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ARTICLE

Disruption of an Atlantic Cod Spawning Aggregation Resulting from the Opening of a Directed Gill-Net Fishery

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Abstract
Atlantic cod *Gadus morhua* exhibit multiyear homing to discrete spawning grounds, where they aggregate in dense schools. Within an aggregation, a series of complex mating behaviors takes place before mate selection and successful spawning. Disruption of these behaviors has been suggested as a cause of diminished reproductive success and poor recruitment in some stocks. An area known to support a spawning aggregation in Massachusetts Bay was closed to both commercial and recreational fishing for the months of May and June 2009. During the closure period, 10 Atlantic cod were captured, tagged with acoustic transmitters, and released back to the aggregation. Four stationary acoustic receivers were deployed in the area to record transmissions from the tagged fish. Overlapping detection ranges of the receivers allowed for the reconstruction of fine-scale movements of the tagged fish over several days. The tagged cod showed a consistent pattern of aggregation prior to the fishery, characterized by limited movement and similar space use. With the opening of the fishery, the aggregation behavior was disrupted, resulting in increased horizontal and vertical movements and dissimilar space use among individuals. Half of the tagged fish appeared to have been caught in gill nets within 9 h of the opening, while the remainder left the area within 18 h. Even though the receivers were maintained for 9 d after the opening, none of the tagged fish that left the area returned. These results indicate that the spawning aggregation was completely dispersed by the onset of the fishery. Managers hoping to protect spawning aggregations should be aware that the effects of fishing on a spawning aggregation go beyond the removals from the spawning stock.

Throughout their range, Atlantic cod *Gadus morhua* form spawning aggregations in locations and seasons that are persistent from year to year (Robichaud and Rose 2001; Espeland et al. 2007; Vitale et al. 2008; Meager et al. 2010; Skjæraasen et al. 2011). This spawning site fidelity has led to the belief that groups of spawning fish represent unique subpopulations and are therefore vulnerable to extirpation. Recent studies have confirmed that spawning groups within the same stock are genetically distinct (Ruzzante et al. 2000; Wirgin et al. 2007; Kovach et al. 2010). Within the Gulf of Maine, several coastal spawning groups have been exploited by fishermen for centuries (Alexander et al. 2009). Unfortunately, these aggregations have diminished in both number and magnitude in recent decades and concerns regarding reduced reproductive capacity of the stock have risen (Ames 2004; ICES 2005). Historically productive Atlantic cod spawning grounds along the coast of Maine are now barren during the spawning season, and the majority of spawning activity in the Gulf of Maine is currently centered along the New Hampshire and Massachusetts coasts in Ipswich and Massachusetts bays (ICES 2005).

In an effort to protect the remaining coastal spawning groups in the Gulf of Maine, two separate Cod Conservation Zones have been created within Massachusetts Bay that prohibit both commercial and recreational fishing during the spawning seasons. One closure, known as the Winter Cod Conservation Zone (WCCZ), protects a spawning aggregation in central Massachusetts Bay in December and January. This study was conducted in the other closure, known as the Spring Cod Conservation Zone (SCCZ), which protects a spawning aggregation in northern Massachusetts Bay in May and June. Before creation

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of the SCCZ, this area had been closed to commercial fishing for the months of April, May and June under a fishing effort control program known as "rolling closures"; however, the area remained available to recreational exploitation (Howell et al. 2008). A dramatic increase in recreational fishing pressure, as well as the scheduled retirement of the rolling closure program, prompted the creation of the SCCZ in 2009. Recent observations of the aggregation indicate that very few cod remain in the area once the commercial fishery opens in July. However, it has previously been unclear whether the aggregation ceased naturally or was dispersed by the onset of the directed commercial fishery.

Within a spawning aggregation, Atlantic cod exhibit a complex set of mating behaviors known as "lekking" (Hutchings et al. 1999; Nordeide and Folstad 2000; Windle and Rose 2007). Males are believed to form a dense aggregation in which they compete with one another for positions of dominance over a small area. This competition occurs in the form of courtship displays, vocalizations, and aggression towards rival males (Brawn 1961). Females visit the aggregation, select a dominant mate from the hierarchy of males and initiate a spawning event (Rowe et al. 2008). Disruption of this complex spawning behavior by fishing activity has been suggested as a mechanism for diminished reproductive success and poor recruitment in some cod stocks (Morgan et al. 1999; Robichaud and Rose 2003; Rowe and Hutchings 2003). However, little direct evidence has been provided thus far that shows an intrinsic biological benefit from protecting fish during the act of spawning (Halliday 1988; Hutchings 1996).

There has been much discussion recently about the design of Marine Protected Areas (MPAs) to achieve fishery management and conservation goals. Small-scale single-species seasonal closures have been disparaged in favor of larger year-round no-harvest reserves that protect a variety of species and habitats (Horwood et al. 1998; Murawski et al. 2000). Furthermore, the utility of area-based closures for temperate migratory stocks in general have been questioned because theoretically any protection offered by the closure is negated if the fish are caught elsewhere once they leave the closure area (West et al. 2009). Yet, seasonal spawning closures may still provide benefits even if the realized reduction in fishing mortality on the overall spawning stock is negligible. If a large portion of the stock-wide fishing mortality is taken from a unique spawning aggregation, it may be exploited beyond its capacity to sustain itself and the evolutionary "knowledge" to spawn at that time and place could be lost (Frank and Brickman 2000). In addition, shielding spawning fish from fishery-induced disruption may also allow adult spawners to more effectively realize their reproductive potential, thereby enhancing recruitment (Halliday 1988; Hutchings 1996).

For several days leading up to and following the lifting of a fishery closure we observed the fine-scale movement patterns of acoustically tagged Atlantic cod individuals in a spawning aggregation in Massachusetts Bay. Our objective was to determine whether the behavior of spawning cod was affected by the sudden rise in concentrated fishing activity.

