Final Report to the Northeast Consortium

Project Title: Activity and distribution of cod in the Ipswich Bay spawning area

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Abstract:

We examined the activity and fine scale distribution of spawning cod in Ipswich Bay using a combination of data storage tags (DSTs) and acoustic telemetry. In April and May of 2006, 200 mature, pre-spawning cod were caught and equipped with external DSTs that recorded depth and water temperature at 12-minute intervals for up to 175 days after release. Thirty of these same cod were also internally implanted with acoustic transmitters, and relocated manually using a directional hydrophone, as well as with six stationary acoustic receivers deployed across the spawning area. Tracking occurred from May through June, with 47 days devoted to manual relocation by boat.

To date, 31 DSTs have been returned (15.5%), and time at liberty has ranged from 8 to 757 days (mean 159). Recapture locations varied across the Gulf of Maine from 88km northeast to 48km southeast of their release sites, but fish recaptured in the summer of 2007 (~1 yr. at liberty) were caught near their release location in Ipswich Bay, supporting the previously reported spawning site fidelity of this group of cod. For several days after release, cod exhibited dramatic vertical movements, probably associated with recovery from barotrauma. After arriving at a consistent depth, vertical activity remained low, and depth remained consistent throughout the spawning period (May through early June). There was a dramatic shift to deeper water from mid-June onward, coupled with increased vertical activity, signaling that individuals had left the study area and changed their behavior. Cod showed daily vertical patterns in their depth profiles.

Positional histories and home ranges were estimated for each acoustically tracked fish. Tracking data indicated that spawning activity, which peaked in May, was concentrated in a small (~35km^2) area on the southern and western edges of an elevated bathymetric feature in the northwestern corner of Area 133 known as “Whaleback”. The shallowest part of this ridge was 40 m deep; about 30 m shallower than the muddy flats south of it. Cod shifted eastward in June before vacating the study site altogether, coinciding with vertical activity changes in DST data. Stationary receivers captured abrupt eastward movements across the study area as some individuals exited, allowing estimates of migratory headings and swimming speed.

These fine-scale movement and spawning data have implications for area closures, defining Essential Fish Habitat, and cod stock assessment.

Introduction:

The Atlantic cod (*Gadus morhua*) historically represents one of the most valuable marine resources of the entire northern Atlantic. Despite well-documented depletion since the 1960s, cod still support significant commercial and recreational fisheries in the Gulf of Maine. Because of their economic value, and prominent role in local marine ecosystems, there have been extensive studies of their life history throughout their range, and concerted efforts have been made to improve their management and conservation.

Data on cod life history characteristics, such as movements and spawning, typically come from research surveys conducted by the National Marine Fisheries Service (NMFS). The limitation with these data is the scale at which they are collected. Most surveys are conducted over large areas (1000s of square kilometers) in which only a few stations are sampled, e.g. one trawl for every 300 square miles (180 km^2) (Pierce and Hughes 1979). While such surveys are useful in providing information about large areas such as the entire Gulf of Maine, they do not provide adequate or detailed information for smaller areas that support important events in the life history of the species.

Cod distribution, on a large spatial scale, in the northwestern Atlantic is well documented, and the locations of spawning sites have been reported (Colton et al. 1979, Ames 2004). Ames (2004) concluded that almost 50% of historical spawning grounds in the western Gulf of Maine became extinct in the 20th century, primarily due to fishing pressure. Of the remaining locations, neither the critical habitat features nor the spawning components that utilize these locations have been examined on an individual basis. Further, our knowledge of cod population dynamics and reproduction is often restricted to large-scale analyses that characterize the Gulf of Maine stock as a whole, and depends on data from widely-spaced NMFS research surveys (Mayo and Col 2006).

Migratory behavior remains undefined in many areas of the Gulf of Maine. Little has been published on the depth preferences, vertical distribution, and patterns of movement of adult cod within US waters. Furthermore, it is unknown how spawning and migratory behaviors vary according to sex and size, and whether lekking behavior exists on Gulf of Maine spawning grounds. It is imperative to collect more fine-scale movement data to make conclusions about the spatial distribution of individuals, behavioral differences between sexes on spawning grounds, and the sequence of events that comprise reproduction.

The foundation for this research was a mark and recapture tagging study conducted at the University of New Hampshire from 2001-2003 (Howell et al. 2008). Adult cod were tagged in several contiguous rolling closure management areas in the western Gulf of Maine to characterize movements and reproductive activity within these areas, and the efficacy of current management strategies. Catch per unit effort (CPUE) and recapture results of the Howell et al. (2008) study indicated two temporal peaks in biomass within Area 133, and associated seasonal movements. Adult, pre-spawning cod assembled offshore of Area 133 in April, to the east on Scantum Basin and Jeffrey’s Ledge (Area 132). They moved inshore into Ipswich Bay in Area 133 during April and May to spawn. Cod appeared to gradually disperse from Ipswich Bay and move offshore throughout June and July. A similar pattern occurred again in the winter, when fish assembled and moved inshore from October through December, and dispersed from Area 133 in February after spawning.

Although this, and other recent tagging work, has begun to indicate general movement patterns around Ipswich Bay, several fundamental questions remain. Among them is the question of where spawning fish arrive from, and where they and move to after leaving. As well, the fine-scale habitat features of peak spawning sites are unknown, and it is unclear what attributes are present in Ipswich Bay that attract multiple spawning components to return there. The fine-scale behavior of cod during their stay in this area is equally unknown, including pre- and post-spawning activity and the precise timing of their movement out of the area.

The overall goal of the project was to study cod activity and fine scale distribution within the Ipswich Bay spawning area. It was anticipated that these data would allow us to determine the spatial use of the spawning habitat, and determine which habitat attributes (e.g. depth, substrate type, bathymetric features) influence the distribution and spawning of cod.

This research utilized a combination of acoustic telemetry and archival data storage tags (DSTs) to collect fine-scale movement data, and expand upon the broad movement patterns observed through previous mark and recapture tagging. Acoustic transmitters and DSTs have been used in a variety of cod studies, including research on residency and spawning site fidelity, juvenile activity patterns, homing, migration patterns, feeding behavior, and spawning abundance (Loekkeborg 1998; Thorsteinsson and Eggertson 1998; Godo and Michalsen 2000; Green and Wroblewski 2000; Robichaud and Rose 2001; Stensholt 2001; Righton and Metcalfe 2002; Palsson and Thorsteinsson 2003; Robichaud and Rose 2003; Cote et al. 2004; Espeland et al. 2007; Lindholm et al. 2007; Svedang et al. 2007). To our knowledge, however, no studies have integrated both data storage tags and acoustic tags to study the activity and distribution of cod. The use of both electronic tag types enabled us to construct profiles of ambient temperature, vertical movement in the water column, and horizontal movement within the spawning area for individual cod.

Null hypotheses and project objectives:

H_o1: There are no daily patterns of activity (vertical movements) of cod in Ipswich Bay.

H_o2: Vertical activity during the spawning period does not differ from vertical activity patterns at other times of year.

H_o3: Habitat attributes and environmental variables such as depth, substrate type, bathymetry, water temperature, and tidal and lunar phases do not influence the fine scale distribution of cod on their spawning grounds.

To test these null hypotheses, we met the following objectives:

1. Quantified daily and seasonal (pre-, spawn, post-spawn) changes in activity and depth distribution of spawning cod in the Ipswich Bay spawning area.

2. Related spawning movements to environmental factors (time of day and water temperature).

3. Determined how the spatial distribution of spawning fish relates to attributes of the spawning habitat.

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Methods:

Adult cod were tagged, released, and acoustically tracked during the spring and summer of 2006 in an area of Ipswich Bay, located 5-13 nautical miles off the northern Massachusetts and southern New Hampshire coasts (Fig. 1). Cod were captured on board the commercial fishing vessel F/V *Stormy Weather*, using a bottom trawl with 6 ½ -inch mesh, in depths ranging from 50-110 m. Trawling locations were based upon the sites having the highest catch per unit effort (CPUE) in tagging studies from 2001-2003 (Howell et al. 2008), as well as local knowledge of productive fishing grounds.

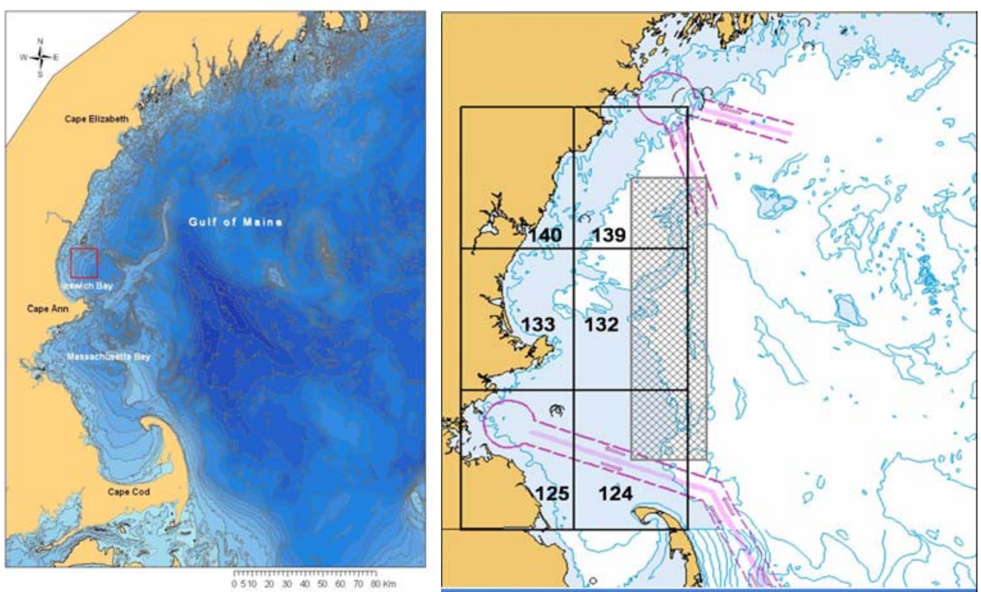

Fig. 1. Western Gulf of Maine, with location of study area outlined in red (left), and location of rolling closures (right). Shaded area is the western Gulf of Maine area closure. Our study was conducted primarily in Area 133.

Electronic tags were attached to adult cod to record data about their behavior, and to track their movements. Two types of electronic tags were employed: external data storage tag

(DSTs), which were attached to 200 cod, and acoustic transmitters, which were implanted in 30 of those same fish. The collective weight of both tags in water was 11g. All tagged fish weighed >1kg, thus the combined tag weight was well under the maximum 2% of fish body weight recommended for aquatic organisms (Winter 1983).

Data storage tags

DSTs recorded pressure (depth), ambient water temperature, and time. The DSTs used, (Star-Oddi DST milli) weighed 5g in water, and were 15 x 46mm in size. The DSTs were programmed to record depth and temperature at 12-minute intervals, allowing data acquisition for 6 months after activation. Archived data were downloaded to a computer when fish were recaptured and the tags were recovered. A reward for $25 per tag was established to encourage tag return, and reward and contact information were printed conspicuously on the side of the DSTs.

Acoustic transmitters

Acoustic transmitter tags (Vemco V13) weighed 6g in water, were 14 x 36 mm in size, and emitted a distinctive series of pulses that identified the individual transmitter. Two types of acoustic transmitters were used. “Coded” transmitters emitted a unique series of pulses that allowed each tag to be distinguished from others. Coded transmitters were detected by stationary receivers as well as by a hand-held, directional hydrophone from vessels associated with the project. The detection range was ~750 m. “Continuous” transmitters emitted a signal, on a different frequency, every second. The continuous transmitters permitted a fish to be continuously tracked by boat once relocated. In this study, 26 coded transmitters and 4 continuous transmitters were employed. We chose to rely primarily on coded transmitters because of their more powerful signals in a large study area, their detectability by stationary receivers, and the limited number of hydrophone channels available to allocate to continuous transmitters. These acoustic tags were able to transmit a signal for ~7 months after activation.

Several preliminary measures were taken to prepare tags before field deployment. The DSTs were designed for external attachment using a pair of steel wires. Prior to tagging, we sheathed each DST’s attachment wires in non-reactive silicone surgical tubing to reduce tissue erosion at attachment sites. In addition, both wires were passed through a silicone pad and the pad was pulled against the side of the DST; the pad acted as a cushion between the DST and the cod’s body to minimize abrasion.

Acoustic transmitters were implanted internally in the body cavity of the fish. Transmitters were coated in a thin layer of melted wax before tagging and allowed to dry in the laboratory, since wax coatings are believed to increase internal tag retention (Meyer and Honebrink 2005; Sakaris and Jesien 2005). The wax coating was composed of a 70:30% paraffin/beeswax mixture to achieve optimal consistency (M. Shane, Hubbs Res. Inst., San Diego, personal communication).

