al.*, 2007). Strongly skewed sex ratios are commonly found in catches made on or near a spawning aggregation, corroborating the idea of spatial segregation of the sexes while spawning (Morgan and Trippel, 1996; Lawson and Rose, 2000; Armstrong *et al.*, 2004; Windle and Rose, 2007). Hydroacoustic observations have indicated that vertical movements play a role during spawning, with individuals typically rising in the water column at night (Ouellet *et al.*, 1997; Fudge and Rose, 2009; Knickle and Rose, 2012). Despite these similarities, it is difficult to reconcile some of the behaviours observed among a small group in a tank with the magnitude of a wild spawning aggregation. For instance, how does a socially determined hierarchy persist among thousands (if not millions) of individuals? At what scale do females and males segregate (causing skewed sex ratios), while still maintaining the proximity necessary for the lek mating system to occur? Does the diel influence on behaviour observed in

the laboratory affect their space use and habitat utilization in the wild? Resolving these questions will help fill the void of information on the spawning behaviour of wild Atlantic cod and allow us to design more informed conservation measures.

Of the different approaches to studying spawning behaviour, acoustic telemetry alone offers the ability to observe the natural movements of individual fish *in situ*. The first applications of this technology to observe spawning cod demonstrated strong site fidelity and gender-related differences in spawning period (Robichaud and Rose, 2001, 2002, 2003). Recent technological advances now permit increased sample sizes, multiyear observation, and expanded detection areas (DeCelles and Zemeckis, 2014). Greatly improved resolution of reconstructed positions can be achieved by locating acoustic receivers in proximity to each other, allowing for the simultaneous detection of tagged individuals by multiple receivers. This receiver configuration, known as a "positioning system", can provide the precise location of tagged fish within a few metres at intervals of less than a minute (Andrews *et al.*, 2011). However, such systems require a significant investment in resources, in addition to *a priori* knowledge of where tagged fish are likely to go once released. Atlantic cod are an ideal candidate for observation with an acoustic telemetry positioning system, given their strong site fidelity and limited space use while spawning (Siceloff and Howell, 2013). Several researchers have recently used positioning systems to reveal fine-scale detail on the movements and behaviour of wild spawning cod (Espeland *et al.*, 2007; Meager *et al.*, 2010; Dean *et al.*, 2012). However, none have accounted for the effect of diel period, despite strong evidence that spawning activity occurs primarily at night. Furthermore, the use of this technology has been limited to relatively small detection areas (≤ 4 receivers) and a single year of observation. In most telemetry studies, spawning cod have been tagged and released with an unknown portion of the spawning season having already transpired. By collecting telemetry data from individuals returning to a spawning ground over multiple seasons, the full spawning period is observed and their movements are more reflective of natural behaviour. The goal of this research was to describe the influence of gender and diel period on cod spawning behaviour through an unprecedented view of fine-scale individual movements of wild cod over multiple seasons.

Material and methods
Study area
This study was conducted within the boundaries of the Spring Cod Conservation Zone (SCCZ), a seasonal fishery closure located ~ 5 km south of Gloucester, MA, USA in the western Gulf of Maine (Figure 1) (Armstrong *et al.*, 2013). The size of the closure area changed over the course of the study, increasing from 23 km^2 in 2009–2010 to 46 km^2 in 2011 (Figure 2). Spawning cod typically aggregate from April through July around a gravel/cobble deposit near the centre of the SCCZ, which has ~ 2 m of relief above a surrounding flat muddy plain that is bordered to the north and east by large outcrops of bedrock that come to within 25 m of the surface. The average depth at low water in the SCCZ is ~ 50 m, with a 3 m tidal range. Over the course of this study, the mean water temperature in April at a nearby oceanographic monitoring buoy was 4°C at the bottom and 7°C at the surface (NERACOOS Buoy "A"—http://www.neracoos.org). By July, the mean temperature rose to 6°C at the bottom and to 19°C at the surface.
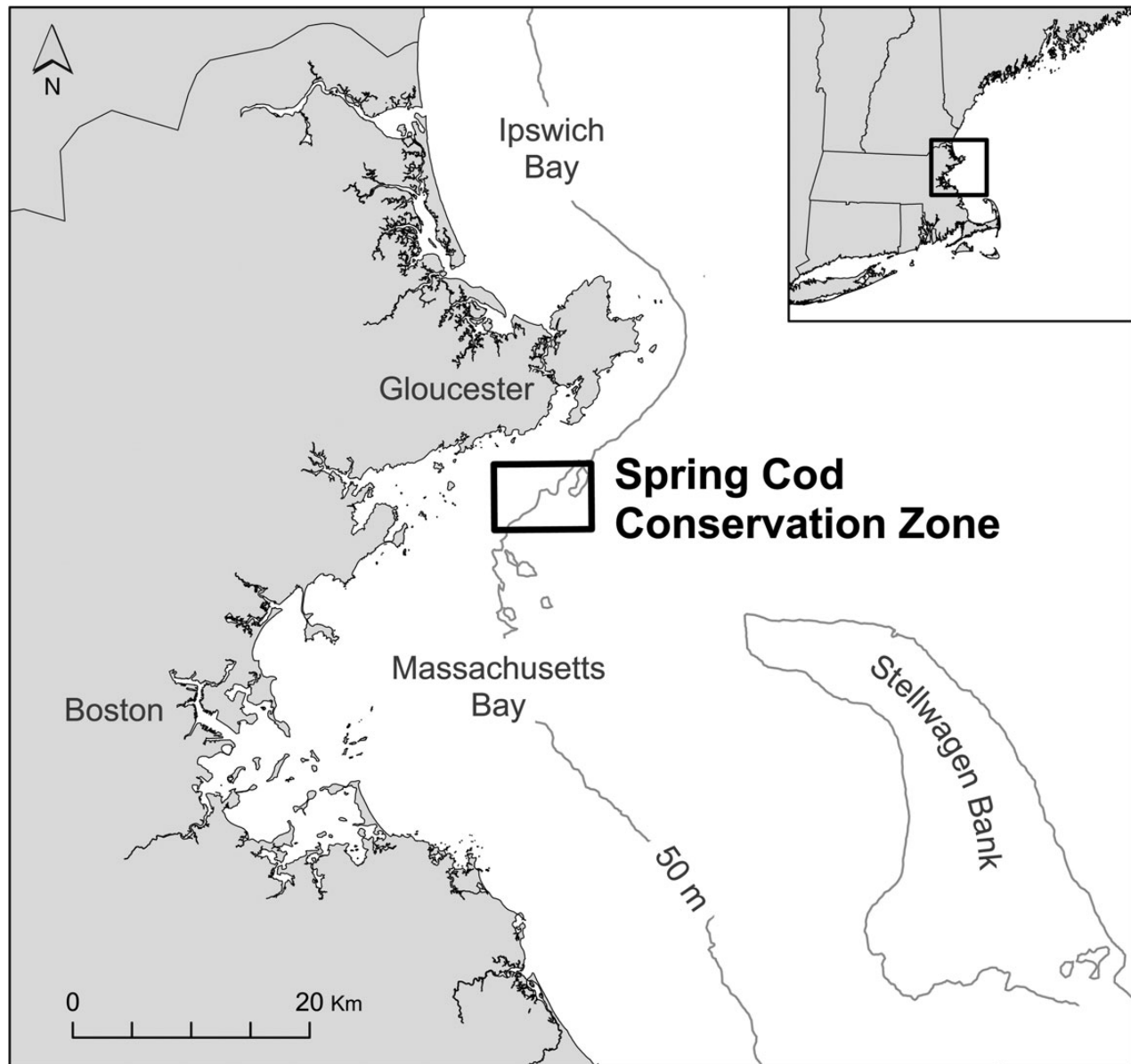
Figure 1. Map of the study area showing the general location in Massachusetts Bay and the western Gulf of Maine. The boundaries of the Spring Cod Conservation Zone in 2011 are shown in bold.