METHODS

Study Site

This study was conducted within the SCCZ, a 4 km × 5.5 km rectangular area in northern Massachusetts Bay located approximately 5 km south of Gloucester, Massachusetts (Figure 1). The sea floor in this area is predominated by fine-grained sediment, occasionally interrupted by cobble and boulder deposits and large bedrock outcrops (Butman et al. 2007). The average depth within the SCCZ is approximately 50 m and the bottom temperature during May and June is between 6°C and 10°C. The prevailing ocean current along this portion of the coast is from north to south, although the complex shoreline of Massachusetts Bay and the proximity to Stellwagen Bank have been shown to produce significant eddies that serve to increase local retention of pelagic cod larvae (Huret et al. 2007).

Tagging

The spawning site was visited regularly beginning in early May 2009 and monitored via commercial echosounder for the presence of aggregating fish. Once the aggregation was detected, Atlantic cod were captured via hook and line to confirm the presence of spawners and for subsequent tagging. Sex and maturity were determined by direct examination of the gonads, unless a fish was selected for tagging, in which case sex and maturity were recorded only when externally visible. A fish was considered to be in spawning condition by the presence of hydrated eggs for females or flowing sperm for males. Because we were unable to determine spawning condition on every tagged fish, only individuals over 65 cm were selected for tagging—that is, larger cod were considered more likely to be reproductively mature and therefore an active member of the spawning aggregation.

Acoustic transmitters tags (Vemco Inc., model V16P-6H) were surgically implanted into the abdominal cavity on the ventral surface directly anterior of the vent. Each tag transmitted a unique identifier and depth reading at random intervals between 30 and 90 s at a frequency of 69 kHz. Tagged fish were allowed to recover for several minutes in a holding tank supplied with water pumped from below the thermocline to minimize thermal stress. Once a tagged fish appeared to recover, it was released to the study area.

Receiver Array

An array of four stationary acoustic receivers (Vemco Inc., VPS system, model VR2W) was maintained for the period May 30, 2009, through July 10, 2009, to record the transmissions from the tagged fish. The receivers were positioned in a diamond pattern, centered on the location where the spawning aggregation was known to occur in prior years (Figure 2). Receivers were spaced 400 m apart, with sufficient overlap in the

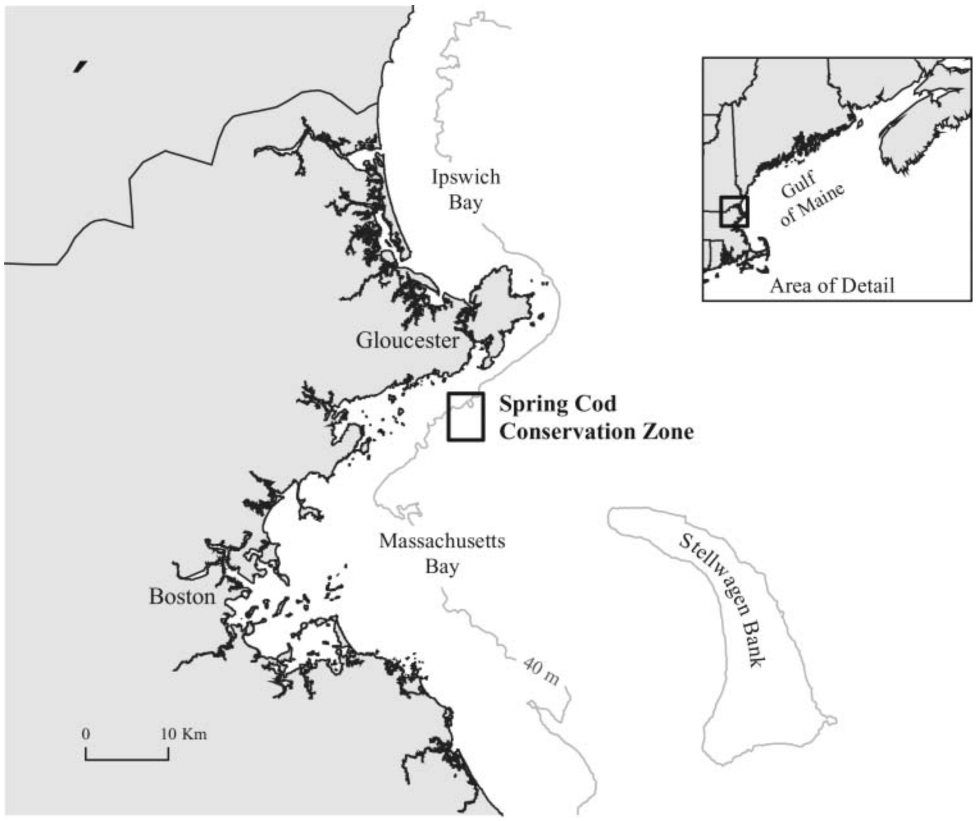

FIGURE 1. Location of the Spring Cod Conservation Zone within Massachusetts Bay in the western Gulf of Maine, which protects an Atlantic cod spawning aggregation.