Although a sterile environment is almost impossible to achieve on a fishing boat deck at sea, measures were taken to disinfect the surgical environment and reduce the risk of infection in fish. Acoustic transmitters, DST tagging needles, scalpels and all suturing tools were immersed in gluteraldehyde (Metricide) for a 12h period prior to tagging trips. Gluteraldehyde is a cold sterilant and one of the more effective techniques to truly sterilize instruments and transmitters prior to tagging (Mulcahy 2003).

Dummy DSTs and transmitters, which were identical to the tags selected for this study but non-functional, were attached and implanted in six captive juvenile cod in January 2006. Behavior, health, and wound healing rate were monitored in a circular, flowing seawater tank at the UNH Coastal Marine Laboratory in the months preceding fish tagging in the field. Additional cod in the tank without tags served as controls. All fish recovered from the anesthesia and tagging procedures within minutes, and were observed to swim and behave normally and in the same manner as untagged control cod.

Tagging methodology

Fish were captured in short, 30-minute tows and brought to the surface as slowly as possible to minimize stress, swim bladder damage, and mortalities. Fish were immediately placed in holding tanks containing flowing seawater, and allowed to acclimate for approximately 30 minutes before tagging. Only fish that appeared active and in good health were selected for tagging; individuals in poor condition were released. Prior to tagging, individuals were removed from the holding tank and submerged in a shallow anesthetic bath of seawater containing 40 ppm tricaine methanesulfate (MS-222). Fish were kept in the anesthetic bath until we observed stage 5 of anesthesia, as described by Summerfelt and Smith (1990), which typically occurred after 3-5 minutes. The anesthetic bath was changed periodically, usually after 10 fish were anesthetized.

After anesthesia, fish were placed on a measuring board and measured and sexed. Only cod greater than 60cm in size were selected for tagging. Sex was determined by initially massaging milt from the genital pore. If no milt was extruded, a gonadal biopsy was taken to confirm female gender. Gonadal biopsy was performed using a small-diameter rubber tube inserted through the genital pore and into the oviduct to retrieve an egg sample. We tagged only ripening females, using the criteria defined by Kjesbu (1994), and spermiating males. Gender was not a factor in selecting fish for DST tagging. Males were more abundant than females in our trawls, and any captured adults meeting the above criteria were tagged to expedite the process. However, a 1:1 sex ratio was chosen for the 30 acoustic transmitter implantations (15 males, 15 females).

During surgery, each fish was placed on a tagging cradle, comprised of a V-shaped wooden board coated with neoprene to support the fish and prevent movement. Following LaVigne's design (2002), the cradle was supported over the anesthesia bath. Water in the bath was oxygenated with a battery-powered aerator. During surgery, the anesthetic seawater was continuously pumped through the oral cavity and across the gills via a battery-powered aquarium pump.

Fish selected for transmitter implantation were placed in dorsal recumbence on the cradle. Transmitters and surgical instruments were removed from a glutaraldehyde bath before surgery and rinsed in sterile saline solution prior to contact with the fish. A 3 cm incision was made with a scalpel approximately 4 cm anterior to the genital pore and 2 cm lateral to the ventral midline. The transmitter was then inserted by hand into the peritoneal cavity, and the incision was closed with non-absorbable monofilament sutures (3-0 Maxon) using a simple interrupted suture pattern as recommended by Wagner & Cooke (2005).

External DST attachment methods were similar to those advocated by the manufacturer (Star-Oddi), as well as Turner et al. (2002), Righton et al. (2006), and others. Anesthetized fish were laid ventral side down in the cradle. A wire attached to the DST was threaded through an 8-inch upholstery needle, and the needle was then passed through the fish's dorsal musculature posterior to the head and 4-5 cm ventral to the first dorsal fin. The needle was pushed along the transverse plane, into one side of the fish and out of the other, and wire and silicone tubing jacket were pulled through. The same process was repeated with the second DST wire approximately 4 cm posterior to the first. Both wires were pulled firmly through the fish until the DST and silicone pad lay snugly against the side of the fish. Both wires were secured on the opposite side of the fish by being passed through a 5 cm-long plastic plate. The wires were then twisted together against the plate to permanently secure the tag. Instructions on how to report the recaptured fish were visible on the DST.

A 5% chlorhexidine solution was used to rinse all incision and tagging wounds, and tagging needles were soaked in this solution between individual tagging. Diluted chlorhexidine is an effective and safe disinfectant for most fish species (Mulcahy 2003). Surgical instruments were also immersed in gluteraldehyde for 10-20 minute periods after each surgery for disinfection. Finally, surgical gloves were changed and the cradle was rinsed with seawater and povodone-iodine solution after each procedure.

After surgery was complete, the fish was immediately placed in a recovery tank. Fish were allowed to recover for approximately 30 minutes, and only those fish considered robust and physically recovered from the effects of surgery and anesthesia were released with tags attached. Following the recommendation of Mulcahy (2003), we released fish as soon as they appeared fully recovered instead of retaining them on board for an extended period. Tag information and release position were recorded for each fish prior to release.

Releases

In total, 17 trawls were completed between 4/21/2006 and 5/17/2006. This period was chosen because we wanted to tag fish at the beginning of the spawning season, and there is evidence that spawning cod move into Ipswich Bay in late April and early May (Howell et al. 2008). During the five days of tagging, we released cod at 18 different sites in Ipswich Bay and western Scantum Basin (Table 1). After tagging, each cod was released < 0.5 km from its capture location (Fig. 2).

Despite several tows in different locations, only 8 fish in spawning condition were caught on April 21. On the next two tagging dates, April 29 & 30, cod were found in abundance, particularly on Scantum Basin and directly west of it. We released the majority of DST tagged cod over that two-day period (n=144). Cod were found further inshore and to the northwest on May 6, in the area believed to be the prime spawning grounds in Ipswich Bay (Fig. 2). Inclement weather prevented tagging trips for over a week in May, and the remaining tags were deployed on May 17. We implanted all acoustic transmitters on May 6 & 17, 2006 (Table 1).

Acoustic tracking methodology

Two types of hydrophones were utilized to relocate acoustic transmitters and track fish movement over time. Stationary receivers (Vemco VR2s) were deployed and anchored to the seafloor at strategic locations to record the presence of tagged fish that came within range. A directional hydrophone and accompanying receiver (Vemco VR100) was used on board commercial fishing boats to locate the acoustically tagged fish. The detection ranges of these receivers were approximately 750 m (0.4 nautical miles) for the VR100 and the 550 m for the VR2. If a transmitter was within detection range, both hydrophone types identified and logged the individual tag number and the time that the signal was received. The manual hydrophone also recorded the strength of the transmitter signal in order to gauge relative distance and direction of the transmitter location.

Six stationary acoustic receivers (VR2s) were deployed throughout the study area on May 8, where they collected data until June 25. They were removed before the commercial fishing season opened in the area in July to ensure that they were not damaged or displaced by bottom trawling gear. The VR2s were periodically retrieved by boat so that detection data could be downloaded to a computer, and then redeployed. The locations of the receivers were based on fishermen's knowledge of locales that have attracted the highest densities of spawning cod in previous years, and potential routes that cod may pass through as they leave Ipswich Bay to disperse offshore. Some VR2s were relocated during the study period if they had no detections at a given location, resulting in ten total deployment sites over the course of the study period (Fig. 3). One VR2 was apparently dragged ~7.5 km by a passing ship, anchors attached, and relocated several weeks later. Its position after being moved is illustrated as the southernmost VR2 location in Figure 3. Manual tracking by hydrophone began on May 6, which was also the first day that transmitters were implanted on cod. Manual tracking was done on 39 days between May 6 and June 30 when weather and scheduling permitted. Tracking was terminated at the end of June in anticipation of the commercial fishing season opening in Ipswich Bay on July 1. At that point, boat traffic and ground fishing gear would make tracking activity difficult and possibly alter fish behavior patterns. Each tracking day consisted of a 10 – 12h excursion for one of the four commercial fishing vessels involved in the project. On each day we attempted to relocate as many of the 30 acoustic transmitters in the study area as possible. Eight of these tracking days were extended over 24h to determine if cod behavior varied throughout a 24h period.

Table 1. Release dates, locations and depths of cod equipped with DSTs and acoustic transmitters. All fish released at a given site were not caught in the same tow, but all were released <0.5 km from where they were brought to the surface. “No. Recap” is the number of fish released at each site that were ultimately recaptured.

Site	Date	Latitude	Longitude	Depth (m)	No. DSTs	No. Transmitters	No. Recap.
1	4/21/2006	42.810	70.569	101	1	-	-
2	4/21/2006	42.842	70.567	97	6	-	1
3	4/21/2006	42.887	70.672	97	1	-	-
4	4/29/2006	42.830	70.560	105	13	-	1
5	4/29/2006	42.819	70.585	93	9	-	1
6	4/29/2006	42.815	70.572	99	15	-	4
7	4/29/2006	42.793	70.529	86	9	-	1
8	4/29/2006	42.824	70.644	74	12	-	4
9	4/29/2006	42.888	70.693	54	22	-	4
10	4/30/2006	42.845	70.573	94	8	-	1
11	4/30/2006	42.819	70.577	96	22	-	6
12	4/30/2006	42.803	70.586	93	18	-	-
13	4/30/2006	42.799	70.588	91	5	-	-
14	4/30/2006	42.829	70.578	96	11	-	1
15	5/6/2006	42.878	70.607	80	15	15	-
16	5/6/2006	42.852	70.668	62	4	-	2
17	5/6/2006	42.859	70.647	70	14	9	3
18	5/17/2006	42.888	70.638	67	15	6	2
				Total:	200	30	31

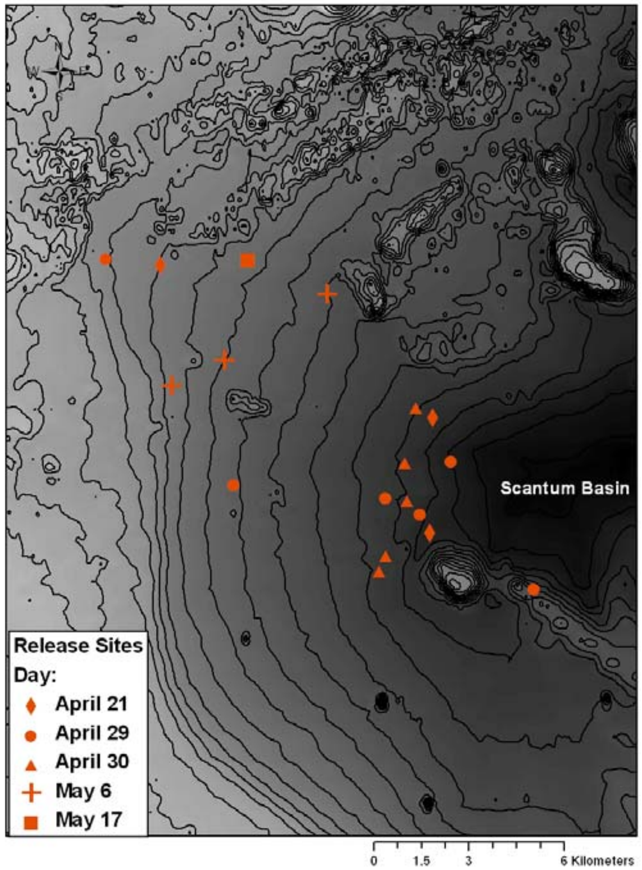

Fig. 2. Release sites (n=18) in Ipswich Bay for all 5 days that cod were caught and tagged. Symbols correspond to different tagging dates. Acoustic tags were released May 6 & 17.