Tagging

Cod were captured from the SCCZ via angling with conventional cod jigs aboard the Massachusetts Division of Marine Fisheries' RV "Alosa". Upon capture, fish were placed in a 500-l tank supplied with continuous seawater flow (a "livewell") for up to 30 min before tagging. Only cod that appeared healthy and vigorous were selected for tagging with acoustic transmitters. In 2009, sex and spawning condition were recorded only when externally apparent (i.e. flowing sperm or eggs); therefore, several individuals of unknown sex and maturity were tagged in that year. In 2010 and 2011, all captured cod were cannulated to determine sex and maturity and only fish in spawning condition were tagged (i.e. males with flowing sperm or females with hydrated eggs). After recording sex, maturity and total length, a wet towel was placed over the eyes of the fish to calm it during the tagging procedure. A small incision (<4 cm)

was made in the lower left side of the abdomen, through which the acoustic transmitter was inserted. The incision was then sutured shut with a sterile needle and braided silk thread. The tagging procedure typically lasted <4 min and fish were allowed to recover in the livewell for up to 30 min before release. Handling time was kept as short as possible to reduce stress and minimize any latent effects on spawning behaviour. Consequently, no anaesthesia was used that would have added significantly to the length of time on-board the tagging vessel. The acoustic transmitters (VEMCO Inc., Model V16P-6H, 69 kHz, 16 × 98 mm, 37 g in air) were configured to transmit a unique identifier and pressure (depth) sensor reading at random intervals between 30 and 90 s. Each tag had an expected battery life of over 4 years, which allowed us to track the movements of cod that returned to the spawning site over multiple seasons.
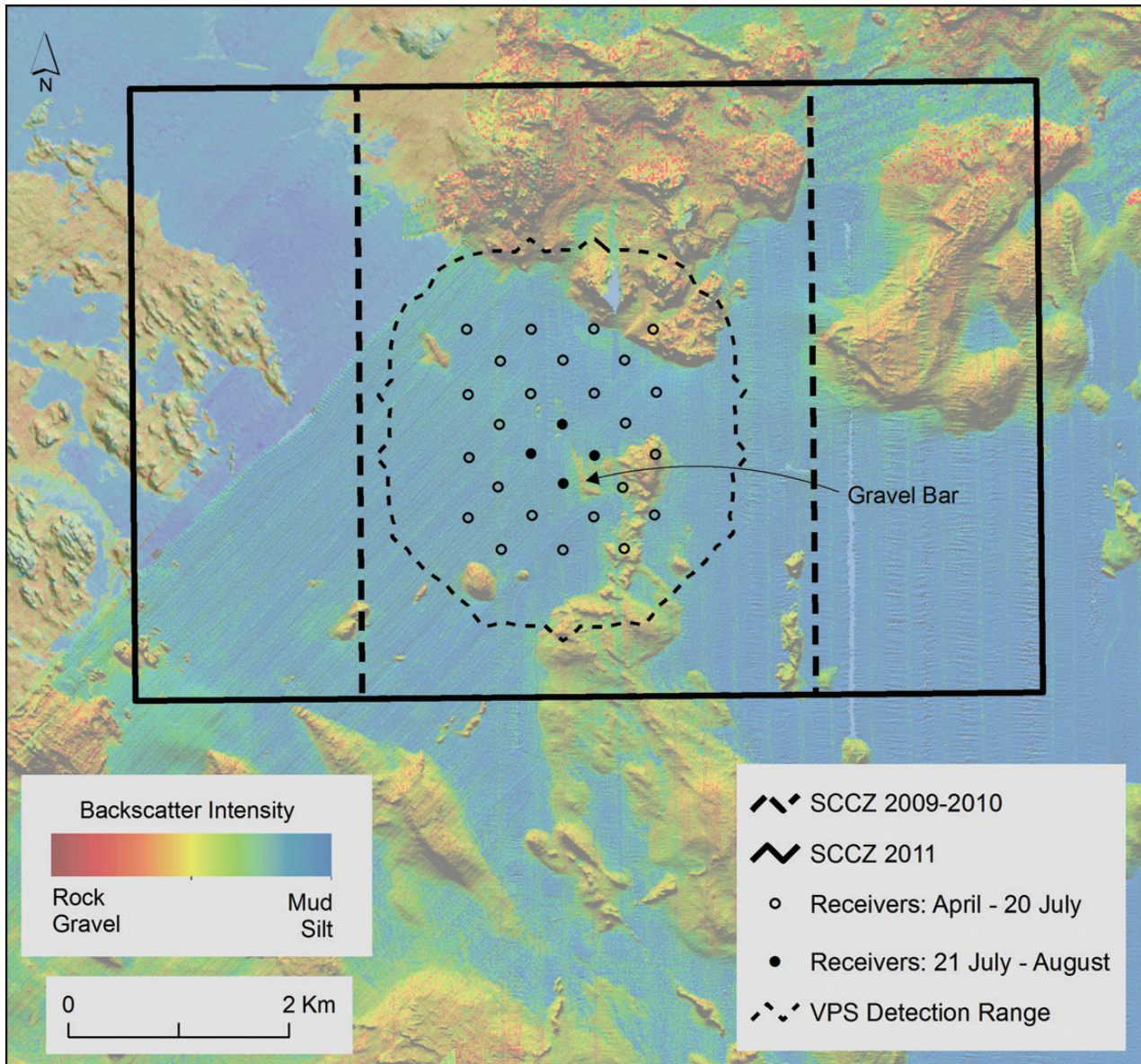
Figure 2. Map of the acoustic receiver array within the Spring Cod Conservation Zone (SCCZ). The width of the SCCZ was expanded in 2011, doubling the size of the closure area. In both 2010 and 2011, all but four receivers (closed circles) were removed on 20 July to minimize conflict with fishers once the SCCZ opened to fishing on 21 July. The background image depicts the bathymetric features of the surrounding area through backscatter intensity and hillshaded topography (Butman *et al.,* 2007). The gravel bar identified at the centre of the array was the focal point of the spawning aggregation in both years.

Acoustic receiver array

To track the movements of tagged fish in 2010 and 2011, an array of 28 acoustic receivers (VEMCO Inc., Model VR2W) was deployed in the form of an isometric grid roughly centred on the main aggregation site (Figure 2). Receivers were attached to vertical lines and moored 2 m above the seabed. Reference transmitters ("synctags¤") were attached to each vertical line to determine the position of receivers in relation to each other. Receivers were spaced 400 m apart, providing substantial overlap in detection areas given the ~1 km detection radius of each receiver. This array was part of a VEMCO Positioning System (VPS), which provided an ~9.5 km² area over which the movements of tagged cod could be observed. All 28 receivers were deployed before the formation of the spawning

aggregation (21 April 2010; 14 April 2011). Just before the lifting of the SCCZ fishery closure on 21 July, all but the four receivers closest to the main aggregation site were removed to minimize the loss of equipment through entanglement with commercial fishing gear. These remaining receivers were removed once all tagged fish had vacated the area (30 August 2010; 24 August 2011).

Data analysis

Raw detection data were downloaded from the receivers at the end of each season and sent to VEMCO Inc. for processing. This procedure involved using the time-difference-of-arrival (TDOA) among receivers to calculate a precise latitude and longitude for each tag transmission (i.e. hyperbolic positioning) (Smith, 2013). Processed data

consisted of tag ID, detection date/time, latitude, longitude, depth, and an estimate of the horizontal position error (HPE) for each relocation. HPE is a unitless error measurement that describes the sensitivity of the positioning system to the variables that affect horizontal accuracy (e.g. array geometry, water temperature, salinity, etc.) (Espinoza *et al.*, 2011). A measure of actual positioning error (HPEm), or the distance separating calculated positions and known locations, is available from the relocated positions of synctag transmissions. Therefore, a linear model was constructed between mean HPEm and HPE (binned in 1 m increments, up to 50 m) for synctag positions (HPEm $\sim 1.3056 + 0.3443 \times$ HPE; d.f. = 45, $r^2 = 0.89$, $P < 0.0001$) and applied to the processed dataset of fish tag transmissions to estimate the mean position error in metres (Smith, 2013). Tag positions with an HPE >25 were omitted from all analyses, as they were estimated to have an actual position error of more than 10 m.

Many demersal physoclistous fish, including cod, suffer the effects of barotrauma caused by the change in pressure when brought to the surface from depth (Heffernan *et al.*, 2004; Nichol and Chilton, 2006). Rapid expansion can cause the swimbladder to rupture, releasing gas that can only be replenished through an internal chemical process. Once released, cod with barotrauma often return to the seabed, but then make frequent ascents to shallower depths to achieve neutral buoyancy. The height of these ascents diminishes as the swimbladder heals and the fish replaces lost gas. Van der Kooj *et al.* (2007) examined this process in Atlantic cod from a variety of regions, and found that the equilibrium period lasted 3.8 days on average, but was influenced by depth of capture and water temperature. In the present study, this pattern of vertical behaviour was apparent in several fish, and appeared to cease within 1 week. For this reason, the first 7 days of observations post-release were omitted from all analyses to minimize the influence of the capture and tagging procedure on behaviour metrics.