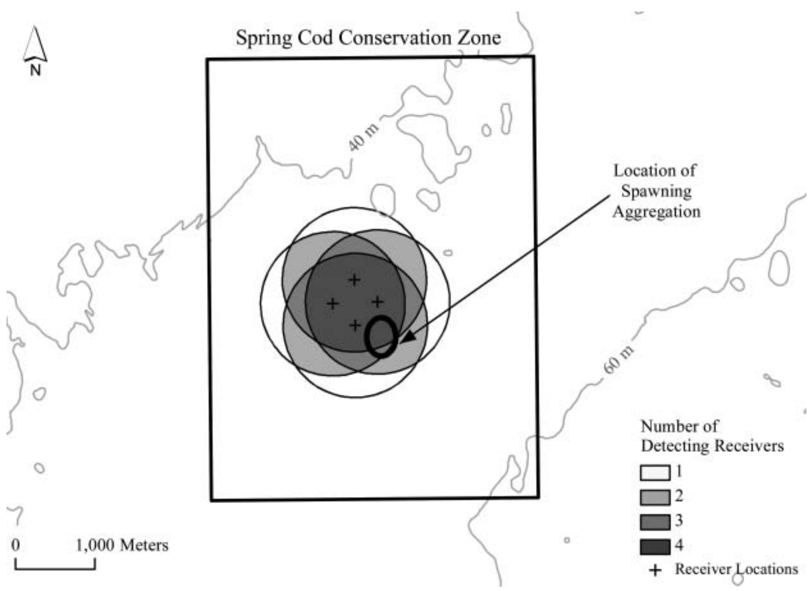

FIGURE 2. Map of the Spring Cod Conservation Zone, showing the location of the Atlantic cod spawning aggregation in relation to the acoustic receivers and their theoretical detection ranges.

detection ranges to permit simultaneous detection of tags by at least three receivers, as needed to calculate each tag's precise location via triangulation. Each receiver was moored 4 m above the bottom by attaching it to a vertical line secured to the seafloor with steel clump weights and Danforth-style anchors and marked at the surface with polyurethane balls and radar reflectors. Vertical lines were also equipped with synchronization tags, which provided a means of calibrating the position of each receiver.

Data Analysis

Raw detection data from the tagged Atlantic cod were downloaded from the receivers and sent to Vemco Inc. for processing. Processing involved using differences in detection time between receivers to calculate a precise latitude and longitude for each tag transmission. Processed data consisted of tag identification, detection time, latitude, longitude, depth, and an estimate of the horizontal position error (HPE) for each relocation. To help describe changes in aggregation behavior, the relocation points from the processed data were used to create a utilization distribution (UD) for each tagged cod for each day that it was tracked. A UD is a measure of space use that describes the probability of an individual occurring in a given area during the time of observation. Because the detection data were highly autocorrelated (relocations points were as little as 30 s apart), a Brownian bridge movement model (BBMM) was used to calculate the UD (Horne et al. 2007) with the ADEHABITAT package (Calenge 2006) of the R statistical software (Version 2.10.1, R Foundation for Statistical Computing). The BBMM creates a probability density around each successive pair of relocation points, known as a "Brownian bridge." The accumulation of these probability densities for each successive bridge yields the UD. In this way, a more precise estimate of space use is created than with a traditional kernel density estimator, which makes no assumptions about the sequence of observed relocation points.

The BBMM relies on two parameters: mean location error (δ) and Brownian motion variance ($\sigma^2{}_m$). In previous applications of this model using global positioning system telemetry, mean location error was assumed to be a single fixed value that is either known or estimated via independent experiment (Horne et al. 2007). In our case, location error was largely dependent upon where a tagged fish was located within the receiver array. Therefore, mean location error was estimated by tag and day via the HPE values from the processed data set. However, because the HPE values represent location error as the radius of a 95% confidence circle, they were converted to the error units required by the BBMM (i.e., standard deviation of normally distributed location error) using the following relationship:

$$\delta = [-\bar{x}^2/2\log_e(\alpha)]^{1/2}, \quad (1)$$

where $\bar{x}$ = the mean of the HPE values, and $\alpha = 0.05$, which is the significance level of the HPE values. Equation (1) relies on properties of the Rayleigh distribution, a circular distribution that describes normal random deviates in both X and Y directions (Evans et al. 2000). The Brownian motion variance parameter ($\sigma^2{}_m$) takes into account the mobility of the tagged fish and was empirically estimated by tag and day using the maximum likelihood approach described in Horne et al. (2007). Both δ and $\sigma^2{}_m$ function as smoothing parameters, higher values acting to distribute the probability density over a wider area.

To evaluate whether a change in behavior occurred, four measures of movement and space use were investigated with respect to the opening of the directed fishery: net movement rate, depth, site affinity, and aggregation.

Net movement rate. —A sample of relocation points at 1-h intervals was selected from the processed data set. The choice of an hourly sample here was intended to describe the amount of directed movement, as opposed to a measurement of swimming speed. The straight-line distance between hourly positions was determined for each tagged fish and divided by the time elapsed between relocations to achieve a series of net movement rates (m/h) for each tag while in range of the receiver array. The mean net movement rate was calculated for each tag and compared prefishery versus postfishery by using a paired two-sample t-test.

Depth. —Each tag was equipped with a pressure sensor that transmitted the fish's depth when within range of the receiver array. Because Atlantic cod are a demersal species, tagged fish remained within a few meters of the seafloor most of the time. As a consequence, depth observations were strongly influenced by the tidal cycle. To account for this, the tidal height for nearby Gloucester Harbor was subtracted from the raw depth observations, yielding a tag depth referenced to mean lower low water (MLLW). Because the MLLW water depth within the receiver array is relatively uniform, it can be assumed that significant changes in observed fish depth represent departures from the seafloor. The mean of the adjusted depth data were calculated for each tag and compared prefishery versus postfishery via a paired two-sample t-test.

Site affinity.—Site affinity was measured via a utilization distribution overlap index (UDOI) from Meager et al. (2010). This method relies on extracting the 95% probability contour from a UD (i.e., the area inside of which there is a 95% probability of locating the tagged fish), which we refer to as the UD_{95}. The similarity of the UD_{95} for a given fish on one day is compared to the UD_{95} for that same fish on the previous day using the following formula:

$$\text{UDOI}_{a,i,j} = 100[\text{overlap}_{a,i,j}/(\text{area}_{a,i} + \text{area}_{a,j} - \text{overlap}_{a,i,j})]; \quad (2)$$

$\text{area}_{a,i}$ = the UD_{95} for fish a on day i;
$\text{area}_{a,j}$ = the UD_{95} for fish a on day j;
$\text{overlap}_{a,i,j}$ = the overlap between the two areas.