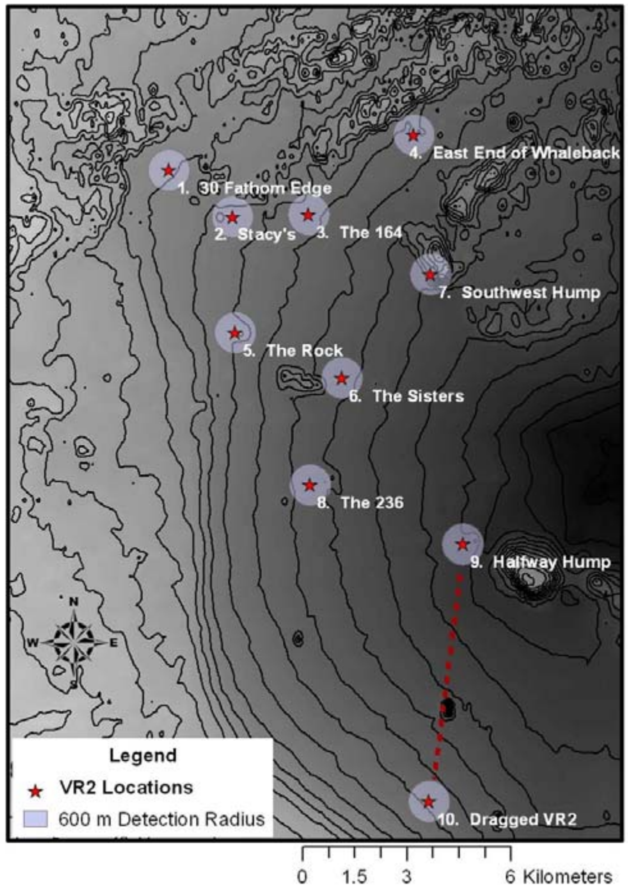

Fig. 3. Locations of VR2 acoustic receivers deployed in Ipswich Bay, including local fishers' names for each site. Buffers illustrate detection radius of each receiver. Northern receivers were deployed along periphery of "Whaleback" area of vertical relief. VR2 at location 9 was dragged to location 10 and relocated weeks later

Under the search protocol developed for this study, stops were made every ~800 m. At each stop, the manual hydrophone was lowered into the water and pointed in four different directions for 90 seconds each while listening for a signal. If no signal was detected, the hydrophone was raised, and the boat moved 800 m to the next stop. For each instance that the hydrophone identified a transmitter, the boat's position and transmitter number were stored automatically in the VR100 unit's memory for download, and also recorded in writing. This position was used as the starting point when searching for the transmitter on the next tracking trip. The size of the study area (95 km^2) made a systematic search grid implausible. The methodology for covering the study area was shaped by previous detection coordinates, tagging and release locations, and fishermen's knowledge of where spawning cod were most likely to aggregate within the area.

Data analysis

Loran positions from recapture reports were converted to latitude/longitude in decimal degrees using the POSAID2™ program, and release and recapture positions and net distance traveled were plotted with Nobeltec Visual Navigation Suite™. DST data were tabulated, analyzed and plotted using the R© programming environment (Ihaka and Gentleman 2008), SYSTAT 10©, Microsoft Excel©, and SigmaPlot 2000©. Acoustic telemetry data were plotted, mapped, and analyzed using ArcGIS 9.0© to assess approximate home ranges and the areas occupied during cod's residence in Ipswich Bay. Minimum convex polygons (MCPs) and kernel distribution estimations (KDEs) were calculated from telemetry data using Hawth's Analysis Tools for ArcGIS (Byer 2004).

To identify cyclical trends in depth behavior, we applied the methods of Neat et al. (2006) to de-trend the depth profiles and apply autocorrelation functions on residual data. First, we ran a loess smoothing function on raw depth data. Selecting the appropriate span width for the loess function is subjective, but an optimal span width produces a smoothed curve that best fits the data and represents the trend of the time series (Neat et al. 2006). We chose a span width of 360 data points, or three days (1/10 of the data set for a month), for the initial smoothing of all spawning phases (Fig. 4a). We then subtracted that smoothed trend from the time series and extracted the residuals, which represented de-trended depth data. Next, we applied a second loess smoothing function with a slightly smaller span width (300 data points, or 1/12 of a month's data) (Fig. 4b). We again subtracted this best-fit curve from the time series. Finally, we applied an autocorrelation function (ACF) to this twice de-trended depth data to reveal short-term temporal rhythms.

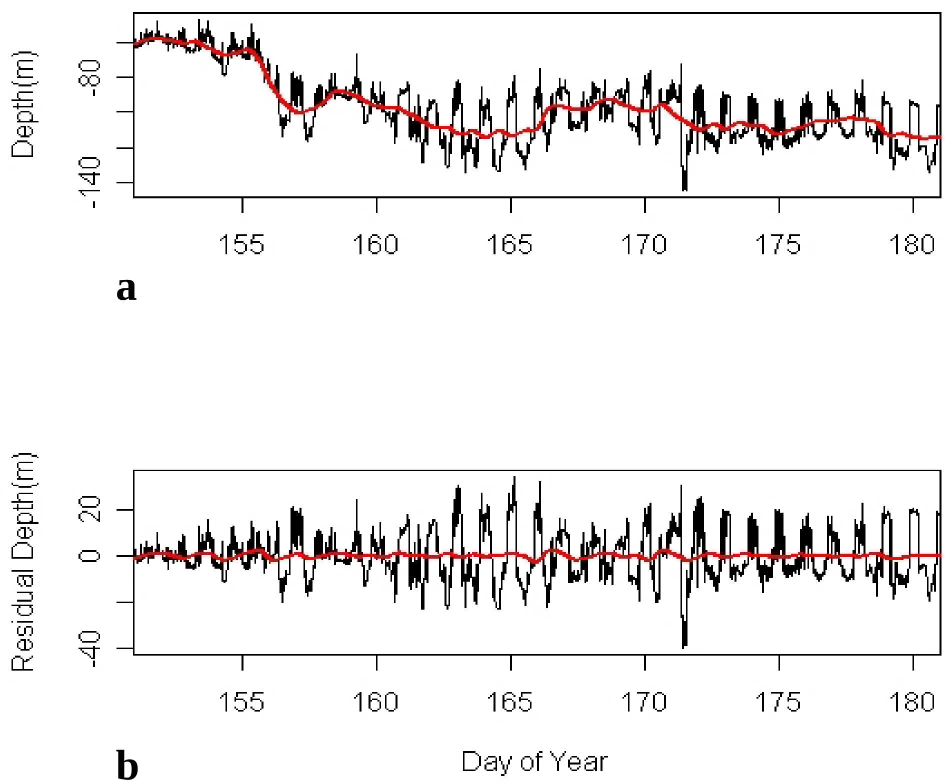

Fig. 4. Example of the smoothing and de-trending steps applied to depth time series. a) Raw depth profile for DST 056 throughout June, overlaid with a best-fit curve produced with loess smoothing (span width=1/10). b) Same depth data and time frame, but with trend in (a) subtracted from time series. Residuals are smoothed again (span width=1/12), and trend is shown overlaid on residuals. Residuals were subsequently de-trended again before applying an ACF.

Data:

Summaries of the data collected are given in the Tables and Figures included in this report. Raw data files include trawling locations and times, catch data, tagging locations, tagging dates and times, sizes of fish tagged, sex of fish tagged, GPS positional information for each acoustically tagged fish over time, and depth and temperature records of each DST-tagged fish we recovered. Some, but not all, of the numerous raw data files have been submitted to the Northeast Consortium Fisheries and Ocean Database. We will post the others in the near future, but this report, and the manuscripts in preparation, result from our analyses of the data, and present our conclusions from the study.

Results and conclusions:

A. DST results

A1. Recaptures

In total, 31 DST-tagged cod (19 males, 12 females) were recaptured and reported by commercial and recreational fishermen, fishery scientists, and seafood processing plants. Total lengths of recaptured fish spanned 64 – 122 cm and averaged 84 cm (s.e.=2.52). Recapture lengths were representative of the total sample of tagged fish (92 cm average, s.e. =1.08). Recapture information for each DST is summarized in Table 2, and a 3-digit ID number hereafter refers to each DST. Four recaptured fish were also fitted with an acoustic transmitter, and their transmitter IDs are also noted in Table 2. Recapture dates and corresponding days at liberty are known for all but one tag. Recaptured fish were at liberty from 8 – 757 days, with an average of 159 days (s.e.=34). The majority of recaptures (68%) occurred in the summer of 2006 (May – August).

Cod were recaptured in one of five general areas targeted by the fishing industry (Table 2). Twelve fish (39%) were recaptured in Ipswich Bay, on the approximate spawning ground or just south of it. Seven cod (23%) were found north of Ipswich Bay in an area of Bigelow Bight, between coastal Maine & Platts Bank, 25-55 km east of Saco Bay. Five cod (16%) were recaptured on Jeffrey's Ledge, directly east of Ipswich Bay. Four cod (13%) were caught on Stellwagen Bank, south of Cape Ann. Finally, one cod (3%) was recaptured off the east coast of Cape Cod. Two DSTs (6%) were returned with no reliable recapture information.

Recapture position coordinates were known for 74% of recaptures (Table 2). We considered the single cod caught off of Cape Cod (DST 064) to be an outlier. It was found 172 km from its release point, about twice as far as the next greatest recapture distance, even though other DSTs were at liberty longer. When this tag is excluded, the net distance traveled for the remaining fish ranges 7-88 km, with a mean of 44 km (s.e.=6.4). Recapture locations for these 22 tags are illustrated in Figure 5.

All cod recaptured through June 2006, and the majority through July, were found in Ipswich Bay. Four cod were caught on May 19 by the Massachusetts Division of Marine Fisheries' Industry-Based Survey, in a single, 30 minute trawl set on spawning grounds that netted over 20,000 lbs. of adult cod (J. Ford, pers. comm.) (Fig. 5). In addition, two tags recaptured in May 2007 and May 2008 were also found in the Ipswich Bay spawning ground <10 km from their release site (Table 2).

Of the 31 reported recaptures, five DSTs could not be incorporated into vertical movement data analysis and are noted in Table 2, including the DST recovered from Cape Cod. These tags were either damaged, or their recaptures were reported but the DSTs were not returned. In total, we utilized 26 DSTs for vertical movement analysis.

Table 2. DST equipped cod recaptures (n=31) by number of days at liberty ("Days" column). "Area" indicates general recapture area: **IB**= Ipswich Bay, **ME**= Offshore Maine, in Bigelow Bight, **JL**= Jeffrey's Ledge, **SB**= Stellwagen Bank, and **CC**= Cape Cod. Under Notes column: "N/A" indicates DST data could not be used. Transmitter ID is listed when present (n=4).

Cod/ DST	Sex	TL (cm)	Recap Date	Days	Area	Lat. / Long.	Net Distance (km)	Depth (m)	Notes
164	M	78	5/8/06	8	**IB**	42.76 70.66	9.31	59	N/A
151	M	95	5/19/06	19	**IB**	42.90 70.63	9.78	70	
165	M	102	5/19/06	19	**IB**	42.90 70.63	7.43	70	
180	M	97	5/19/06	19	**IB**	42.90 70.63	9.78	70	
074	F	76	5/19/06	20	**IB**	42.90 70.63	8.39	70	
231	F	90	6/3/06	28	**IB**				TF81
093	F	102	5/29/06	29	**IB**	42.87 70.62	6.95	74	
176	M	74	6/5/06	36	**IB**	42.84 70.69	9.47	48	
010	F	74	6/19/06	51	**ME**	43.39 69.83	87.70	133	
084	F	64	6/21/06	53	**ME**	43.24 69.75	86.47	127	N/A
184	F	90	7/12/06	56	**ME**	43.37 70.01	73.89	161	N/A
077	M	73	7/7/06	69	**JL**	42.87 70.25	32.27	115	
140	M	81	7/17/06	78	**ME**	43.36 69.89	80.97	155	
976	F	77	7/9/06	79	**IB**	42.75 70.60	10.86	73	
004	M	66	7/18/06	80	**JL**	42.87 70.25	24.09	115	
056	M	84	8/2/06	306	**?**				
207	M	73	8/3/06	89	**SB**	42.44 70.48	48.39	57	T61
241	F	94	8/26/06	101	**IB**				T76
006	M	73	8/9/06	102	**ME**	43.36 69.89	82.11	163	
014	M	75	8/9/06	102	**ME**	43.26 69.92	72.30	158	
033	F	80	8/9/06	102	**SB**	42.49 70.38	39.68	81	
086	F	122	8/19/06	112	**ME**				
061	M	85	9/12/06	136	**SB**	42.44 70.48	52.84	55	
060	M	71	9/14/06	138	**SB**	42.40 70.27	56.29	57	
228	M	76	10/22/06	169	**JL**	42.93 70.26	32.60	145	T73
981	M	91	4/10/07	346	**?**				
147	M	70	5/21/07	380	**IB**				
163	F	114	?/?/07	?	**JL**				N/A
020	M	90	8/1/07	459	**JL**				
064	F	72	8/23/07	474	**CC**	41.57 69.51	171.51	54	N/A
017	M	100	5/25/08	757	**IB**	42.89 70.63	8.55	70	