To examine diel differences in behaviour, the relocated positions were assigned to the following periods, using astronomical data from the US Naval Observatory (http://aa.usno.navy.mil/): Day = 1 h after sunrise to 1 h before sunset; Night = 1 h after sunset to 1 h before sunrise; Dawn/Dusk = the 2-h period surrounding either sunrise or sunset. Night observations after midnight were assigned to the previous date, so that a single contiguous Night period existed for each calendar date. For most analyses of diel patterns, only Day and Night periods were compared, because the Dawn/Dusk period appeared to be a time of transition between two relatively stable behaviour states.

Patterns in space use were described through the creation of utilization distributions (UDs) from the processed dataset. A UD is essentially a map of the probability of locating a tagged animal over a given period (Worton, 1987). Because the detection data were highly autocorrelated, a Brownian bridge movement model (BBMM) was used to construct each UD with the adehabitat package (version 1.8.12; Calenge 2006) of the R statistical software (version 3.0.2; R Development Core Team 2012). This model leverages the information contained in the sequence of observations to obtain a more precise measure of space use than a traditional kernel density estimator, which assumes that observed positions are a random sample of all possible locations along the trajectory of a tagged animal. The BBMM relies on two key parameters: mean position error (δ) and Brownian motion variance (σ_m^2, related to circuitousness of movement), both of which were estimated via the maximum likelihood approach of Horne *et al.* (2007). Because of the expected heterogeneity in movement

patterns, δ and σ_m^2 were estimated independently for each fish, date, and diel period. Some tagged fish periodically left the array; as such, UDs were calculated in multiple "bursts" when necessary. A burst was defined as a sequence of observations with no more than 1 h between positions. Burst UDs were then averaged together, weighting by the burst length (hours) to achieve a single UD for each fish, date, and period combination. This step ensured that each UD described the space use of a fish only when it was within the array.

Four measures of individual movement or space use were derived from either the UD or the processed point dataset directly: area occupied, height above bottom, site affinity, and aggregation intensity. These behaviour metrics were then examined for differences between genders, diel periods, or years with a mixed-effect generalized linear model (GLMM), using the R package lme4 (version 1.0−5). Fish ID was defined as a random intercept to account for within-fish variation. For each behaviour metric, error was best represented by the Gamma distribution with a log link function. Before analysis, each dataset was summarized to establish the individual fish as the unit of observation. For example, the mean height above the bottom per individual, diel period, and year were calculated and used as input to the model, as opposed to relying on the raw or daily observations. This step avoids the pitfalls of autocorrelation and pseudoreplication common to acoustic telemetry studies that rely on individual positions as the unit of observation (Rogers and White, 2007). Best fitting models for each behavioural metric were selected using backwards stepwise regression and the Bayesian information criterion.

Area occupied

The area occupied by an individual fish is related to its swimming speed and the directionality of its movement. Both are subject to change as it switches between behaviour modes (i.e. foraging, courtship, spawning, etc.), yet are difficult to measure directly. The estimation of swimming speed is affected by the interval between calculated positions, which in turn is affected by the number of tagged fish simultaneously present in the array. Because receivers can detect only one tag transmission at a time, the more fish that are within range of a single receiver increases the chance that two tags will transmit at the same time and cancel each other out. This leads to longer intervals between positions and a substantial downward bias in estimated swimming speed (Løkkeborg *et al.*, 2002). Determining the directionality of movement is equally problematic, particularly when aggregated fish are making limited movements relative to the level of horizontal position error. The BBMM accounts for both the variability in position intervals and the level of position error in the estimation of the UD. To represent the area occupied by an individual fish, the 95% and 50% probability contours were extracted from each UD, referred to here as the UD$_{95}$ and UD$_{50}$. In wildlife telemetry studies, these values are commonly referred to as the "home range" and "core area" of a tagged animal, respectively (Downs and Horner, 2008). The former is more inclusive and describes nearly all the areas that a tagged individual might visit over a given period, while the latter is more indicative of just the areas where that individual spent the most time.

Height above bottom

Both laboratory and field studies of cod spawning behaviour have observed some level of vertical movement (Meager *et al.*, 2009; Knickle and Rose, 2012). Measuring the position of spawning cod in the water column provides a third dimension with which to illustrate their patterns of behaviour. However, the raw tag depth data are

not inherently informative, given that the study area encompasses water depths of 25–65 m with a tidal range of 3 m. For a demersal species like Atlantic cod, a more relevant measure of vertical behaviour is the position of the tagged fish in relation to the seabed. As such, tag depths from the processed dataset were converted to heights above the bottom according to the following procedure: first, the tidal height from nearby Gloucester Harbor obtained from the National Oceanographic and Atmospheric Administration (http://tidesandcurrents.noaa.gov/) was subtracted from the tag depth to achieve a depth referenced to Mean Lower Low Water. The tag height above the bottom was then calculated by subtracting the depth of the water column at each position, which was obtained from a high-resolution bathymetric survey of the study area (Butman *et al.,* 2007). While the tag depth data were highly precise, as is evident from the clearly defined tidal cycle, each tag appeared to be biased by up to a few metres, a fact acknowledged by the tag manufacturer (i.e. the calculated height of several fish indicated they were several metres *below* the seabed). To correct for this bias, a synthesized "bottom line" was constructed for each tag by subtracting 1 m from a loess smoother (span = 5 days) of each tag's minimum height above the bottom per hour. Tag height data were then adjusted by making this synthesized bottom line the new zero height level. This assumes that when the tidal cycle is evident in the depth data, a fish is ∼1 m above the bottom, which appeared to be a reasonable assumption given video observations of the aggregation. Since the tidal cycle was apparent for each fish for some portion of each day, it was possible to use this technique to discern the location of the seabed from the recorded depth data. A loess smoother was used instead of a scalar adjustment, because the amount of sensor bias appeared to drift slightly over the course of a tag's life.

Site affinity

The relationship between spawning fish and their surrounding habitat is of critical importance for their protection and conservation. Describing the affinity for particular locations helps us to understand what constitutes optimal spawning conditions and can help explain potential mechanisms for genotypic divergence. The level of site affinity was measured using a UD overlap index (UDOI) as described in Dean *et al.* (2012), originally adapted from Meager *et al.* (2010). This method calculates the similarity in space use (i.e. per cent overlap between two UD_{95}) from one date to the next for a given fish and diel period. Only periods separated by one calendar day were used to calculate site affinity (e.g. from day_t to day_{t+1}, or from $night_t$ to $night_{t+1}$). A UDOI score of 0 means that a fish occupied completely different areas on consecutive periods; whereas a score of 100 indicates that it returned to the exact same area. A value of 0.01 was added to all UDOI scores to satisfy the assumptions of a Gamma-distributed variable in the GLMM (i.e. no zero values).

Aggregation intensity

Many field studies of spawning cod refer to the formation of dense aggregations, yet observations in captivity have shown that courtship and gamete release occur primarily in pairs. Understanding how these two phenomena function within a single mating system requires measuring the amount of overlap in space use between individuals in an aggregation. We quantified aggregation intensity among fish of the same gender using the same UDOI employed to measure site affinity. However, in this instance we measured the similarity in space use (i.e. per cent overlap in UD_{95}) between all possible inter-fish combinations (within a gender) on a given date

and period. A UDOI score of zero indicates complete disaggregation, or no overlap in space use among individuals; larger values indicate more overlap between individual fish, and a higher aggregation intensity. As with site affinity, a value of 0.01 was added to all UDOI scores to satisfy the assumptions of a Gamma-distributed variable in the GLMM.

Aggregation scale and location

Interannual variation in the focal point and extent of an aggregation helps determine the spatial predictability of a spawning event and therefore the appropriate size of a fishery closure. Substantial variation in spawning location from 1 year to the next implies that much larger spatial management measures are necessary to provide meaningful protection. Little interannual variation in aggregation location demonstrates fine-scale spawning site fidelity, which underscores the uniqueness of a spawning component and the need to protect it from overexploitation. The persistence of the aggregation focal point was evaluated by calculating the distance separating the overall average position of individuals and comparing between years, genders, and periods. To measure the average position of a group of individuals, the mean latitude and longitude were first determined for each fish, then the mean of those coordinates was calculated, ensuring that individuals with more detections did not exert undue influence on this measure of aggregation location.