The resulting units can be interpreted as the percentage of the area occupied by a fish that is the same from one day to the next. Therefore, a higher UDOI score in this instance indicates a higher level of site affinity. The mean daily site affinity UDOI score was calculated for each fish and compared prefishery versus postfishery via a paired two-sample *t*-test.

Aggregation.—A similar UDOI method was used to measure the level of aggregation among the tagged fish. In this instance, the UD_{95} for a given fish was compared to the UD_{95} of other tagged fish on the same day via

$$\text{UDOI}_{a,b,i} = 100[\text{overlap}_{a,b,i}/(\text{area}_{a,i} + \text{area}_{b,i} - \text{overlap}_{a,b,i})]; \quad (3)$$

$\text{area}_{a,i}$ = the UD_{95} for fish *a* on day *i*;
$\text{area}_{b,i}$ = the UD_{95} for fish *b* on day *i*;
$\text{overlap}_{a,b,i}$ = the overlap between the two areas.

In this case, the units can be interpreted as the percentage of the area occupied by two tagged fish that is the same on a given day. When averaged across all possible interfish combinations, higher UDOI values indicate more similar space-use among fish and therefore a higher level of aggregation. The mean daily aggregation UDOI score was compared prefishery versus postfishery via an unpaired two-sample *t*-test.

RESULTS

A total of 55 Atlantic cod were captured from the study area between May 6 and June 29, 2009. Males accounted for 73% of fish caught; their total length averaged 61 cm (range, 31–78 cm). Females were somewhat larger at 67 cm (range, 46–101 cm). Of the fish where maturity stage was determined, 92% were found to be in spawning condition (i.e., either ripe or recently spent gonads). The remainder were mostly smaller individuals, with either immature, developing or resting gonads.

We selected 10 cod for tagging over five dates in June (Table 1). Although sex and maturity were undetermined for six of these fish, it is likely that most were female, based on a mean size of 86 cm. Four fish that were tagged on earlier dates left the area before the fishery opening (tags F01, F02, F03, and F08; Figure 3). While one of these fish (F08) did return briefly on July 3, the fishery was already under way, and therefore its reaction to the fishery could not be assessed. As such, the majority of the analysis presented here focuses on the six tagged fish that were within range of the receiver array when the fishery opened at midnight (0000 hours) on July 1 (tags F04, F05, F06, F07, F12, and F13). These six fish were tracked for an average of 5.6 d each, yielding a total of 26,441 relocation points. The spatial and temporal resolution of these relocation data were sufficient to determine when a tagged fish was caught in a gill net. Several cod traced the outlines of a gill net minutes before becoming

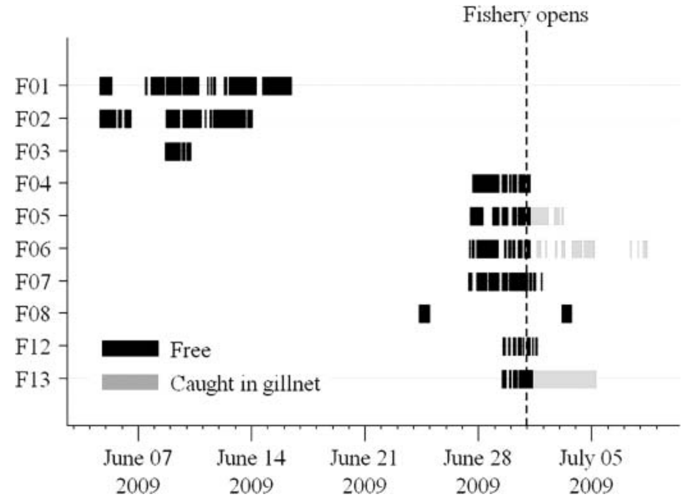

FIGURE 3. Detection times (i.e., presence in acoustic array) for acoustic-tagged Atlantic cod in Massachusetts Bay during June 2009. Black bars indicate when free-swimming tagged cod were detected by the receiver array, and gray bars indicate when tagged cod were detected but determined to be caught in a gill net.

TABLE 1. Individual fish data and relocation summary for Atlantic cod tagged with acoustic transmitters in the Spring Cod Conservation Zone of Massachusetts Bay in June 2009. Blank cells mean that status was not determined. Fate describes whether the tagged fish left the array area before (BF) or after (AF) the fishery opened on July 1 or was caught in a fishery gill net.

Tag	Length (cm)	Weight (kg)	Sex	Maturity	Date and time of day (hours) tagged	Last detection date and time of day (hours)	Days tracked	Fate
F01	68	3.7			Jun 4 at 1515	Jun 16 at 1025	11.8	Left BF
F02	71	3.8			Jun 4 at 1509	Jun 14 at 1234	9.4	Left BF
F03	73	3.2	M	Ripe	Jun 8 at 1609	Jun 10 at 0545	1.6	Left BF
F04	94	8.5	F	Ripe	Jun 27 at 1045	Jul 1 at 2138	4.5	Left AF
F05	79	5	F	Ripe	Jun 27 at 1045	Jul 3 at 0513	5.8	Caught: gill net
F06	105	12			Jun 27 at 1045	Jul 8 at 0947	11.0	Caught: gill net
F07	107	12.7			Jun 27 at 1045	Jul 1 at 2045	4.4	Left AF
F08	77	4.6			Jun 24 at 0913	Jul 3 at 1709	9.3	Left BF
F12	85	6.3			Jun 29 at 1045	Jul 1 at 1432	2.2	Left AF
F13	101	10.6	F	Ripe	Jun 29 at 1045	Jul 5 at 0607	5.8	Caught: gill net

enmeshed, where relocations were stationary for 2–7 d before the nets were hauled (Table 1). We concluded these three fish were caught in gill nets within 9 h of the fishery opening. The remaining three fish appeared to leave the area within 18 h of the fishery opening and did not return before the receivers were removed 9 d later on July 10. The objective of this study was to describe the change in behavior of live free-swimming cod, so relocation points after being caught in gill nets were omitted from the analyses because they would introduce significant bias to the calculation of movement rates, depths, and utilization distributions.