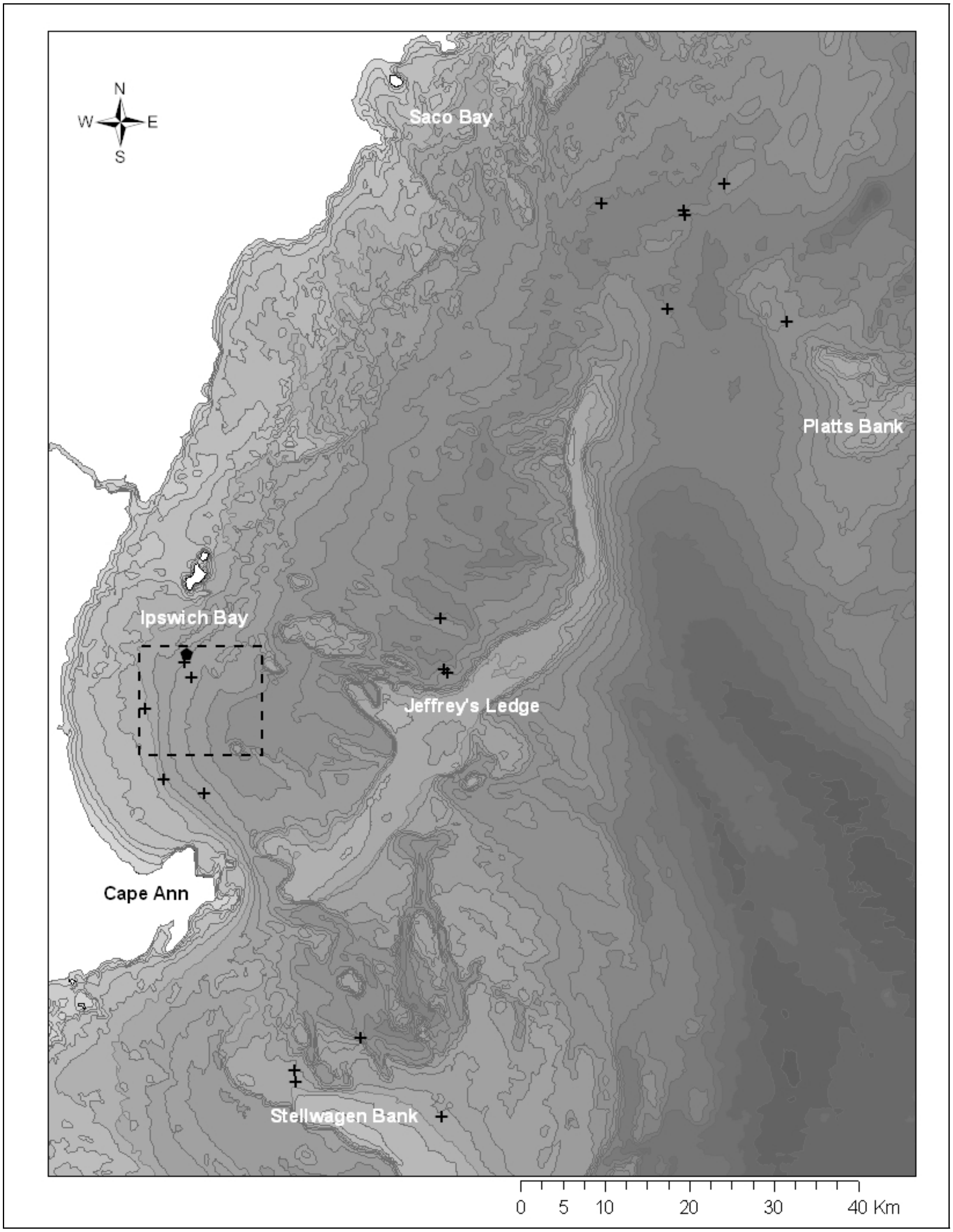

Figure 5. Recapture locations for cod equipped with DSTs with known position coordinates (n=22). Cod recaptured off Cape Cod not shown. Tag and release area indicated by dashed square. Enlarged dark spot near the northern boundary of the tag and release area is the location of Massachusetts Division of Marine Fisheries survey tow where four DST equipped cod were recaptured.

A2. Tagging Recovery Phase

All 26 cod displayed several days of vertical behavior, immediately after tagging, that were distinct from the rest of their DST records. During this recovery phase, cod exhibited uneven and sporadic activity, including dramatic ascents and intervals both at the surface and on the seafloor (Fig. 6 & 7).

Recovery phase was determined by visual observation for each depth profile, and we deemed it to end when the fish arrived at a consistent depth range of 55-90 m and a pattern of activity that was typical during the spawning ground residency (Fig. 6d). Recovery phases spanned 4 – 18 days (Table 3), and all measurements from the recovery phase of each fish were excluded from subsequent analysis of spawning behavior and depth/temperature trends.

Much of recovery activity consisted of irregular depth changes. However, three distinctive behavioral patterns were identified within this phase, and most cod alternated between more than one behavior. Behavior 1 was a period of activity near the surface immediately after release, likely caused by over-buoyancy, and was seen in six out of 26 of fish (23%) (Fig. 6a). Behavior 2 was a sharp escape dive to the bottom, after which the fish remained on the seafloor for several days (6b). We determined the fish to be sedentary on the seafloor when its depth profile showed a smooth, sinusoidal wave caused by the tidal signature, indicating the fish was stationary but the tide was rising and falling around it. This resting period was punctuated by brief, sporadic ascents, but predominantly lacked discernible movement. Seventeen fish (65%) showed this behavior.

Behavior 3 was a series of depth fluctuations observed in previous DST studies of cod (Godo and Michalsen 2000; Heffernan et al. 2004), and described as recuperation or equilibration behavior after release (Nichol and Chilton 2006; van der Kooij et al. 2007). This pattern often followed Behavior 1 or 2. In Behavior 3, the cod made a gradual descent from the surface in the form of oscillatory vertical movements that shifted to greater mean depth over several days (Fig. 6c). Oscillations often occurred in a regular diel cycle in which the cod was deep by day and shallow by night. The peak of each subsequent oscillation increased in depth, often at a similar rate among individuals (Fig. 7). The end result was that the oscillations diminished in magnitude over time as the fish approached its target depth, before finally dissipating altogether as the fish achieved a consistent depth range. Fifteen fish (58%) exhibited some form of this equilibration behavior (Fig. 7).

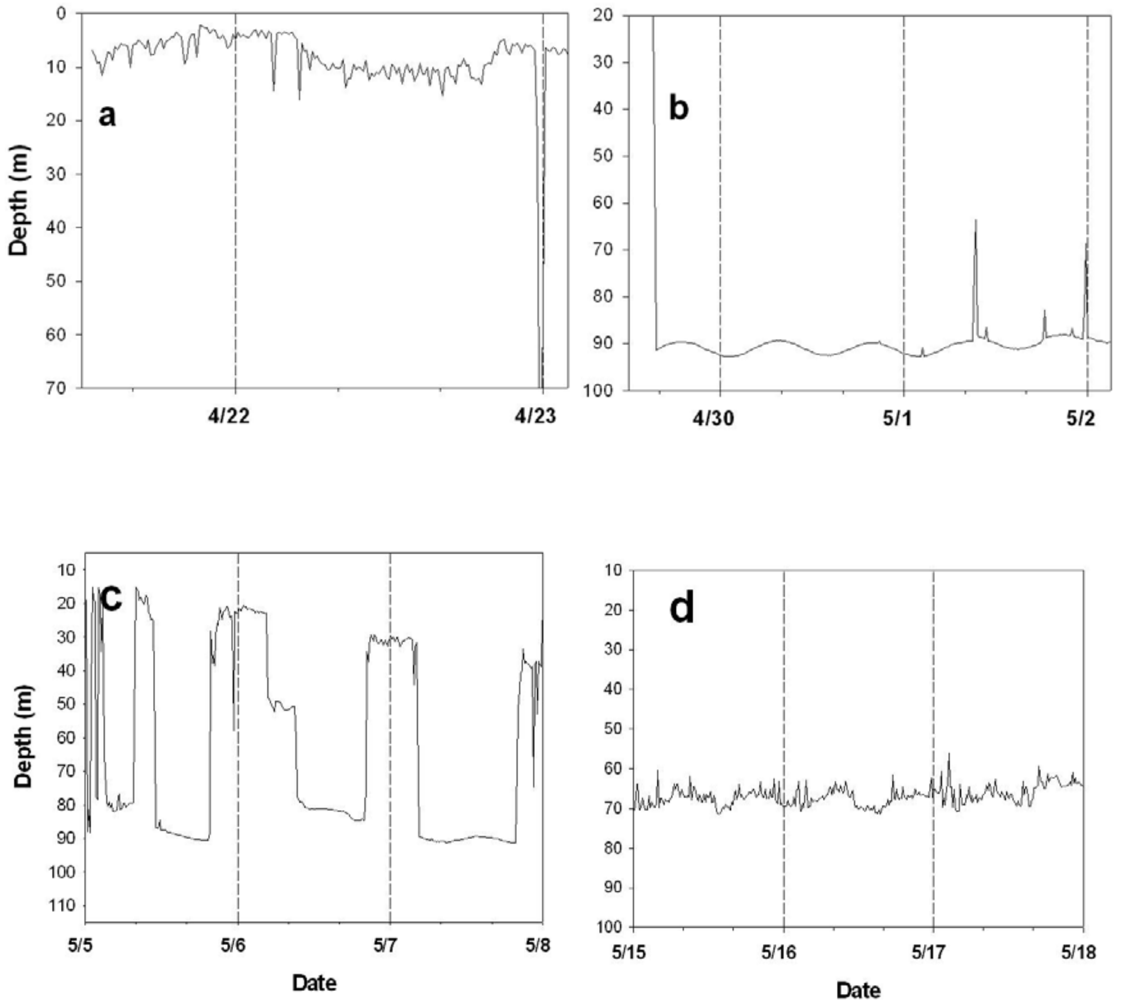

Fig. 6. Tagging recovery phase behaviors and typical subsequent spawning phase activity. a) Shallow period after release during recovery phase. b) Escape dive and sedentary period during recovery phase. c) Oscillatory descent behavior during recovery: deep by day, gradually decreasing ascents at night. d) Typical behavior during spawning phase: constant activity, small vertical range, and 55 – 80 m depth.

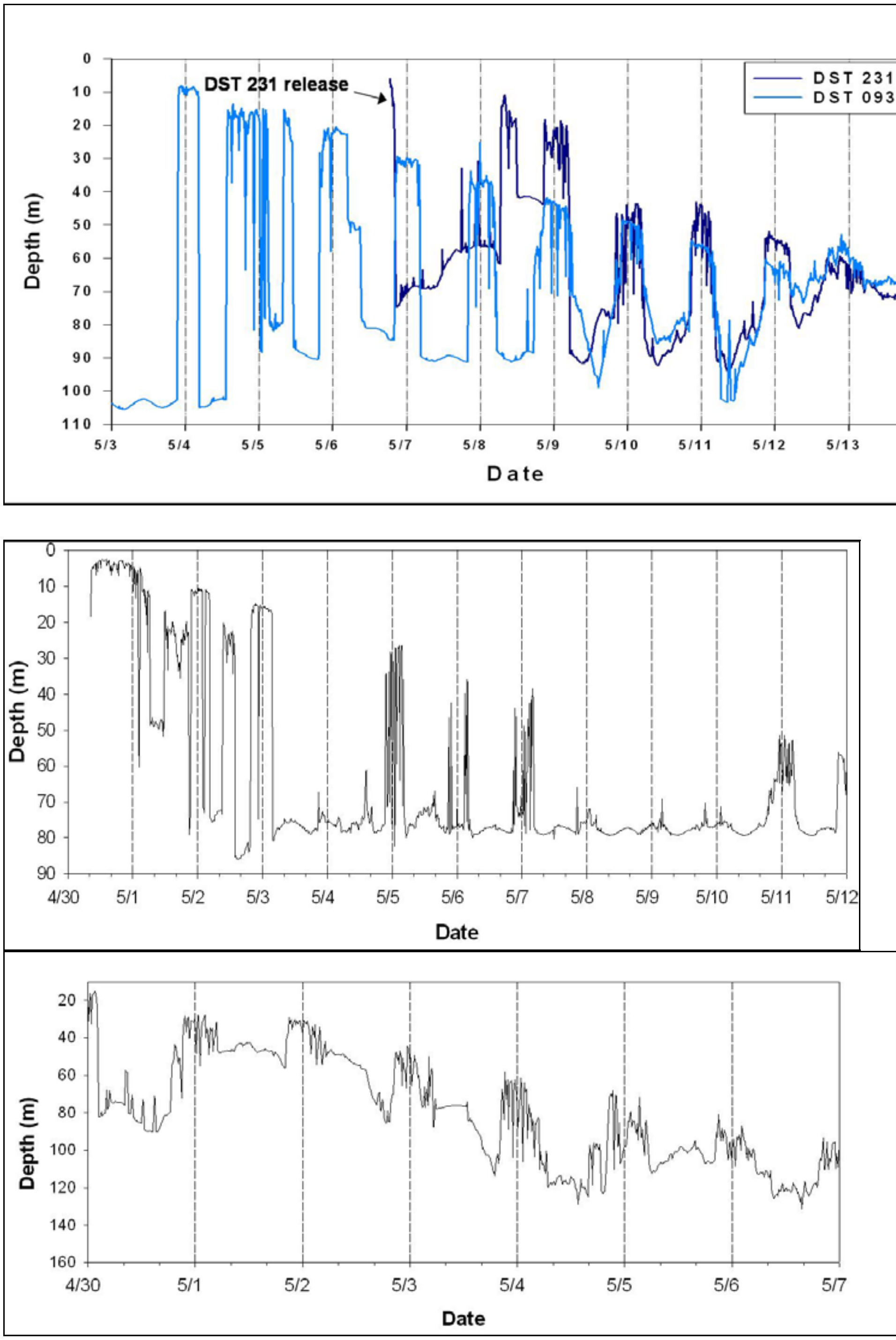

Fig. 7. Oscillatory descent behavior during the recovery phase. Dotted gridlines indicate 12:00am on successive days. Top plot shows overlapping recovery phases of two DSTs. The first was tagged a week earlier and displayed an initial bottom interval. Both adopted diel oscillations that diminished in similar increments each night. Both entered spawning phase by May 13 and adopted narrow depth range of 55 -- 80 m. The other two plots show additional forms of oscillatory behavior.