The physical extent of the aggregation as well as the use of space in relation to the surrounding habitat was described through the creation of composite UDs. Composite UDs were constructed by first averaging the UDs from all dates for each individual, diel period, year combination, then averaging across all individuals. Thus, each composite UD represents the probability of locating an average tagged cod of that gender during that diel period over the entire season. The area inside the composite UD_{95} and UD_{50} was used to describe the area occupied by the group.

Results

A total of 2,032 cod were caught in the SCCZ between the months of April and July from 2009 to 2011. These were predominantly large fish in spawning condition, with the majority (60%) being female (Table 1). Males were significantly smaller (two-sample *t*-test; d.f. = 1621.5; $P < 0.0001$) and more likely to be in spawning condition than females (two-sample *z*-test; d.f. = 1; $P < 0.0001$). Despite cannulation, we were unable to determine the sex and maturity of a small number of fish (5% in 2010; 7% in 2011). A total of 70 uninjured cod with a minimum size of 65 cm were tagged with acoustic transmitters, in approximately equal proportions of males and females. Some of these fish were tagged in 2009 and did not return in 2010 or 2011 (*n* = 8), while others were determined to have died soon after release based on depth sensor data (*n* = 3). The remaining 59 fish were tracked in either 2010, 2011 or both years (Figure 3). Only 1 tagged fish (Fish ID = 19) was not in spawning condition when released; data from this transmitter were omitted from all analyses. Most tag releases occurred in 2010 and were distributed over multiple dates to encompass the entire spawning period (Figure 3). On average, tagged cod were tracked for 20 d (range = 1–53 d) in the year of their release. However, 19 tagged fish (29%) returned to the array in subsequent seasons and were tracked for an average of 36 d (range = 3–101 d) in those years. All but four fish tracked in 2011 were released in prior years, providing the best description of the full natural spawning season in that year: the first tagged fish arrived on 18 April and the last fish was

Table 1. Number; mean, standard deviation, minimum and maximum total length (cm); and spawning condition of cod caught and tagged with acoustic transmitters in the SCCZ by gender, 2009–2011.

	2009		2010		2011	
	Caught	Tagged	Caught	Tagged	Caught	Tagged
Female						
Number	13	3	598	31	519	1
Mean length	67.3	91.3	82.8	94.5	82.6	97.0
SD length	17.3	11.2	14.3	15.1	15.3	–
Min length	46	79	43	68	39	97
Max length	101	101	140	125	122	97
% spawning	69.2	100	67.7	100	59.2	100
Male						
Number	35	1	325	24	417	3
Mean length	60.6	73.0	68.3	80.2	69.1	114.7
SD length	9.6	–	13.8	9.1	14.7	4.2
Min length	31	73	40	65	40	110
Max length	78	73	106	99	118	118
% spawning	91.4	100	94.5	100	96.4	100
Unknown						
Number	7	7	52	–	66	–
Mean length	84.6	84.6	60.1	–	42.4	–
SD length	15.5	15.5	21.0	–	13.4	–
Min length	68	68	31	–	30	–
Max length	107	107	117	–	109	–
% spawning	0%	0%	0%	–	0%	–

detected on 1 August. The peak number of tagged fish simultaneously present in the array (15 fish) in 2011 occurred on 28 May.

Over eight million tag detections were recorded in 2010 and 2011. However, the majority were duplicate detections of tags simultaneously within the range of multiple receivers. Consequently, the VPS processing algorithm yielded a total of 363 272 individual positions with an estimated HPEm below our maximum threshold of 10 m (Table 2). After cropping the dataset for the post-release interval (7 d), a total of 47 fish (23 males; 24 females) had sufficient positions for estimating UDs. The median interval between positions was <3 min in both years, but was slightly higher in 2010 due to the larger number of fish tracked that year. Some fish occasionally left the array during their spawning season, which was defined as the period between the first and last detections in a given year. Any interval between positions more than 1 h was considered a departure from the array. On average, males spent approximately twice as much time outside of the array than females (Table 2; Wilcox rank-sum test, $P = 0.0212$); however, the median departure from the array was <3 h for both sexes.

The receiver array was dramatically reduced in size (from 28 to 4 receivers) upon the opening of the fishery on 21 July. During the closure period, each individual appeared to make daily visits to the area covered by the smaller array. Therefore, it seems reasonable to assume that the smaller array adequately documented the end of the spawning period. However, due to its limited detection area, the smaller array did not prove useful in the creation of UDs. Fortunately, more than 90% of the tagged fish had left the area before the opening of the fishery in both years. Therefore, it appears that the larger VPS array during the closure period captured the majority of the spawning season for most individuals. The GLMM analyses revealed a strong SEX effect in the best fitting model for all behaviour metrics (Table 3). PERIOD or

SEX:PERIOD interactions were significant predictors in each model as well, indicating a strong diel influence on behaviour, with each gender responding differently to the change in diel period. A lack of a significant YEAR effect in all metrics indicates little interannual variability in spawning behaviour.

Males exhibited a two- to fourfold diel difference in the core area occupied by individual fish (UD_{50}), ranging from 0.5 ha at night to 1.4–2.4 ha during the day (Table 4, Figure 4). Females showed less diel change in area occupied, remaining within a UD_{50} of 0.6–0.7 ha at night and 0.9–1.2 ha during the day. A similar pattern was also apparent in the broader measure of home range (UD_{95}). Females showed a higher affinity for a particular location than males, both during the day and at night. Both genders exhibited a three- to eightfold increase in site affinity during the day, indicating that tagged cod tended to seek out new areas each night but returned to the same area each day. On average, females were ~3 m above the bottom during the night, and within a metre of the bottom during the day. Males had less diel difference in depth, typically remaining within 2 m of the bottom both day and night. Both males and females exhibited higher aggregation intensity during the day; however, females were more aggregated than males both day and night.

The location of the spawning aggregation was remarkably consistent between years. The year-to-year change in average position of females was only 9 m at night and 104 m during the day (Table 5). Similarly, the interannual change in average male position was higher during the day (360 m) than at night (75 m). Males tended to move west at night, while females tended to move to the north. Interestingly, the average male position was consistently west of the average female position by several hundred metres in both years, regardless of diel period, suggesting some amount of segregation among the sexes.

The composite UDs of all tagged individuals showed that during the daytime, males were active over a 160–256 ha area (UD_{95}) extending west from the gravel bar out over the muddy plain (Table 6, Figure 5). The core area of male activity (UD_{50}) during the day increased from 5 ha in 2010 to 46 ha in 2011, which is potentially a result of an increase in the size of the fishery closure area. At night, the area occupied by all males either increased (2010) or stayed roughly the same (2011), despite individual males occupying much smaller areas. As a result of male disaggregation at night, the composite UD appears as a patchy pattern resulting from the accumulation of individual territories (Figure 6). Regardless of diel period, males restricted their movements to the muddy plain west of the gravel bar. Female's collective use of space was slightly larger at night (139–170 ha) than during the day (113–125 ha), as measured by the UD_{95}. However, the core area of female activity (UD_{50}) was seven to eight times larger at night than during the day. In both years, all tagged females could be found inside of a 1.6 ha UD_{50} during the day, essentially outlining the limits of the gravel bar at the centre of the SCCZ. The tendency of females to make periodic excursions from the gravel bar at night causes the composite UD to appear as a tangle of linear trajectories radiating from a single core area (Figure 6).