A significant prefishery–postfishery change was detected in all four behavior metrics that we evaluated. Before the fishery opening, tagged fish moved relatively little, achieving a mean net movement rate of 63.2 m/h. After the fishery opened, this rate increased fourfold to 261.0 m/h, a significant change ($t = -2.899$, df = 5, $P = 0.034$; Table 2; Figure 4). For all six fish, the movement rate peaked within the first 5 h of the fishery. Tagged cod also remained close to the bottom for the days preceding the fishery: mean tidal-adjusted depth of 56.0 m (Table 2; Figure 5). However, every fish rose in the water column immediately after the fishery opened, some by as much as 29 m. The mean postfishery depth of tagged fish was significantly shallower, by an average of 6.1 m, than prefishery depths ($t = 4.085$, df = 5, $P = 0.009$). The shallowest depth observations occurred within the first 3 h of the fishery for all six fish.

The mean location error (δ) for all relocation points used in the UD analysis was 22.4 m (Table 3). Because we focused on a relatively stationary spawning aggregation, estimates of Brownian motion variance (σ^2_m) were comparatively small: overall mean of 1.23 m^2. The daily UD_{95} for individual tagged fish ranged from 11.2 to 36.1 ha (mean = 20.0 ha; Figure 6). On average, tagged fish had a prefishery site affinity UDOI score of 28.6, meaning that 28.6% of the area occupied by a tagged fish was the same from one day to the next. Once the fishery opened, this value dropped significantly to 5.3% ($t = 3.464$, df = 5, $P = 0.0180$; Table 4; Figure 7). A similar response was seen in the amount of aggregation between fish. Preceding the fishery, the mean daily aggregation UDOI score was 21.2, meaning the average amount of prefishery overlap between any two tagged fish was 21.2%. After the fishery opened, this value decreased significantly to 6.5% ($t = 5.741$, df = 83.827, $P = <0.001$; Table 4; Figure 8).

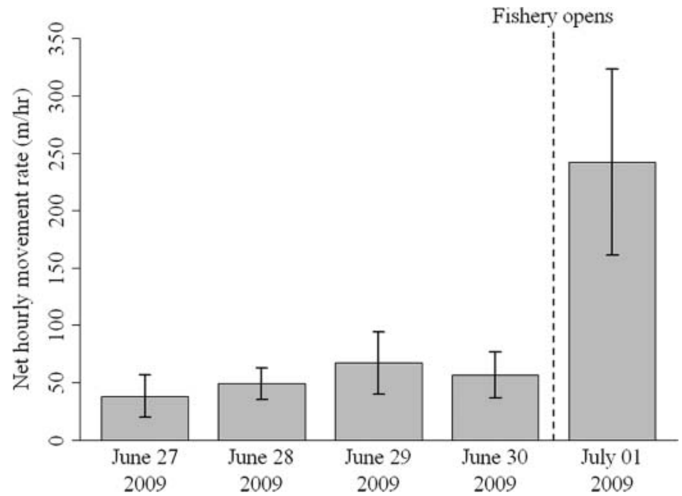

FIGURE 4. Mean net hourly movement rate of Atlantic cod tagged with acoustic transmitters by date (i.e., before and after the fishery opening on July 1). Error bars represent 2 SEs.

TABLE 2. Average movement rates and depths of individual Atlantic cod by date preceeding and following the fishery opening at 0000 hours on July 1, 2009. Data during the fishery are means from the opening to the last live detection. Blank cells indicate that the fish had not yet been tagged on that date.

	Before fishery				During fishery
Tag	Jun 27	Jun 28	Jun 29	Jun 30	Jul 1
		Mean net hourly movement rate (m/h)			
F04	27.2	44.9	51.2	21.4	548.5
F05	50.4	79.4	18.0	19.9	94.6
F06	52.0	55.3	205.0	30.5	282.7
F07	13.5	33.0	41.3	43.3	272.8
F12			45.6	73.4	166.6
F13			31.7	152.2	200.5
		Mean tide-adjusted depth (m)			
F04	54.0	54.7	54.7	54.4	44.5
F05	53.7	53.0	54.2	54.6	54.2
F06	54.0	53.7	51.3	52.5	45.6
F07	55.2	55.5	55.4	55.4	48.5
F12			55.9	55.1	52.8
F13			56.3	53.7	48.1

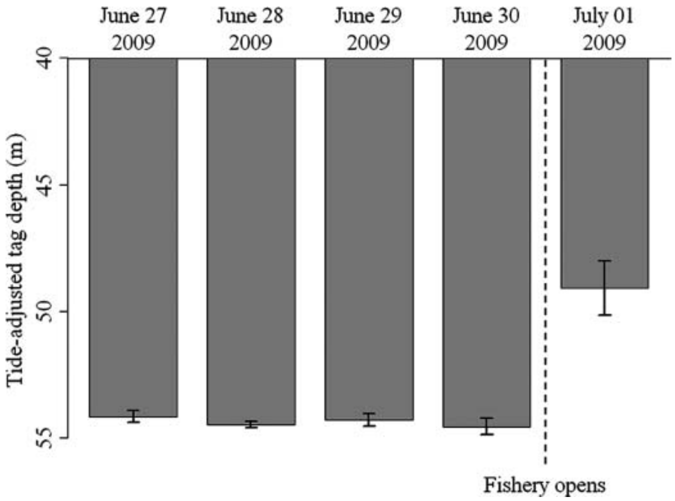

FIGURE 5. Mean tide-adjusted depth of Atlantic cod tagged with acoustic transmitters by date (i.e., before and after the fishery opening on July 1). Error bars represent 2 SEs.