A3. Spawning Phase

As tagging recovery behaviors diminished, most cod adopted a similar pattern of reduced vertical activity with a consistent and restricted depth range (Fig. 6d). This phase lasted 1-5 weeks, beginning in May and ending between late May and mid-June, and both recaptures and occupied depths indicate fish were present in Ipswich Bay during this time. Because cod are known to spawn at this time in this location, we refer to this period as the spawning phase. Each spawning phase was deemed to begin after the recovery phase, and end when the fish was recaptured in Ipswich Bay or we confirmed it had left Ipswich Bay based on its depth profile. The dates and durations of DST recovery and spawning phases are summarized in Table 3. Three cod lacked identifiable spawning phases because they migrated to depths greater than Ipswich Bay within days of release (976, 060, & 241).

The occupied depth during the spawning phase was concentrated at 55 – 80 m, which is consistent with the range of bottom depths found in Ipswich Bay inshore of Scantum Basin (Fig. 8). Fish recaptured during this phase were all caught in Ipswich Bay within 10 m of the bottom. Vertical movement during the spawning phase was mostly confined to a narrow range of ~20 m, yet fish appeared to be in constant motion (with continuous minor and irregular depth changes) and were not sedentary. Movement was often minimal enough that a semi-diel tidal pattern can be vaguely seen in the depth profile (Fig. 6d). Table 4 includes each DST-equipped cod's mean depth during its individual spawning phase (SP). For six fish, this phase persisted until they were recaptured in Ipswich Bay in May or June (Table 3). These were presumably caught before their spawning phase was completed. For the rest, the spawning phase ended when each fish adopted a new vertical activity pattern, typically associated with a dramatic shift to deeper depths (Fig. 8). The maximum depth in Ipswich Bay is approximately 100 m, and therefore any movement deeper than 100 m is confirmation the fish must have moved offshore out of Ipswich Bay, into deeper waters such as Scantum Basin, Jeffrey's Basin, or the trenches east of Cape Ann. We marked the end of each spawning phase as the date a cod first descended below 100 m, followed by several days of deep-water activity and no confirmed return to the spawning ground. Six cod also showed a noticeable ascent to shallower water (50-60 m) for several days immediately preceding their deep-water descent (Fig. 8).

Fifteen cod were observed to make these offshore descents; occurring 17 – 43 days after their spawning phases began (Table 3). Only two cod left Ipswich Bay without ever descending below 100 m, and were recaptured on Jeffrey's Ledge and Stellwagen Bank (004 & 061). Their vertical activity patterns and depth during May and early June were consistent with other cod's spawning phases, however, and we chose the mean date of offshore descent, June 8, as a rough estimate for the end of their spawning phase.

Table 3. Tagging recovery phase (RP) and spawning phase (SP) durations for cod equipped with DSTs.

Cod/ DST	Release	RP Duration (days)	SP Start	SP Duration (days)	SP End
151	April 30	13	May 13	*6*	*May 19*
165	April 30	13	May 13	*6*	*May 19*
180	April 30	6	May 6	*13*	*May 19*
074	April 29	5	May 4	*7*	*May 19*
093	April 30	12	May 12	*17*	*May 29*
176	April 30	9	May 9	*27*	*June 5*
231	May 6	7	May 13	*21*	*June 3*
010	April 29	9	May 8	30	June 7
976	April 21	8	-	-	-
077	April 29	5	May 4	37	June 10
014	April 29	13	May 12	33	June 14
140	April 30	12	May 12	17	May 29
006	April 29	7	May 6	39	June 14
033	April 29	11	May 10	12	May 22
207	May 6	8	May 14	31	June 14
004	April 29	7	May 6	34*	June 8*
056	April 29	13	May 12	25	June 6
061	April 29	4	May 3	37*	June 8*
241	May 17	18	-	-	-
086	April 29	7	May 6	43	June 18
060	April 29	8	-	-	-
147	May 6	6	May 12	32	June 13
228	May 6	5	May 11	24	June 4
017	April 29	12	May 11	38	June 18
020	April 29	13	May 12	34	June 15
981	April 29	12	May 11	23	June 3

* Two cod never made deep-water shift when leaving spawning ground; mean offshore descent date of June 8 is used as substitute and indicated with asterisks.
Italicized SP end dates for first six cod indicate SP ended when they were caught on spawning ground in May-June. All other cod's SP end dates signify offshore descents.

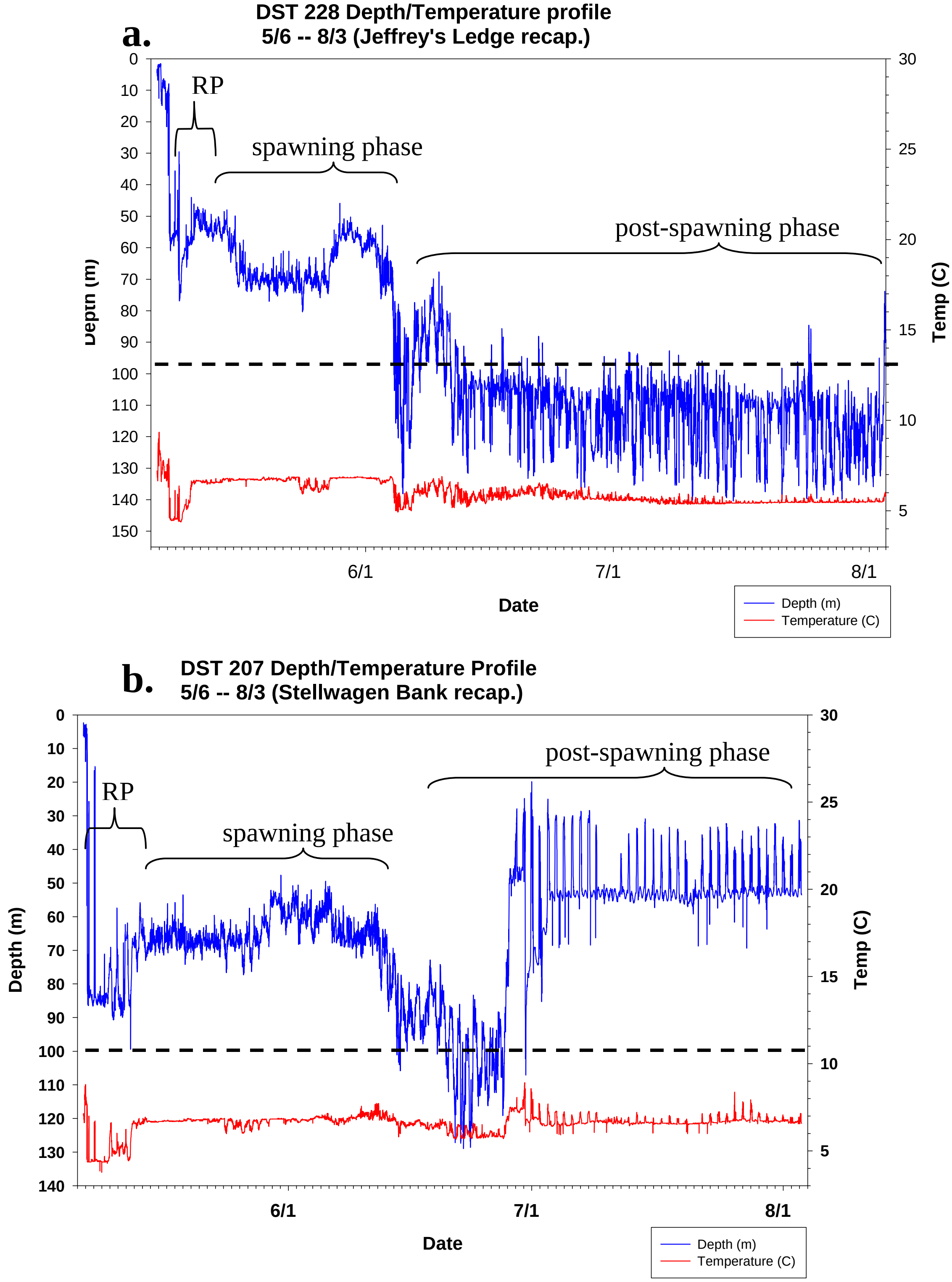

Fig. 8. DST depth & temperature profiles, illustrating recovery phase (RP), spawning phase, offshore descent in June, and post-spawning phase. Dotted line indicates maximum depth in Ipswich Bay. One DST shows consistent deep-water activity after the spawning phase (a), while the other (b) ascended to a bank shallower than the spawning ground.

A4. Post-Spawning Phase

Most cod (73%, n=19) were at liberty long enough (>5 weeks) to exhibit a post-spawning phase, or activity outside of Ipswich Bay. All spawning phases ended by June 18 and most cod demonstrated a shift in vertical behavior in conjunction with their move to deeper water. The DSTs programmed in this study reached their memory capacity and ceased recording after six months, usually in late October 2006. Thus the recorded post-spawning phase lasted several months in some cases, and this phase was divided into month blocks to examine behavioral trends on a finer scale. Table 4 gives each cod's mean depth for all post-spawning months. For each cod, data were only analyzed for a given month if the DST recorded at least two weeks of data during that month. The post-spawning month of "June" is defined here as the remainder of June after each cod's spawning phase ended.

A5. Trends in DST data

A5.1 Depth

Spawning phase depth ranged from 6 – 105 m, but these extremes represent brief forays to deep water, and unusual vertical ascents observed in only a few cod. Cod depths were highly similar during this period (Table 4). Cod released on the edge of Scantum Basin (Fig. 2) initially inhabited deeper waters during their tagging recovery phase, but most cod moved into a typical spawning phase range of 55 – 80 m by mid-May.

Depths occupied in post-spawning months spanned 25 – 203 m. Vertical behavior changed considerably after the spawning phase ended, and two general trends are evident in Table 4. The most common trend (n=10) was characterized by consistent deep-water activity after leaving Ipswich Bay, with mean monthly depths often greater than 100 m (Fig. 8a). The second trend (n=5) was an offshore descent followed by a return to depths comparable to Ipswich Bay, or even shallower (Fig. 8b).

Table 4. Mean depth (m) for cod equipped with DSTs by spawning phase and post-spawning month.

			Time Period					
Cod/ DST	Sex	Size (cm)	SP	June	July	August	Sept.	Oct.
151	M	95	68.6					
165	M	102	71.0					
180	M	97	70.3					
074	F	76	72.9					
093	F	102	67.5					
176	M	74	65.4					
231	F	90	64.0					
010	F	74	75.7	129.2				
976	F	77	109.9*	77.8				
077	M	73	81.3	78.7				
014	M	75	74.4	124.2	137.7			
140	M	81	69.6	138.4	150.6			
006	M	73	65.7	122.4	131.4			
033	F	80	61.9	89.3	73.0			
207	M	73	65.3	88.4	51.3			
004	M	66	62.4	64.5	67.2			
056	M	84	69.2	103.9	125.0			
061	M	85	56.9	55.2	50.8	50.6		
241	F	94		93.7	80.6	86.0		
086	F	122	68.5		115.7	98.5		
060	M	71	72.8*	71.0	62.8	61.9	64.2	
147	M	70	58.6	79.6	81.3	75.8	79.3	94.0
228	M	76	64.2	104.6	115.0	112.0	121.0	132.5
017	M	100	64.3		125.4	132.5	137.2	136.2
020	M	90	62.6	107.5	122.2	120.6	126.4	131.1
981	M	91	70.1	80.9	49.9	32.3	33.9	32.8

* Cod 976 & 060 had no clear spawning phase; mean May depth is given in the SP column. Cod 241 had no clear spawning phase and did not recover from release until June. Spawning phases for cod 086 & 017 extended through most of June; therefore no June mean is given

Table 5. Mean vertical range (m) by spawning phase and post-spawning month.