Discussion

Our results identify clear gender-related diel patterns in movement and space use among Atlantic cod on a spawning ground. During the day, females remained aggregated close to the bottom in one small location that varied little within and between years. Males were also aggregated during the day, but occupied a much larger adjacent
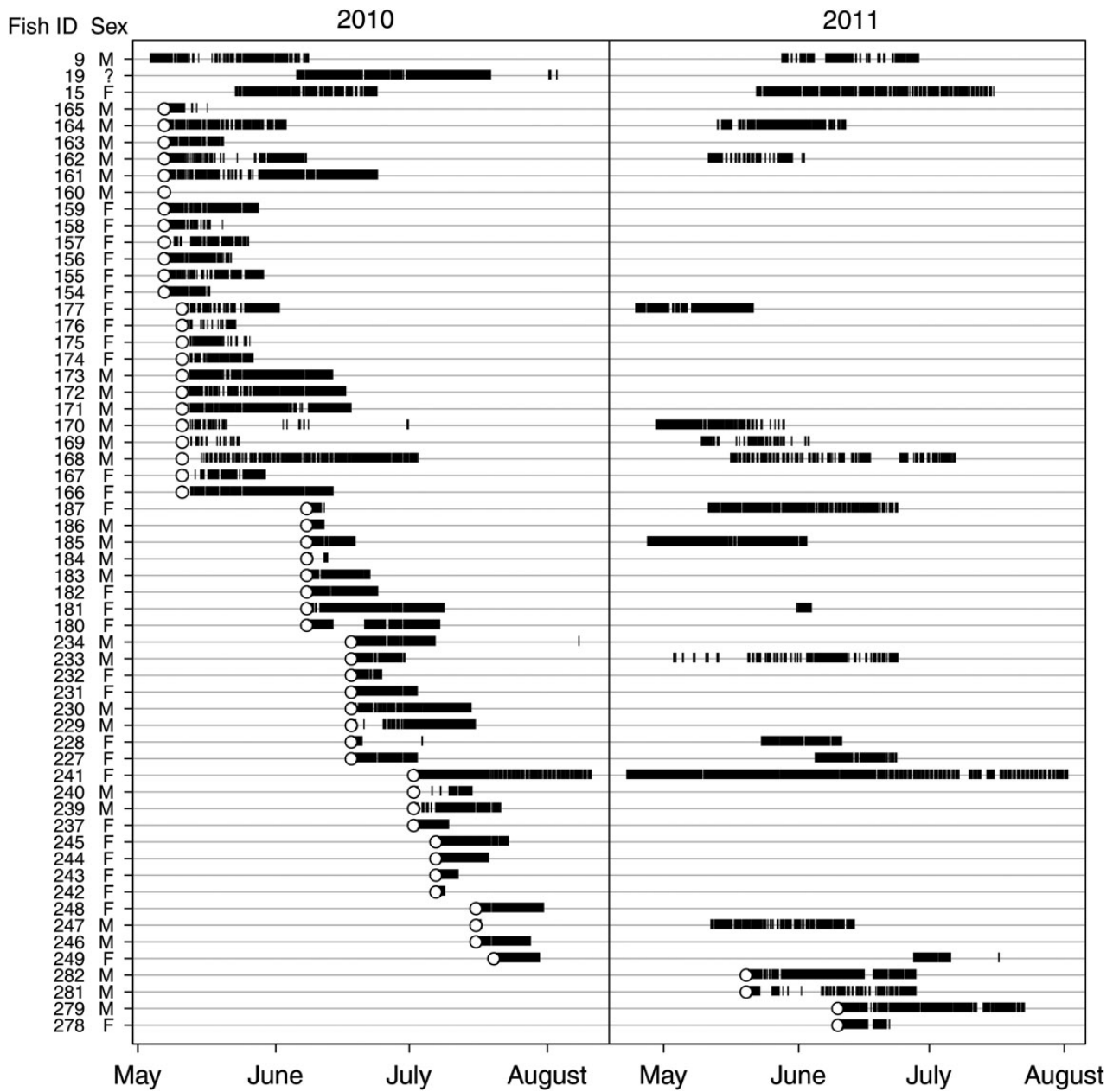
Figure 3. Detection timeline for acoustically tagged cod in the Spring Cod Conservation Zone (SCCZ) in 2010 and 2011. Open circles indicate the release date, whereas black bars indicate detections. Fish IDs 9, 15, and 19 were released in 2009.

area to the west. At night, these behaviours changed as both genders disaggregated, males more so than females. Individual males sought out separate small territories each night, while females generally remained near their daytime aggregation site, making periodic excursions into the surrounding area. Females moved higher in the water column at night, while males tended to remain close to the seabed both day and night. These patterns in behaviour were surprisingly stable over the 2 years of observation (Figures 5 and 6).

In many ways, our observations are consistent with the results of tank experiments describing cod spawning behaviour. The limited space use and disaggregation by males at night supports the notion of individual territories for display and courtship (Brawn, 1961; Hutchings *et al.*, 1999). Several studies reported that females

were segregated from males during the spawning period (Brawn, 1961; Kjesbu, 1989; Meager *et al.*, 2009). Similarly, we found that males and females favoured different areas, although substantial overlap remained both day and night. Both Brawn (1961) and Kjesbu (1989) found that spawning occurs primarily at night, with most individuals joining a "passive" aggregation during the day. Our results support this concept, as both genders were more aggregated during the day, and spawning-related behaviours (male territories, female excursions, vertical movement) were more common at night.

However, our findings differ from these studies in a few key ways. Both Brawn (1961) and Hutchings *et al.* (1999) support the concept of a dominance hierarchy wherein only the largest, most dominant

males form territories that they defend from other males through agonistic interactions. Female cod have been shown to preferentially select dominant males with territories for mating (Brawn, 1961) and paternity analysis of the offspring from captive cod has shown

Table 2. Summary of tag positions calculated from detections made by the acoustic receiver array in 2010 and 2011.

	Females	Males
2010		
Individuals tracked	25 (1/24/−)	21 (1/20/−)
Relocated positions	78 894	77 485
Median position error (HPEm)	2.8 m	2.9 m
Median position interval	150 s	162 s
Mean % of season outside array	20.7%	37.0%
2011		
Individuals tracked	9 (1/7/1)	12 (1/8/3)
Relocated positions	104 737	102 606
Median position error (HPEm)	3.0 m	3.1 m
Median position interval	116 s	128 s
Mean % of season outside array	20.3%	41.0%

Notes: The number individuals tracked in a given year is provided in total, and by year tagged in parentheses (2009/2010/2011). Position error is the estimated distance (m) separating a calculated position and the true location. Position interval (s) is the amount of time separating consecutive detections for an individual fish. The per cent of a fish's season spent outside the array was calculated as the sum of the detection "gaps" (time between consecutive detections separated by more than 1 h) divided by its "season" (time difference between the first and last detections).

Table 3. *P*-values associated with independent variables of best fitting models for each behaviour metric.

Dependent variables	Independent variables		
	Period	Sex	Period × sex
Area occupied (UD_{50})	0.2055	0.0030	0.0034
Area occupied (UD_{95})	0.0389	0.0027	0.0180
Height above bottom	<0.0001	0.0013	<0.0001
Site affinity	0.0083	<0.0001	−
Aggregation	<0.0001	0.0003	0.0050

that larger, dominant males achieve the highest reproductive success, a phenomenon known as "mating skew" (Bekkevold *et al.,* 2002; Rowe *et al.,* 2008; Skjæraasen and Hutchings, 2010). Furthermore, male dominance hierarchies have been found to be stable over the course of an entire season (Hutchings *et al.,* 1999), or until the dominant male is depleted of sperm (Bekkevold *et al.,* 2002). Our findings suggest that the presence of these behaviours in captive spawning cod may result from confinement, and extrapolation to wild spawners may be unwarranted. If the natural size of an individual male territory is greater than or equal to the dimensions of a laboratory tank, only one fish would be expected to form a territory. Furthermore, it seems logical that only the largest male would be successful at defending this territory from competitors. In the wild, physical space is not as limited and mature males may choose to establish their own territory, rather than challenge a larger male for his. Our observations indicate that males are not faithful to a specific location when they form individual territories at night. It seems unlikely that a social hierarchy determined through agonistic interactions in defence of a specific territory would persist if a new location is chosen each night, and that location is abandoned during the day; any investment in securing a position in the hierarchy would be lost and have to be re-established each night. Furthermore, it seems somewhat implausible that a social hierarchy would persist within an aggregation of thousands, if not millions of conspecifics. A persistent male dominance hierarchy and strong mating skew are common in avian leks, but they typically contain less than a hundred individuals (Widemo and Owens, 1999), with mating skew increasing as the size of the lek decreases (Widemo and Owens, 1995). While female mate choice is likely a universal component of the cod mating system, the extent to which male dominance hierarchies and mating skew play a role may be amplified by the artificially smaller lek caused by a laboratory tank. However, it should be noted that regional variation in reproductive strategy may exist, and while there is little evidence supporting a male dominance hierarchy in the present study, this may not be the case elsewhere.