DISCUSSION

Concerns about the impacts of fishing on spawning aggregations have previously centered around overexploitation, loss of genetic diversity, or damage to critical habitat (Sadovy and Domeier 2005). There has been comparatively little focus on the impacts of fishing on the behavior of spawning fish. Yet, reproductive ecology has been identified as a key factor in the success or failure of managing Atlantic cod stocks, particularly in ones that have already been depleted (Rowe and Hutchings 2003). This study provides a clear empirical example of the impact that fishing can have on cod spawning behavior. We found that members of a spawning aggregation displayed an abrupt and dramatic change in behavior as a result of concentrated fishing activity. Tagged cod showed a consistent pattern of aggregation before the fishery, characterized by limited movement, high site affinity, and similar space use among individuals. Coinciding with the opening of the fishery, this aggregation behavior was disrupted, resulting in increased horizontal and vertical movement, little site affinity, and dissimilar space use among individuals. Tagged cod that were not caught by the fishery fled the area within hours and did not return despite the receiver array being maintained for 9 d beyond the opening of the fishery.

The conclusions drawn from this study rely on observations of a limited number of tagged individuals ($n = 6$) that were tracked for a relatively short window of time. Furthermore, because the fishery opened less than a week after tagged fish were released, it is possible that the capture and tagging process influenced their behavior in some way. However, despite these shortcomings, we believe the abrupt, significant, and consistent (across individuals) change in behavior coincident with the fishery opening indicate a real and meaningful reaction to the fishery. The four cod tagged on earlier dates that left the area before the fishery opening (Table 1: tags F01, F02, F03 and F08) and were therefore omitted from fishery-effect analysis, showed an affinity for the same spawning site as those included in the analysis. However, these four fish did not leave the area in a synchronized fashion; rather, their departures were separated by several days, in contrast to the coordinated exodus of the six tagged cod present when the fishery opened. One fish (tag F08) left the area shortly after being tagged on June 24 and returned eight days later on July 3, when the fishery was already in progress. Like the tagged cod present at the onset of

TABLE 3. Parameter estimates used in the Brownian bridge movement model to create daily utilization distributions for each tagged Atlantic cod by date preceeding and following the fishery opening at 0000 hours on July 1, 2009. Data during the fishery are means from the opening to the last live detection. Blank cells indicate that the fish had not yet been tagged on that date.

	Before fishery				During fishery
Tag	Jun 27	Jun 28	Jun 29	Jun 30	Jul 1
			Mean location error (δ)		
F04	23.19	16.92	10.38	16.42	12.00
F05	12.79	18.97	24.94	17.73	5.36
F06	22.55	11.69	15.81	23.18	17.31
F07	27.81	29.11	15.96	11.21	10.73
F12			28.52	84.40	16.26
F13			26.50	183.84	2.46
			Brownian motion variance (σ^2_m)		
F04	2.44	0.00	1.18	1.63	2.39
F05	0.79	1.42	1.11	1.25	1.02
F06	1.12	1.20	1.11	1.34	2.33
F07	0.00	0.52	1.52	1.28	1.99
F12			1.12	0.12	1.89
F13			0.46	1.60	1.33

TABLE 4. Site affinity utilization distribution overlap index (UDOI) scores and mean daily aggregation UDOI scores by tag and date.

	Before fishery				During fishery
Tag	Jun 27	Jun 28	Jun 29	Jun 30	Jul 1
Site affinity (utilization distribution overlap index) score[a]					
F04		19.5	32.0	45.8	0.0
F05		7.1	32.9	38.2	0.0
F06		13.7	14.1	31.4	6.5
F07		56.9	38.5	36.3	4.3
F12				16.5	17.7
F13				18.2	3.1
Mean aggregation UDOI score[b]					
All 6 tags	19.1	17.9	24.6	19.8	6.5

[a]Percentage of the area occupied by a tagged fish on a given day that was the same as on the previous day (e.g., 19.5% of the area occupied by fish with tag F04 was the same on June 27 and June 28).

[b]Average percentage overlap for all possible two-fish combinations on a given day.