Cod/DST	SP	June	July	August	Sept.	Oct.
151	19.1					
165	13.7					
180	22.1					
074	13.4					
093	12.0					
176	11.0					
231	10.6					
010	21.7	40.5				
976	35.0*	26.2				
077	19.1	34.2				
014	16.2	*51.5*	*66.2*			
140	18.4	*48.7*	*51.9*			
006	16.9	*49.2*	*47.3*			
033	21.6	38.3	36.0			
207	13.7	33.6	26.8			
004	13.4	26.4	24.4			
056	17.5	*38.8*	*44.6*			
061	14.2	16.2	23.5	23.3		
241		30.7	11.5	14.2		
086	23.5		*9.9*	11.9		
060	24.9*	24.0	28.7	17.9	9.2	
147	20.5	24.9	21.9	28.1	23.6	39.9
228	12.8	*33.5*	*34.2*	*33.2*	*36.9*	*31.2*
017	12.8		*33.4*	*34.3*	*41.3*	*27.4*
020	15.0	*65.2*	*54.6*	*35.4*	*33.2*	*27.4*
981	12.6	29.1	13.3	4.3	7.4	4.5

*Cod 976 & 060 had no clear spawning phase; mean May vertical range is given in the SP column. Cod 241 had no clear spawning phase and did not recover from release until June. Spawning phases for cod 086 & 017 extended through most of June; therefore no June mean is given. *Italics* indicate months where mean depth > 100 m.

Table 6. Mean temperature (°C) by spawning phase and post-spawning month.

Cod/DST	SP	June	July	August	Sept.	Oct.
151	6.7					
165	6.7					
180	5.9					
074	6.6					
093	6.6					
176	6.7					
231	6.7					
010	6.0	5.9				
976	5.0*	6.7				
077	6.0	6.1				
014	6.6	5.7	6.1			
140	6.5	5.8	6.1			
006	6.5	5.9	6.0			
033	6.5	6.1	6.4			
207	6.8	6.4	6.7			
004	6.4	6.2	6.1			
056	6.6	6.1	6.0			
061	6.5	7.1	6.7	6.9		
241		6.0	6.1	6.5		
086	6.4		5.9	6.6		
060	6.2*	6.7	6.5	6.9	7.4	
147	6.9	6.3	5.9	6.6	7.3	7.5
228	6.7	5.9	5.5	5.9	6.3	6.3
017	6.8		5.7	5.9	6.1	6.5
020	6.8	5.8	5.6	5.9	6.1	6.3
981	6.5	6.2	6.9	7.8	8.9	10.6

* Cod 976 & 060 had no clear spawning phase; mean May temperature is given in the SP column. Cod 241 had no clear spawning phase and did not recover from release until June. Spawning phases for cod 086 & 017 extended through most of June; therefore no June mean is given

A5.2 Vertical range

We also examined the vertical range of depths occupied by cod. Vertical range is defined as the difference between minimum and maximum depths for each day in a DST record. From these values, mean daily vertical range was calculated for each time block (spawning phase and post-spawning month) and presented in Table 5.

Vertical range was found to consistently increase with depth. All cod exhibited an average daily vertical range of 10-23 m during their spawning phase. Almost all cod (14 out of 15) that made a deep-water shift exhibited a corresponding increase in daily vertical range that doubled or even tripled their spawning phase ranges (Fig. 9). The majority of large vertical ranges (>30 m) were observed in months where a cod's mean depth was over 100 m (Table 5). The cod without spawning phases not only exhibited their deepest activity in May and June, but also their largest vertical ranges during these months. Cod that moved offshore into deep water, but later settled in waters shallower than Ipswich Bay, show vertical ranges that decreased as their depth decreased (fish ID numbers 207 & 981). Interestingly, however, the two cod that never entered deep water still showed an increase in vertical range over time, suggesting that their behavior changed as they migrated, even if depth did not (fish 004 & 061). Using values from Tables 4 & 5, a simple linear regression of mean depth vs. mean daily vertical range for each time period found that the effect of depth on vertical range was significant for all time periods ($p<0.05$) except during the spawning phase and in the month of October.

Most cod in the post-spawning phase displayed an interval, however brief, of sedentary behavior. During these periods, cod became motionless at a fixed depth, apparently resting on the seafloor similar to recovery phase behavior. Frequently cod became diurnally sedentary but active at night, and showed sizeable vertical ranges. Mean vertical ranges less than 15 m in post-spawning months, however, indicate where cod became fully sedentary for extended periods, and made vertical excursions only rarely (fish 241, 086, 060, & 981). Sedentary behavior was typically associated with depths <80 m. It is notable that most cod recaptured in the post-spawning phase (72%) became sedentary for at least a day immediately before capture. Nevertheless, with the exception of a few cod that adopted extended sedentary modes in late summer, this behavior did not dominate DST records and the spawning phase represents the time block of smallest vertical range and lowest activity for most cod (Table 5).

The vertical activity of cod 086 proved to be an anomaly among the data set in numerous ways. This 122 cm female was over 20 cm larger than any other recapture, and had the distinction of attaining both the minimum depth and highest vertical range of any fish in the spawning phase, despite a mean depth similar to others (Tables 4 & 5). Its spawning phase was distinguished by two separate week-long sequences of remarkably high vertical ascents, occurring in late May and again in mid-June, both presumably after any tagging recovery phase, and neither showing a gradual descent as equilibration

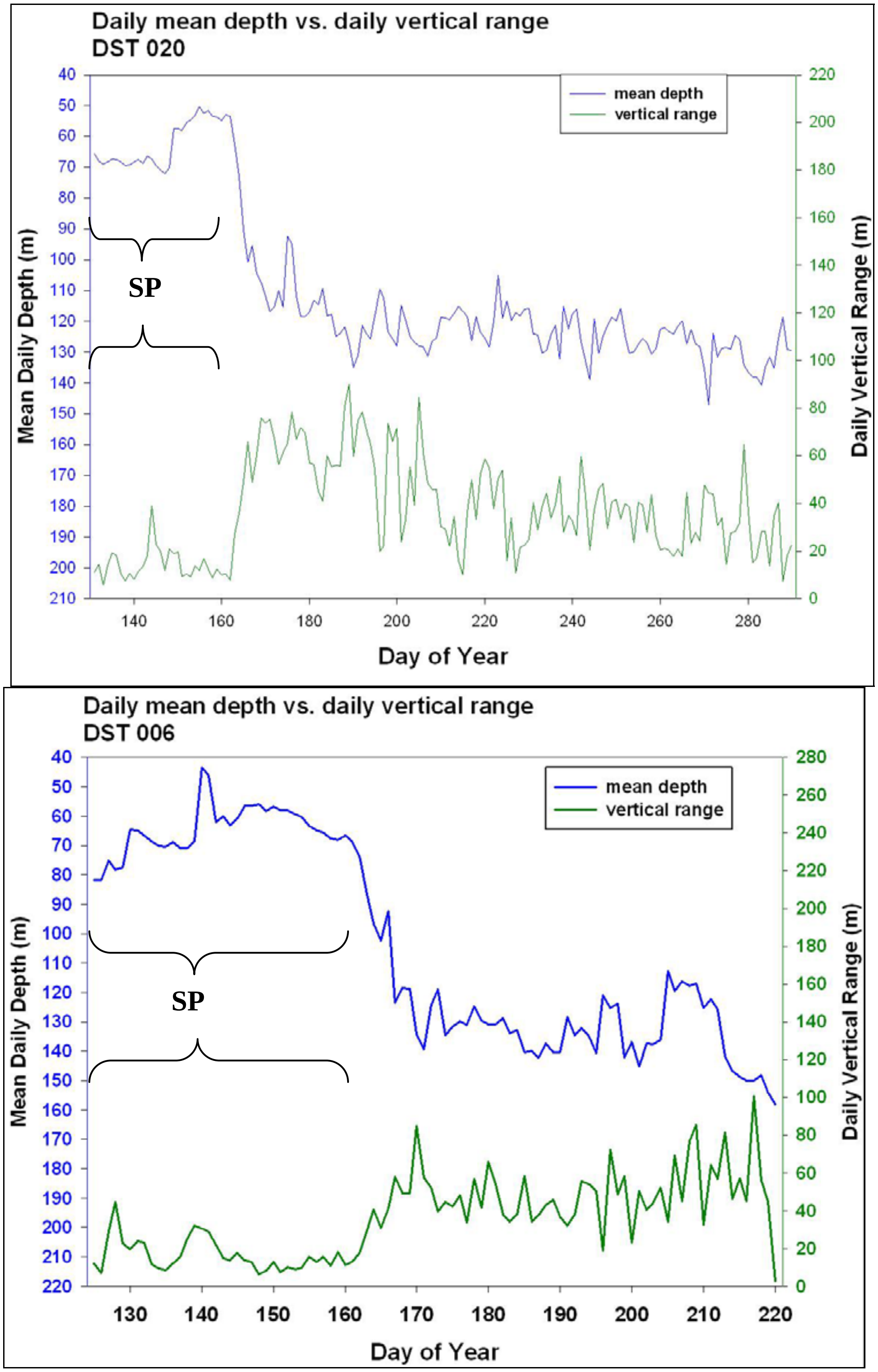

Fig. 9. Examples of the positive relationship between depth and vertical range. For each DST, daily mean depth and daily vertical range are plotted together. Spawning phases (SP) are indicated.

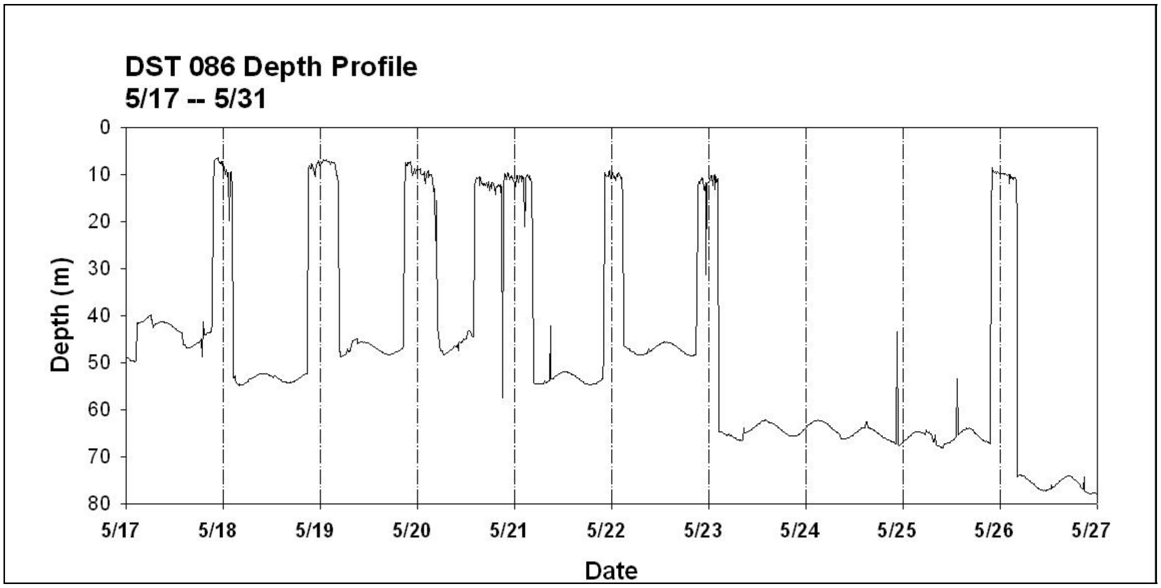

Fig. 10. Depth profile of DST 086 illustrating a series of unusual nocturnal ascents in May during its spawning phase that do not appear to be equilibration behavior. A second series during its spawning phase occurred in June.

behavior does. During these nocturnal ascents, this female rose up to 70 m above its sedentary depth, and each ascent peaked just 6-15 m below the surface; up to 22 m shallower than any other cod in May after the recovery phase (Fig. 10).

Cod 086 made a deep water shift in mid-June and was recaptured offshore of Maine in August 2006. Despite migration, its profile was characterized by an absence of fine-scale vertical activity. The fish spent intervals of several days at a fixed depth, then smoothly shifted depth up or down and fixed its depth again. After a depth shift, its activity became so minimal again that it was largely masked by a tidal signature, producing low mean vertical range values in deep water (Tables 4 & 5).

A5.3 Temperature

Temperature records from all DSTs show cod inhabited water temperatures ranging from 4 – 13°C in the summer and fall of 2006, although temperature was usually within a 5.5 – 8°C range for all time blocks (Fig. 11). Mean temperature by time block is given in Table 6. The spawning phase, which represents the time block with the highest number of cod at liberty and the most data points, also represents the narrowest temperature range, with most values between 6 and 7°C (Fig. 11). As expected, shallower depth was frequently associated with higher temperature, and many cod showed minor temperature drops following deep-water shifts. Using values from Tables 4 & 6, a simple linear regression of mean depth vs. mean temperature for each time period found that depth had a significant effect on temperature for all time periods ($p<0.05$). DSTs also display temperature increases from July to October, suggesting an additional seasonal effect. Although deep-water temperatures were not measured in this study, data from the Gulf of Maine Ocean Observing System's weather buoy on the coast of Maine demonstrates that water temperature at 20 m and 50 m gradually increased through mid-October (Fig. 12, GoMOOS Western Maine Shelf Buoy B).