The vertical movements of spawning cod have been directly observed in captivity, and remotely described via telemetry and hydroacoustic surveys. Laboratory studies have typically found
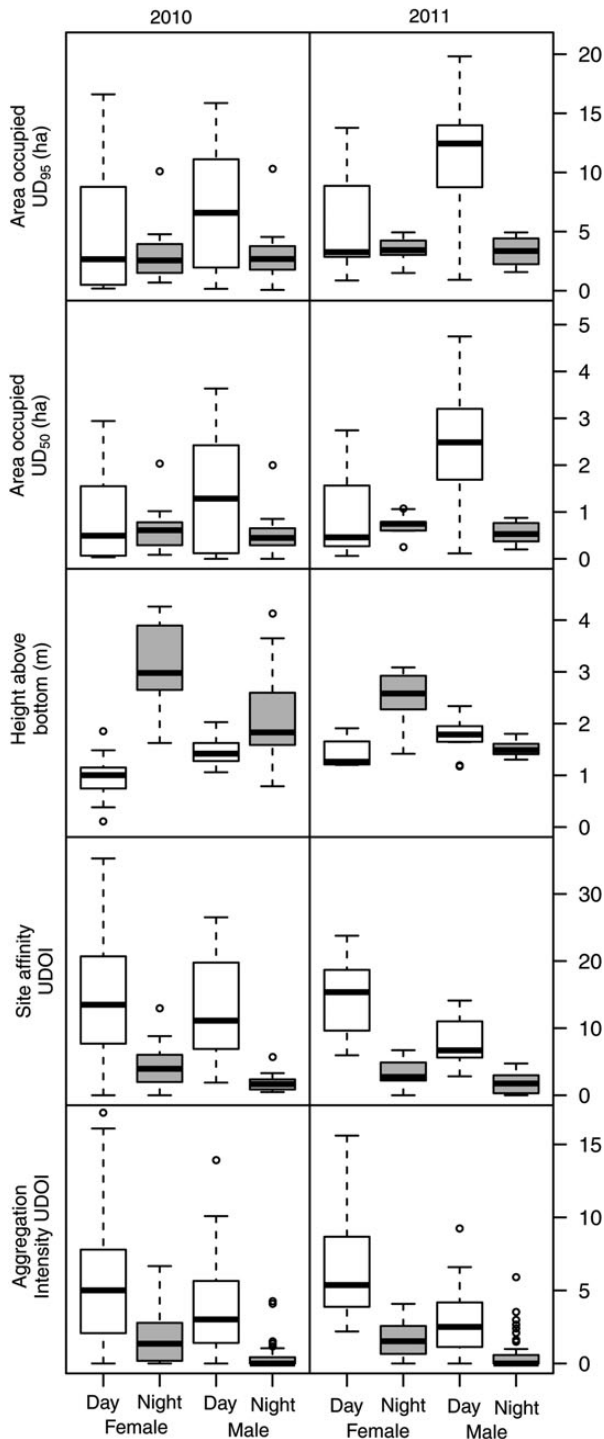
Table 4. Mean values (standard deviation) associated with each individual behaviour metric by year, gender, and diel period.

	Area occupied (ha)		Height above bottom (m)	Site affinity (UDOI)	Aggregation intensity (UDOI)
	UD_{50}	UD_{95}			
2010					
Female					
Day	1.17 (1.7)	5.79 (7.1)	0.90 (0.5)	14.76 (9.9)	5.82 (4.9)
Night	0.61 (0.4)	3.05 (2.1)	3.20 (1.0)	4.28 (3.1)	1.82 (1.7)
Male					
Day	1.43 (1.3)	7.37 (5.6)	1.50 (0.3)	14.05 (11.2)	3.71 (3.2)
Night	0.54 (0.4)	3.09 (2.1)	1.96 (0.8)	1.84 (1.3)	0.35 (0.8)
2011					
Female					
Day	0.91 (0.9)	5.51 (4.3)	1.32 (0.5)	14.65 (6.6)	7.09 (5.1)
Night	0.73 (0.3)	3.59 (1.1)	3.12 (2.0)	3.41 (2.3)	1.67 (1.3)
Male					
Day	2.37 (1.3)	10.96 (5.4)	1.79 (0.3)	7.83 (3.8)	2.74 (2.0)
Night	0.56 (0.2)	3.30 (1.4)	1.48 (0.1)	1.85 (1.7)	0.59 (1.1)

Notes: UD_{50} and UD_{95} represent the area inside the 50th and 95th probability contours of individual fish UDs. Site affinity is measured by the amount of UD_{95} overlap (UDOI) on consecutive dates for a given fish. Aggregation intensity is measure by the average amount of UD_{95} overlap (UDOI) between all possible inter-fish combinations within a group.

Figure 4. Box plots of mean behaviour metrics, by year, gender, and diel period (from top to bottom): mean area occupied per individual, as measured by the UD 50% and 95% probability contours; mean height above bottom per individual (m); mean site affinity per individual, as measured by the UD overlap index (UDOI) between consecutive periods; aggregation intensity, as measured by the mean UDOI of all possible inter-fish combinations within a group.

that females occupy a higher place in the water column than males when not actively engaged in courtship or spawning events (Hutchings *et al.,* 1999; Meager *et al.,* 2009). Courtship activity

Table 5. Distance (m) between the average position of each gender, diel period, and year combination.

	2010				2011			
	Female		**Male**		**Female**		**Male**	
	Day	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**
2010								
Female								
Day	0	198	182	768	104	191	542	704
Night		0	247	765	105	9	531	692
Male								
Day			0	586	225	238	360	522
Night				0	794	758	234	75
2011								
Female								
Day					0	101	561	725
Night						0	524	686
Male								
Day							0	164
Night								0

Table 6. Total area occupied by all tagged individuals of a group by year, gender, and diel period.

	Area occupied (ha)	
	UD$_{50}$	**UD$_{95}$**
2010		
Female		
Day	1.6	125.3
Night	11.4	138.8
Male		
Day	4.5	160.0
Night	34.6	215.7
2011		
Female		
Day	1.6	112.9
Night	13.6	169.9
Male		
Day	45.5	255.7
Night	41.6	240.1

Notes: UD$_{50}$ and UD$_{95}$ represent the area inside the 50th and 95th probability contours of a composite UD.

appears associated with the seabed, while the ventral mount and actual spawning release occurs near the surface (Brawn, 1961; Hutchings *et al.,* 1999; Meager *et al.,* 2009). However, it should be noted that the vertical dimensions of the experimental tanks in all studies were 3 m or less, limiting their relevance to natural spawning conditions. In our study, we never recorded tagged cod more than 20 m above the seabed, which was still ∼35 m below the surface. While reports of the vertical behaviour of spawning cod in captivity are fairly consistent, there appears to be substantial diversity among regions in the wild. In some areas, spawning cod favour a pelagic distribution (Godø, 1989; Nielsen *et al.* 2013), while in other locations they are associated with the seabed (Lawson and Rose, 1999; Meager *et al.*, 2009; Siceloff and Howell, 2013). In Newfoundland, spawning aggregations of cod are typically close to the bottom during the day, yet become pelagic at night (Ouellet *et al.;* 1997, Rose, 2003; Fudge and Rose, 2009). Large pelagic "columns" of cod have been observed via echosounder during the spawning season (Rose, 1993; Knickle
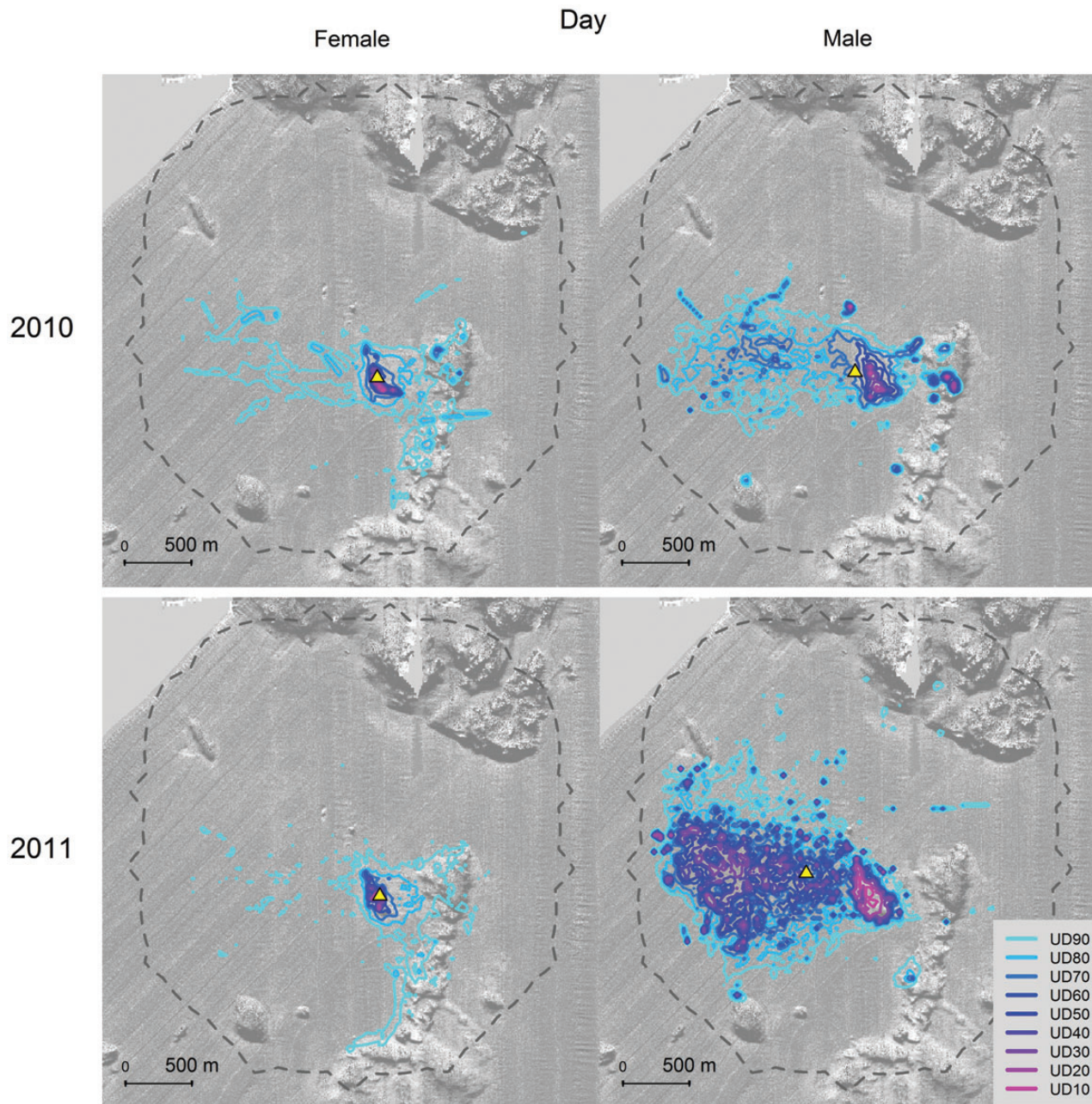
Day