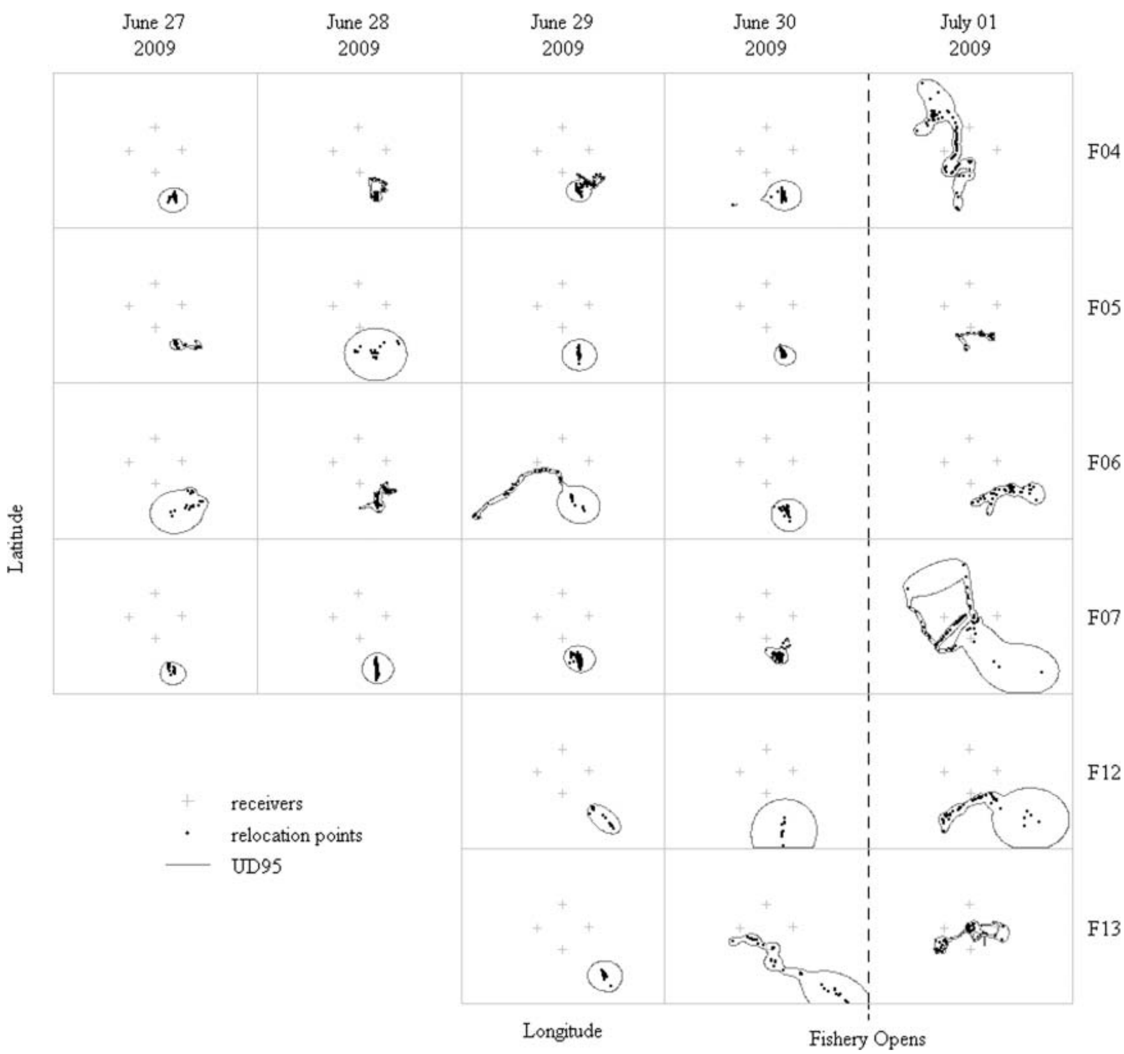

FIGURE 6. Observed relocation points and the 95th percentile of the utilization distribution (UD_{95}) for Atlantic cod tagged with acoustic transmitters by tag and date. Tags F05, F06 and F13 were concluded to be caught in gill nets shortly after the fishery opened on July 01.

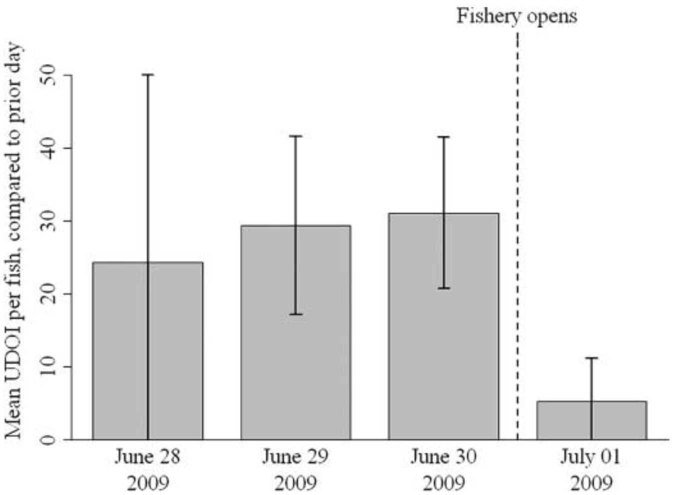

FIGURE 7. Mean utilization distribution overlap index (UDOI) score for site affinity, by date, of acoustic-tagged Atlantic cod. As presented here, the site affinity UDOI score represents the percentage of the area occupied by a cod on one day that was the same on the previous day. Error bars represent 2 SEs.

the fishery, this fish left the area again after only 13 h and did not return.

In Newfoundland, Morgan et al. (1997) used hydroacoustics to observe the reaction of spawning Atlantic cod to a single bottom trawl. While the much larger aggregation in their experiment did not completely disperse, an avoidance "hole" five times the width of the trawl was observed for over an hour in the trawl's passage corridor. In our study, it appears that the aggregation was disrupted to the point of complete abandonment of the spawning ground. This disparity in response to fishing activity may be a function of the concentration of the fishery in both time and space across the entire aggregation. In the Newfoundland trawl experiment, a single trawl was used to examine the impact on an undisturbed aggregation that spanned several kilometers. In our case, the entire aggregation was less than 300 m wide in any direction and was fished on by several vessels simultaneously.

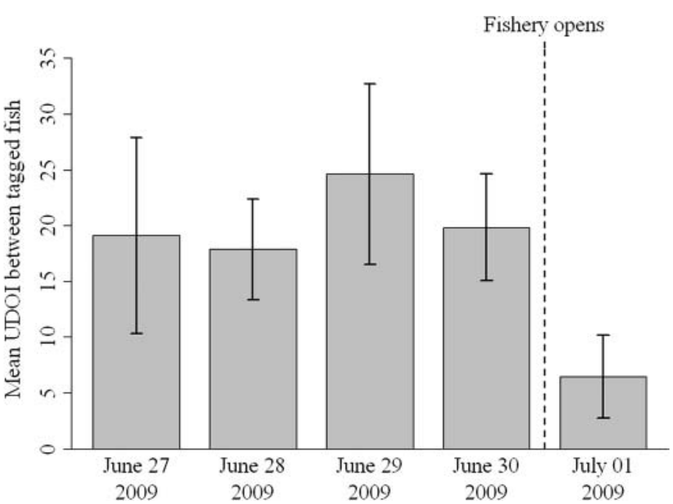

FIGURE 8. Mean utilization distribution overlap index (UDOI) score for aggregation between all acoustic-tagged Atlantic cod by date. The aggregation UDOI score can be interpreted as the percentage of the area occupied by any two cod that is the same on a given day. Error bars represent 2 SEs.