A5.4 All data by time block

In addition to individual comparisons between cod, time series data from all DSTs were pooled together for each time period (i.e. all spawning phase data was pooled, all July data was pooled, etc.). The overall distribution of depth, daily vertical range, and temperature for each time period was calculated and illustrated in Figure 13. These box plots demonstrate a uniform, narrow depth range for the majority of the spawning phase, and correspondingly low vertical range and narrow temperature range. Post-spawning months all show an increase both in overall depth and the range of depths occupied. Similarly, post-spawning months show higher vertical ranges but also greater variation in vertical range within each month. No clear depth trend is obvious within post-spawning months, other than a slight depth decrease in August and a corresponding decrease in vertical range. Temperature decreased in June after offshore descents, but then warmed over time, and the thermal range occupied by cod expanded concurrently (Fig. 13).

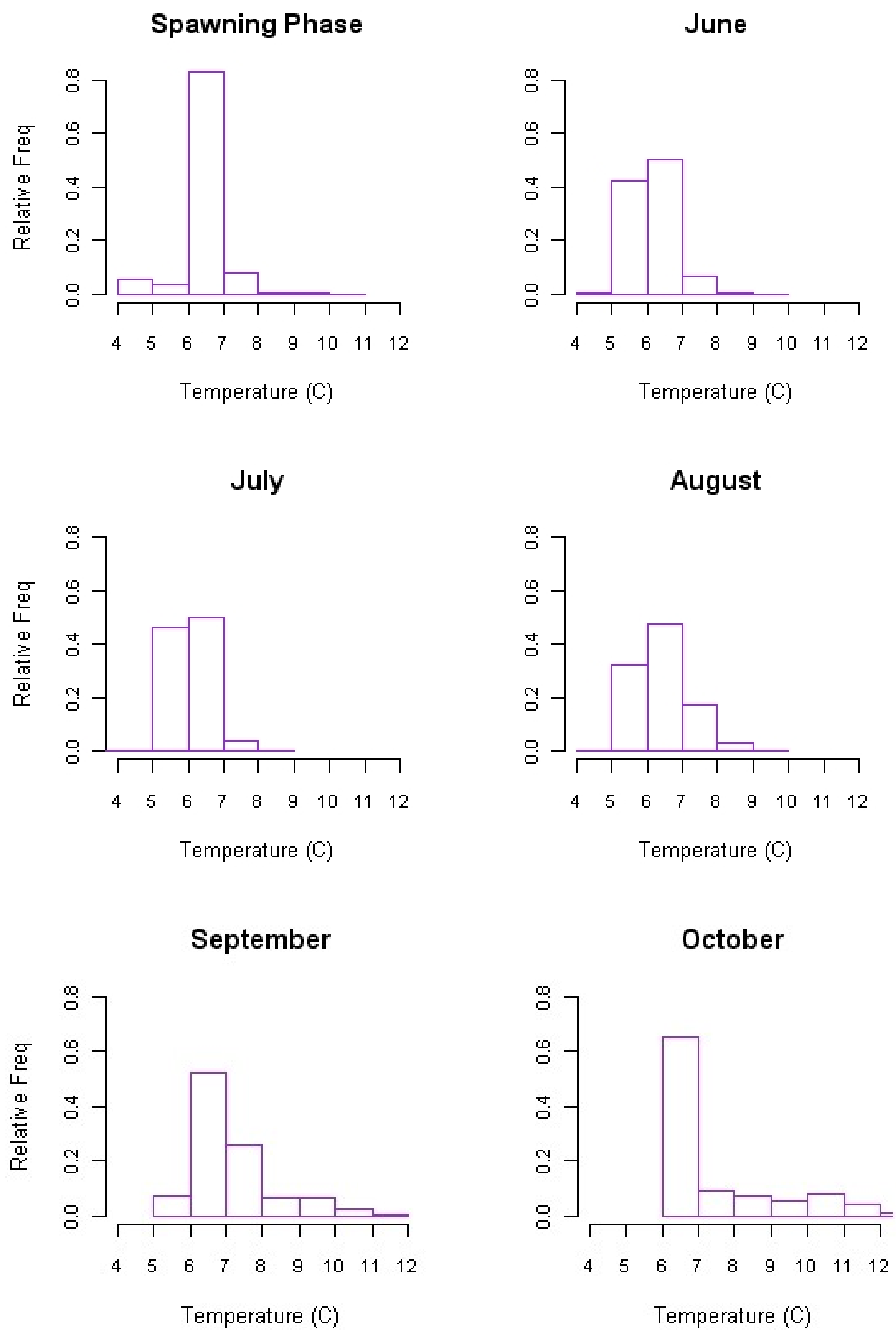

Fig. 11. Relative frequency distribution histograms of temperature (°C) using pooled data from all DSTs. Divided into spawning phase and post-spawning months.

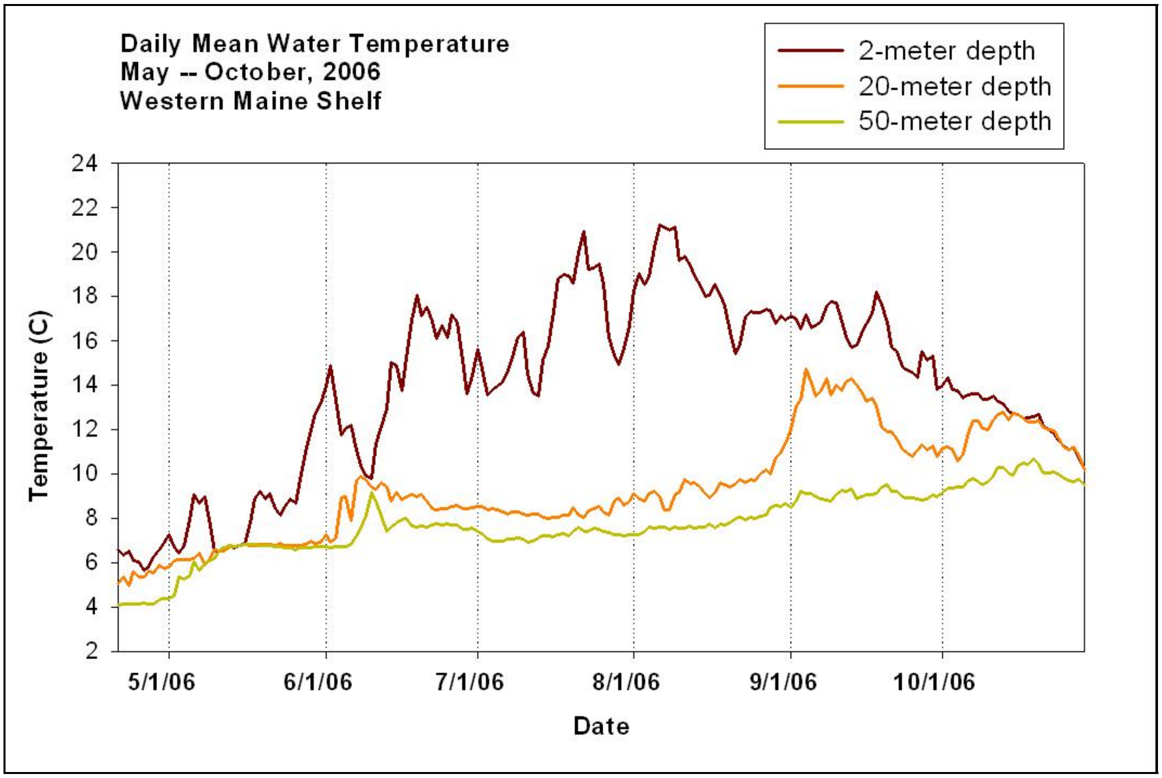

Fig. 12. Mean daily water temperature profile at 2 m, 20 m, and 50 m depths on southwestern Maine shelf during study period. Obtained from GoMOOS buoy B01. Bottom temperature gradually increases throughout the study period. A small increase in temperature occurs in early June, just preceding the majority of offshore descents.

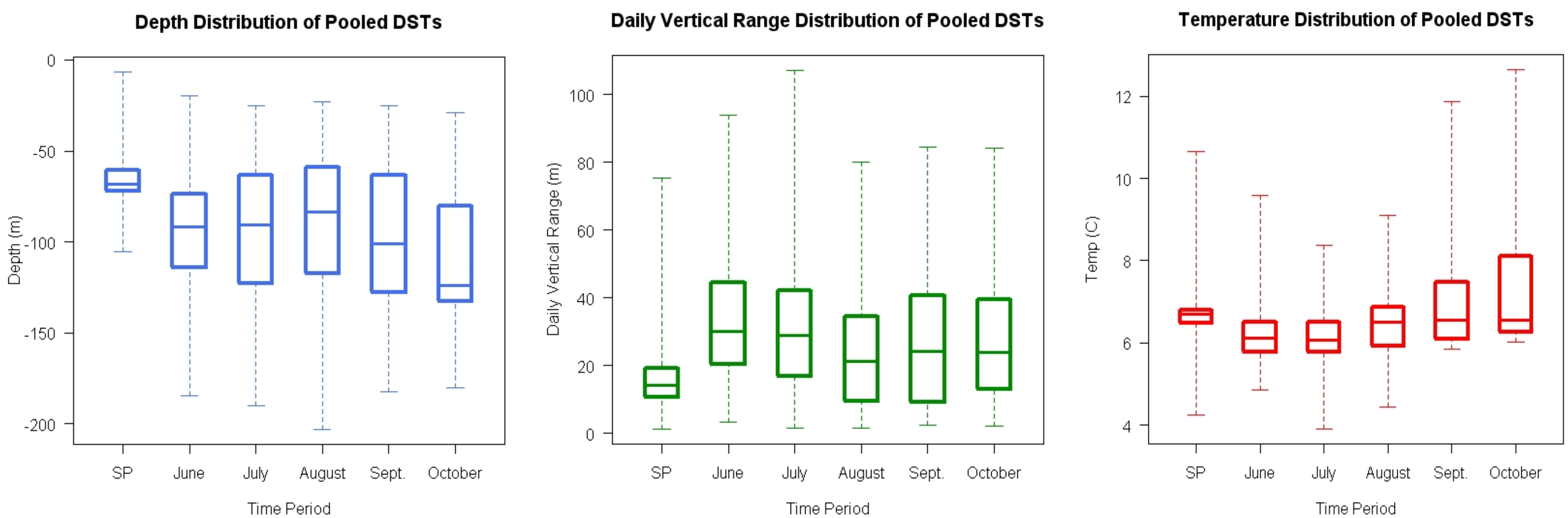

Fig. 13. Box plots of depth, daily vertical range, and temperature distribution by time period for all DST data combined. Whiskers extend to data extremes. SP=spawning phase.

A5.5 Differences by size and sex

The effect of size and sex on depth, vertical range, and temperature were examined for each time period using the mean values from Tables 4–6. Mean values were found to be normally distributed within each time period (Shapiro-Wilk, $p>0.05$). Initially, a general linear model (GLM) was applied using the mean depths of the spawning phase as the dependent variable. Size, sex, and the interaction between size and sex all served as independent variables. This GLM was repeated for each post-spawning month, and in turn this series of GLMs was repeated for daily vertical range and temperature. Neither size nor sex were found to have a significant effect on depth, range or temperature for any time period ($p>0.1$ for all results).

A6. Temporal rhythms of depth data

We examined temporal rhythms of depth profiles by combining visual inspection of raw depth data with the construction of autocorrelation function plots (ACF). In particular, fine-scale temporal rhythms during spawning and post-spawning phases were characterized and compared to patterns observed in post-spawning months.

Results of the autocorrelation function are illustrated in plot form (Fig. 14). The ACF plot indicates the strength of autocorrelation between depth values that are a given number of observations apart, with 1.0 as the maximum autocorrelation strength. The x-axis shows the lag, or the number of observations (data points) separating depth measurements. A positive peak at a lag of 120 indicates that throughout the spawning phase, depth values 24h apart (120 depth readings) are consistently similar. If the peak repeats at multiples of 120 on the lag axis, depths values at 48h, 72h, 96h, etc. apart are also correlated. Negative peaks at a lag of 60 indicates depths werre consistently different when only 12h apart. A pattern of positive peaks at 24h intervals, and negative at 12h intervals, indicates a diel rhythm in vertical movement, particularly when it persists as lag increases (i.e. to several days between depth measurements) (Fig. 14).

For each cod at liberty more than a week, an ACF was also created for each post-spawning time block. These month-long blocks were smoothed just as spawning phases were (span widths = 360 & 300). Month blocks were further subdivided and an ACF was created for every two-week period a fish was at liberty after its spawning phase (span widths = 280 & 336). The focus of this analysis was fine-scale rhythm, such as diel or semi-diel cycles, and ACF plots were run with a maximum lag (x-axis) of 600 observations, or a difference of 5 days between depth values.