Figure 5. Probability contours extracted from the composite daytime UD of acoustically tagged cod, by year and gender. The dashed grey line represents the approximate detection limit of the acoustic array. The yellow triangle identifies the average daytime position for that gender and year.

and Rose, 2012), yet this behaviour is rarely observed outside of Canada. Despite extensive behavioural plasticity, there are some common elements to the studies describing individual vertical movements (i.e. laboratory and telemetry observations): females generally occur higher in the water column than males, and females move higher in the water column at night. Our findings are consistent on both these points.

Cod spawning grounds have often been identified by an abundance of ripe fish in survey or fishery catches (Lawson and Rose, 2000). In addition, it is common to find strongly skewed sex ratios on a spawning ground, typically with the majority being male (Morgan and Trippel, 1996; Nordeide, 1998; Jakobsen and Ajiad, 1999; Armstrong *et al.,* 2004). From these observations, it has

been inferred that males arrive on the spawning ground first and remain there more consistently than females. Females are believed to be more widely dispersed and less consistently present on the spawning ground. Per the theory, females periodically enter the male-dominated aggregation from the periphery when ready to spawn. However, the idea that sex ratios can be used to infer patterns in distribution is based on the assumption that there is a negligible difference in catchability between the genders. Our results indicate that not only are females more consistently present, they are also more densely aggregated and more faithful to a particular locale. This gender disparity in aggregation behaviour could explain the male-skewed sex ratios commonly found on spawning grounds. While still aggregated, males are far more wide ranging than
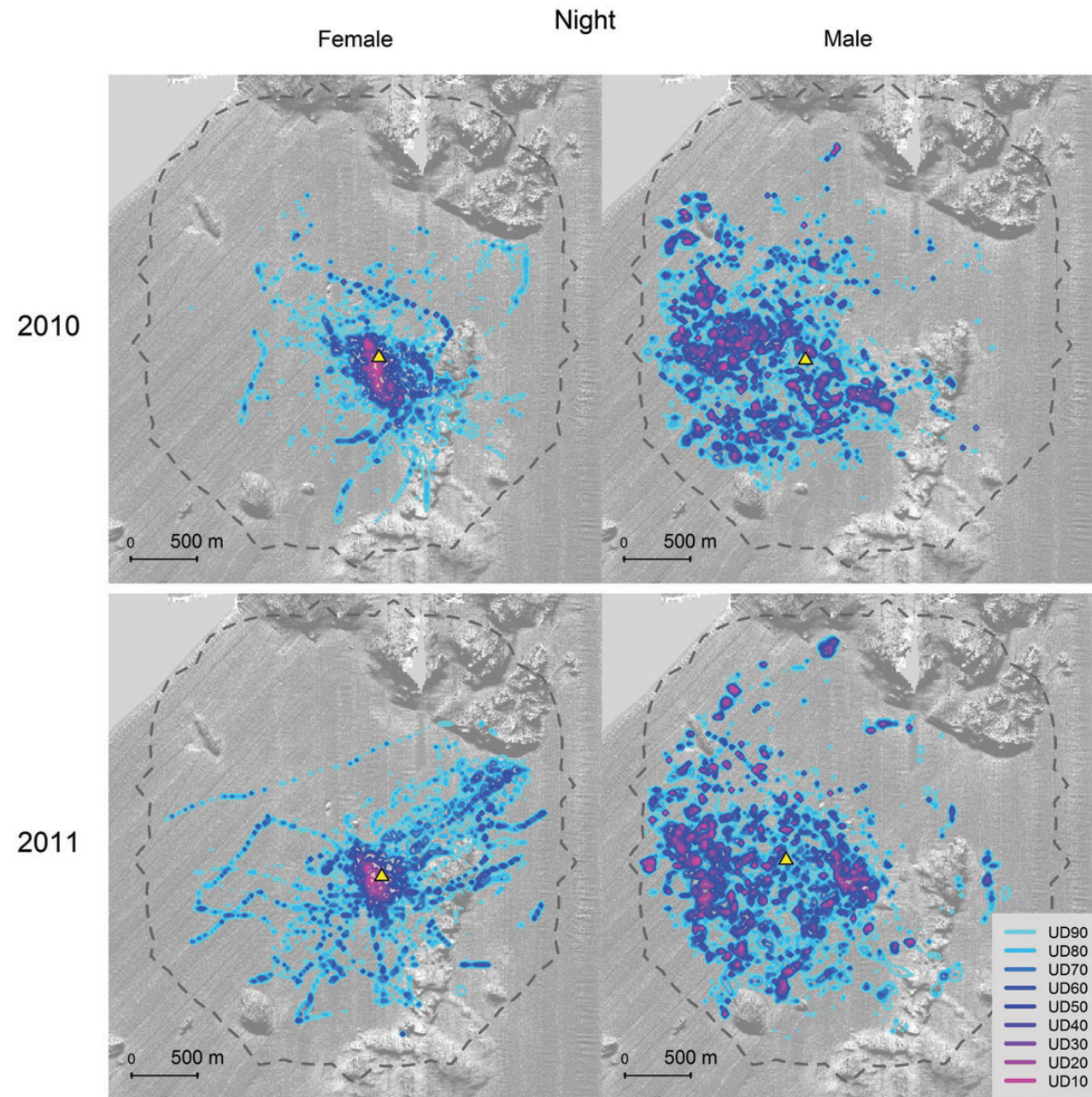
Figure 6. Probability contours extracted from the composite night-time UD of acoustically tagged cod, by year and gender. The dashed grey line represents the approximate detection limit of the acoustic array. The yellow triangle identifies the average daytime position for that gender and year.

females, making them more susceptible to encounters with fishing gear. Our experience with angling for cod in the SCCZ supports this idea. The initial telemetry work in this area in 2009 identified the site of the female-dominated aggregation (Dean *et al.,* 2012). Since this was the most productive fishing location, much of our angling effort was focused here in 2010 and 2011. Consequently, the overall sex ratio of our catches was dominated by females (Table 1). Yet, whenever the research vessel drifted off of this location, the sex ratio of catches quickly became more male-dominated.