The commercial fishery that occurs in this portion of Massachusetts Bay is predominated by unbaited gill nets. As the fish dispersed, they were observed to follow the face of several gill nets before either being caught or leaving the area. Based on these observed movements, it is possible to discern the approximate location of at least six gill nets aligned parallel to one another within the detection range of the receiver array, an area of approximately 115 ha. Observations of gill-net surface buoys in the days following the fishery opening confirmed this density of fishing activity. Such a concentration of nets in this small area essentially precludes the use of other gear types, indicating that the observed change in behavior was due to the presence or deployment of gill nets alone. Kallayil et al. (2003) found that acoustic-tagged Atlantic cod made directed movements towards baited gill nets; however, these fish were not part of a spawning aggregation and were presumably more influenced by the scent of the bait than the presence of the net.

The vulnerability of the Atlantic cod mating system to disruption by fishing has been theorized as a mechanism for the rapid decline and lack of recovery in many depleted stocks (Rowe and Hutchings 2003). At low densities, the ability to encounter and select a high-quality mate may already be impaired, thereby reducing reproductive output and negatively impacting the population growth rate, a phenomenon known as the Allee effect (Frank and Brickman 2000). Disrupting spawning aggregations can exacerbate this situation by making it increasingly difficult for individuals to spawn successfully. Cod in particular are vulnerable to disruption because their mating system involves a complex sequence of male competition and courtship, resulting in female mate selection (Rowe and Hutchings 2003). In captivity, female cod have been found to release their eggs only after a courtship sequence has been performed and her mate has rolled upside down beneath her to align their vents (Rowe et al. 2008). Ovulated eggs lose their viability quickly if not released (Kjesbu 1989), and if the sequence of behaviors preceding egg release are disrupted, otherwise healthy ripe eggs may go unfertilized. Furthermore, cod exposed to stressors during mating have been found to produce more abnormal larvae than undisturbed cod (Morgan et al. 1999). These negative impacts to reproductive success caused by the disruption of spawning aggregations could help explain poor recruitment and the loss of unique spawning groups in many depleted stocks.

Once an Atlantic cod spawning group has been extirpated, it may be impossible to restore. Despite optimal habitat conditions for all life stages and minimal directed fishing, coastal spawning groups off Maine have not been recolonized after several decades (Ames 2004). Similar patterns of stock collapse and failure to rebuild despite austere fishing restrictions have occurred elsewhere, particularly in Canadian waters (Smedbol and Stephenson 2001). Previous studies have theorized that recolonization could come from the settling out of pelagic larvae spawned elsewhere (Bradbury et al. 2008) or from the straying of adult spawners that have been displaced from adjacent overcrowded spawning aggregations (Wroblewski et al. 2005). The larval drift theory requires that ocean circulation patterns advect pelagic larvae from an existing spawning aggregation to a fallow spawning ground. The possibility of this recolonization mechanism is extremely low in locations that are isolated from ocean currents or have no upstream "seed" spawning groups, as appears to be the case in coastal Maine (Huret et al. 2007). Either recolonization theory requires the existence of healthy spawning aggregations to act as a source of either adults or larvae. Clearly, primary emphasis should be placed on preventing the loss of remaining spawning groups. Extirpated spawning groups mean a portion of the reproductive capacity of the stock has been lost, and historical biomass levels may no longer be attainable (Frank and Brickman 2000; Reich and DeAlteris 2009).

The rolling closures on spring-spawning Atlantic cod in Massachusetts and Ipswich bays once offered substantial protection from commercial exploitation during the months of April to June (Howell et al. 2008). Our results indicate that further protection may be necessary because the aggregation was still intact on July 1 when the fishery opened. It remains unknown how much longer the aggregation would persist if left undisturbed. It is possible that the bulk of the individuals that utilize this spawning ground had already spawned by the time the fishery opened and only the last remnants were dispersed. Alternatively, a considerable proportion of the spawning group could have been present at the onset of the fishery and were therefore prevented from spawning successfully. In 2010, the SCCZ closure was extended through July 21 and preliminary results from a continuing study indicate that the spawning aggregation was still intact through that time. Additional research is warranted to further characterize the spawning season, residence time and behavior of individual fish on the spawning ground, as well as the relative size of this and other GOM cod spawning aggregations.

Under the current Northeast Multispecies Groundfish Management Plan, which began in May 2010, the commercial fishing mortality rate for Atlantic cod is controlled via a quota system that is divided into individual catch shares, which are pooled into self-organized groups of fishermen, known as "sectors" (NOAA 2010). As a consequence, fishing-effort controls, such as daily possession limits and rolling closures, have been lifted for most fishermen. While this new system may provide a more direct method of controlling fishing mortality for the Gulf of Maine cod stock as a whole, it also greatly increases the potential for overexploitation of individual spawning groups. The Cod Conservation Zones enacted by Massachusetts have extended the spawning protection once offered by rolling closures in the immediate vicinity of the aggregations. Yet, other cod spawning aggregations exist in the gulf that will probably face the brunt of relatively unrestricted fishing pressure, unless similar conservation zones are established.

Our study clearly demonstrates the adverse effect of gill netting on an Atlantic cod spawning aggregation. All tagged cod were either caught or left the area within 18 h of the opening of the fishery. If the reactions of the tagged cod are representative of untagged cod in the area, the opening of the gill-net fishery ended the spawning activity at this site. This was a surprising find and has significant implications for the management of spawning closures. There is often pressure on fishery managers to allow for a controlled harvest with the assumption that removing some small portion of the spawning biomass will not have a deleterious effect on the stock. In the case of gill netting, this assumption appears to be false because the onset of the fishery caused the spawning aggregation to disperse. The use of other gears such as trawls and hooks should be investigated for similar interactions with spawning behavior. Fishery managers attempting to achieve spawning protections need to consider that fishing on spawning aggregations may have adverse effects that go beyond the simple removal of biomass.

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