The influence of spawning behaviour on the observed sex ratio has important implications for the assessment and management of this species. Stock demographics (e.g. size distribution, fecundity, sex ratio, etc.) can vary dramatically over time; yet, it is common to

use spawning-stock biomass (SSB) as a measure of the reproductive potential of the stock, which assumes constancy in the demographic variables that influence egg production and thus recruitment (Marshall *et al.,* 2006). Recently, efforts have been made to incorporate more biological information into assessments, and measures such as female spawning biomass and total egg production have been favoured over SSB (Marshall *et al.,* 2006; Morgan, 2008; Lambert, 2013). The proportion of females in the population (i.e. sex ratio) is an integral component to these alternative measures of stock reproductive capacity. Our findings caution reliance upon sex ratio information collected near known spawning grounds, as these data are likely biased towards males, which would underestimate female-based measures of spawning stock.

The behaviours observed in this study could inform the spatial distribution of cod on spawning grounds elsewhere. Tank studies from both sides of the Atlantic have indicated that spawning occurs mainly at night, and that the sexes are typically segregated during spawning (Brawn, 1961; Kjesbu, 1989; Hutchings *et al.,* 1999). Our observations corroborate both these points, which lead us to believe that there are aspects of the cod mating system that are common to all cod stocks. Yet, the scale on which these spawning behaviours occur remains unclear. The spawning component protected by the SCCZ is a relatively small aggregation within a relatively small cod stock (NEFSC, 2013). In contrast, spawning aggregations in Canada and Norway have been shown to span many kilometres and contain millions of fish (Ouellet *et al.*, 1997; Nordeide and Kjellsby, 1999; Rose, 2003). If these larger groups of fish exhibit comparable diel and gender patterns in behaviour, do they form a single large female aggregation? Or, are there multiple smaller groups of densely aggregated females distributed sporadically throughout the spawning ground? It would seem energetically impractical to have all members of one gender many kilometres apart from the other gender, as was previously suggested from the examination of sex ratios from bottom trawl surveys (Morgan and Trippel, 1996). Interestingly, both Morgan and Trippel (1996) and Nordeide (1998) found a small portion of female-skewed sets scattered among most of the male-dominated sets on the spawning ground, providing evidence of a network of multiple small female-dominated aggregations.

Both Espeland *et al.* (2007) and Meager *et al.* (2010) used an acoustic telemetry positioning system to describe the space use of wild spawning cod in two separate Norwegian fjords. The home ranges (UD$_{95}$) of individual fish in both studies (Espeland: 3–77 ha; Meager: 2–51 ha) were somewhat larger than our estimates (0.2–27 ha), but this is to be expected given their kernel density approach to estimating the UD. In contrast to our findings, Meager *et al.* (2010) found that males as a group occupied a smaller area than females, and males exhibited more overlapping space use than females. However, with only three receivers, perhaps a significant portion of the movements of their tagged fish went unobserved. In fact, 20 of their 48 tagged fish did not yield sufficient positions to estimate a UD. In the SCCZ, our perception of the aggregation extent was broadened significantly between the 4-receiver array of 2009 (Dean *et al.*, 2012) and the 28-receiver array of 2010–2011. Furthermore, our results identify a strong diel component to cod spawning behaviour, and for this reason it is difficult to make direct comparisons to these earlier studies that did not evaluate day/night differences. Regardless, all acoustic telemetry studies of spawning cod (present study included) confirm the observations made in captivity of sexually dimorphic behaviour.

The dramatic diel difference in behaviour observed in this study has important implications for the monitoring and protection of cod spawning aggregations. The location, intensity, and spatial extent of the spawning aggregation varied significantly from day to night. Ignoring this spatio-temporal pattern in the design of spawning protection measures can have negative consequences. For example, the initial SCCZ fishery closure in 2009 was based around knowledge of the female-dominated daytime aggregation. However, upon reviewing the telemetry observations included in this paper, it was clear that many fish (primarily males) were leaving the closure at night. Consequently, managers doubled the size of the SCCZ in 2011 to ensure the integrity of the spawning aggregation and prevent overexploitation and fishery-induced disruption (Dean *et al.*, 2012; Armstrong *et al.,* 2013). This change in the

size of the closure could explain the larger spatial extent of the aggregation in 2011 (Table 5; Figure 5). Spawning cod have been shown to react to and avoid both gillnet and trawl fishing activity (Morgan *et al.*, 1997; Dean *et al.*, 2012). Although speculative, fishing pressure immediately outside of the closure may have caused individual fish to avoid the margins and restrict their movements to the interior. Interestingly, both the closure and aggregation extent expanded in an east–west direction in 2011.

In the present study, space use did not appear random with respect to local bathymetric features. In both years, the main focal point of the aggregation was a 2 ha gravel bar near the centre of the array with ∼2 m of vertical relief (Figure 2). Both males and females frequented the surrounding flat muddy area at night, but appeared to avoid entirely the bedrock ledges to the north and east (Figure 2). This preference for a particular habitat during spawning is similar to observations of spring-spawning cod in nearby Ipswich Bay (Siceloff and Howell, 2013). In that study, spawning cod were active over "muddy flats" in 60–70 m of water, bounded by a series of "rocky humps" with 30 m of vertical relief, and were most frequently observed around a small bathymetric feature (∼6 ha) with 4 m of relief. This similarity in habitat utilization between Massachusetts Bay and Ipswich Bay cod suggests a common reproductive strategy among genetically related spring-spawning components (Kovach *et al.*, 2010). It is not evident what distinguishes this particular gravel bar from others in Massachusetts Bay, as there are a number of seemingly similar bathymetric features within a 10 km radius. Presumably, this location is associated with other favourable oceanographic conditions suitable for the survival of early life stages; Massachusetts Bay in general has been shown to be an area that promotes the local retention of cod larvae (Huret *et al.*, 2007; Churchill *et al.*, 2011) and provides suitable habitat for juveniles (Howe *et al.*, 2002).

In many regions, Atlantic cod are a migratory species, often wandering hundreds of kilometres in search of forage or favourable environmental conditions before returning to their spawning ground each year (Robichaud and Rose, 2004). This interannual spawning site fidelity is well documented and has been shown to occur on the scale of <1 km (Robichaud and Rose, 2001; Skjæraasen *et al.,* 2011). The level of homing to a particular site observed in the present study was astonishing, with only 9 m separating the mean night-time position of females in 2010 and 2011 (Table 5). Although not presented here, telemetry observations from 2009 (Dean *et al.*, 2012) and 2012 confirm the persistence of this aggregation focal point in those years as well. Such extreme site fidelity underscores the need to protect spawning aggregations, as their spatial and temporal reliability make them particularly vulnerable to overexploitation and disruption from fishing activity (Sadovy and Domeier, 2005; Dean *et al.*, 2012). Furthermore, the fine scale on which spawning site fidelity occurs suggests a potential mechanism for evolutionary divergence in populations that share adjacent spawning grounds (e.g. Nordeide 1998; Kovach *et al.* 2010; Grabowski *et al.* 2011).

The ability of these spawners to navigate to an exact location each year is particularly intriguing. With individual fish returning to the same fixed location each day of each season, it seems visual cues must play a role in how they orient themselves on the spawning ground. Some species of fish have been shown to use landmarks to return to a particular location (Dodson, 1988). Both field and laboratory experiments have shown that fish have the ability to learn the position of and route to a desirable location (e.g. for feeding or spawning) from more experienced "demonstrators" (Brown and Laland,

2003). Rose (1993) used hydroacoustic observations of migrating cod off Newfoundland to propose that smaller fish followed the lead of larger "scouts". The mere existence of such extreme site fidelity in an open marine system suggests that social learning plays a role in the spatial persistence of spawning aggregations, and that cod may experience diminished recruitment success if the age structure becomes truncated and the evolutionary "knowledge" to spawn at an optimal location is lost.

This study furthers our understanding of cod spawning behaviour by providing critical details that connect the findings of earlier laboratory experiments and field observations. Our results identify strong diel and gender-based differences in the spatial distribution and aggregation behaviour of spawning cod. However, it remains to be seen whether the behaviours observed in this study are a property of spring-spawning Gulf of Maine cod, or of the species in general. Similar investigations made elsewhere in the Gulf of Maine or in other stocks would contribute greatly to answering this question. Regardless, our findings provide an empirical example of how spawning behaviour can influence the fine-scale distribution of Atlantic cod. Acknowledging and understanding these patterns can aid in the design of more effective management measures and help reduce biases in stock assessments.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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