The summary results of the ACFs by spawning phase and post-spawning month for each cod are shown in Table 7. For each time block, the strength of the ACF and the type of rhythm are given. “None” indicates no consistent signal above the plot’s confidence intervals. “Weak” indicates a signal below 0.2 that breaks down as lag increases. “Moderate” indicates a consistent or gradually diminishing signal in the 0.25–0.5 range. “Strong” indicates an ACF signal that is consistently over 0.5, and only slightly diminishes as lag increases to the 5d maximum (Fig. 14).

Three types of fine-scale movement rhythms are given in Table 7. “Semidiel” indicates a pattern of positive correlation at 12h and 24h apart, and negative correlation at 6 and 18h apart. This demonstrates a tidal pattern, and was detected when the sinusoidal rise and fall of the tide was evident in the depth profile of a few cod with highly reduced spawning phase activity, or completely sedentary modes in later months (e.g. fish 060 & 981 in Fig. 15a). We defined “DVM” (diel vertical migration) as the behavior in which the cod is deeper during the day and ascends to shallower depths at night. “DVM” was indicated in Table 7 when a diel ACF signal was detected and DVM was obvious in the depth profile. If a diel ACF signal was detected, but a different, or more ambiguous 24h movement pattern was observed in the depth profile, the pattern was classified simply as “diel” in Table 7.

A7. Tidal adjustment

One concern when applying ACF to depth profiles was the potential effect of the tide on any observed temporal patterns. We attempted to address this potential bias by removing the tidal signature from depth data. We obtained 2006 tidal data from the mouth of Portsmouth harbor, New Hampshire, ~20 km northwest of the spawning ground. Using a time series of water level measurements above mean low-low water (MLLW), we adjusted depth data by subtracting the water level value from each DST depth value at the corresponding point in time.

The tidal adjustments had minor effects on spawning phase ACFs, including slight signal enhancements or reductions and a smoothing of some semi-diel correlation peaks. We opted to use the tidally-adjusted ACFs for all spawning phase results given here. In post-spawning months, tidal adjustment had no discernible effect for most ACFs, but completely removed semi-diel signals for some (but not all) sedentary cod. Due to the unpredictable (albeit mostly negligible) impact of tidal adjustment on later months, possibly due to variable distance between the cod and the monitoring station, tidal adjustment was only employed for the spawning phases.

Trends in temporal patterns

The spawning phase of most fish, often characterized by a narrow depth range and low vertical activity, usually revealed a weak to moderate diel signal not immediately obvious to visual inspection (Fig. 16). This rhythm often shifted subtly between slight DVM and reverse DVM, or sedentary or more active behaviors during regular intervals at other times. Several cod with particularly low vertical activity produced a semi-diel ACF. In total, 87% of cod with a defined spawning phase displayed a weak or moderate cyclical pattern during that period. Only 13% revealed consistent DVM however.

The months following the spawning phase were dominated by a shift to moderate and strong diel and DVM rhythms (Fig. 16). Semi-diel signals were only observed when cod were sedentary for extended periods. Seventy four percent of cod at liberty past their spawning phase adopted visible DVM in their depth profiles during June and July, and 53% had strong diel or DVM ACF signals during these months.

There were several cases in post-spawning months where an ACF returned a weak diel signal, but visual inspection of the depth profile revealed a powerful, consistent 24h rhythm to vertical movement. In some cases (061, 147, 207, 033), cod appeared to reach shallow banks and adopt strong diel rhythms in which they were sedentary by day and vertically active at night. However, they displayed variable nocturnal activity – sometimes descending from their daytime bank to greater depths, sometimes ascending above their resting place, and often performing both deep and shallow excursions in one night (Fig. 15b). This diel pattern of activity/inactivity could not be captured by ACF.

The goal of autocorrelation analysis was to examine short-term temporal patterns, but we extended the lag beyond 5 days in some cases to investigate longer-term patterns. Most ACF signals continued to diminish with increasing lag, but a few showed a two-week signal, in which correlation began to increase beyond a 7d lag until reaching a second, weaker peak at a 14d lag. This is possibly a tidal cycle corresponding to spring and neap tides, and there is no apparent behavioral component to this pattern.

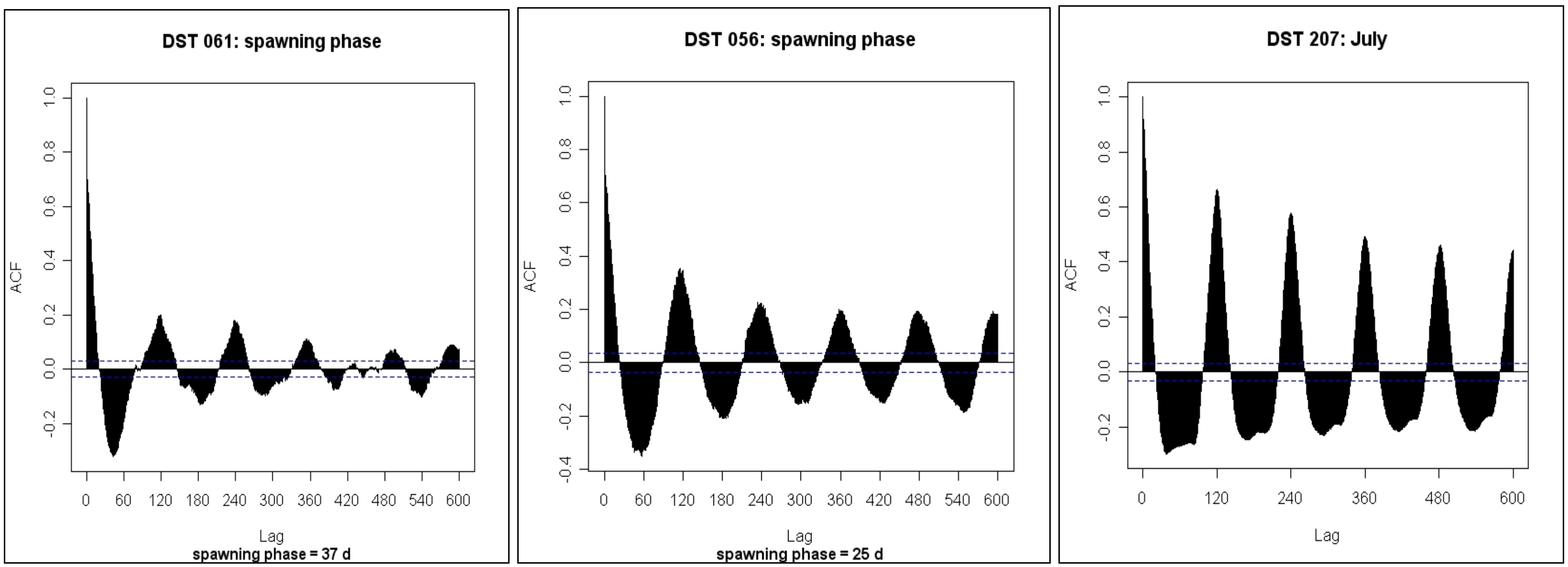

Fig. 14. Three ACF plots that provide examples (left to right) of weak, moderate, and strong ACF signals. Plots are from different DSTs and time periods. All are examples of a diel pattern of vertical movement, where depths are consistently similar 24 hrs apart and consistently different 12 hrs apart. In ACF plots, depth is positively correlated at 24 hr intervals (lags 120, 240, 360, etc.), and negatively correlated at the intervening intervals (lags 60, 180, 300, etc.).

Table 7. Fine-scale rhythms of vertical activity for cod with DSTs by spawning phase and post-spawning month.

Cod/DST	Spawning Phase	June	July	August	September	October
151	none					
165	none					
180	mod. DVM					
074	weak semidiel					
093	strong DVM					
176	mod. semidiel					
231	mod. DVM					
010	weak diel	strong DVM				
976	mod. diel*	mod. DVM				
077	weak diel	mod. DVM				
014	mod. diel	strong DVM	strong DVM			
140	weak semidiel	strong DVM	strong DVM			
006	mod. diel	*mod. DVM*	*mod. DVM*			
033	mod. diel	weak diel	mod. diel			
207	weak diel	*weak DVM*	strong DVM			
004	mod. DVM	weak semidiel	mod. diel			
056	mod. diel	strong DVM	strong DVM			
061	weak diel	*weak diel*	*weak diel*	*weak diel*		
241		strong DVM	strong DVM	strong DVM		
086	mod. diel		mod. semidiel	weak semidiel		
060	weak semidiel*	strong DVM	strong DVM	weak semidiel	weak semidiel	
147	weak diel	strong DVM	strong DVM	*mod. diel*	*mod. diel*	*weak diel*
228	weak diel	mod. DVM	mod. DVM	weak diel	weak diel	weak diel
017	mod. diel		strong DVM	strong DVM	strong DVM	strong DVM
020	weak diel	strong DVM	strong DVM	mod. diel	weak diel	none
981	mod. diel	mod. diel	weak diel	strong semidiel	weak semidiel	strong semidiel

ACF signal strength is ranked as weak, mod.(moderate), or strong. Rhythm type indicated by diel, DVM, or semi-diel.
Italics: ACF indicated weak/mod. signal but strong diel rhythms observed in the depth profile.
* Cod 976 & 060 had no clear spawning phase; May ACF is given in SP column. Cod 241 had no spawning phase and did not recover from release until June. Spawning phases for cod 086 & 017 extended through most of June; no June ACF is given.

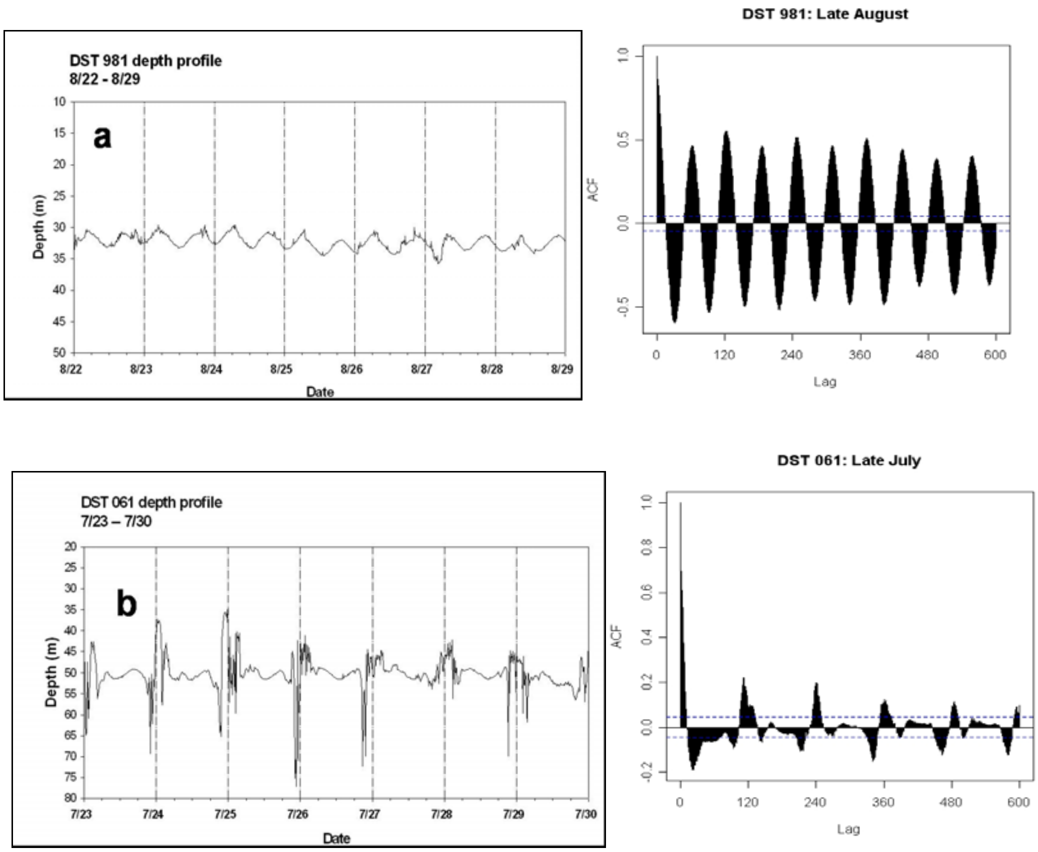

Fig. 15. Examples of fully sedentary and partially sedentary depth profiles and their corresponding ACF plots. Gridlines indicate 12 a.m. on successive days. a). Fully sedentary behavior at constant depth and a smooth, sinusoidal tidal signature (on left, location unknown). A strong semidiel ACF signal results from the tidal signature's dominance (on right). b). Sedentary behavior at constant depth by day on Stellwagen Bank, and activity at night (both ascents and descents, on left). Nocturnal depth variability results in a weak ACF signal (on right).

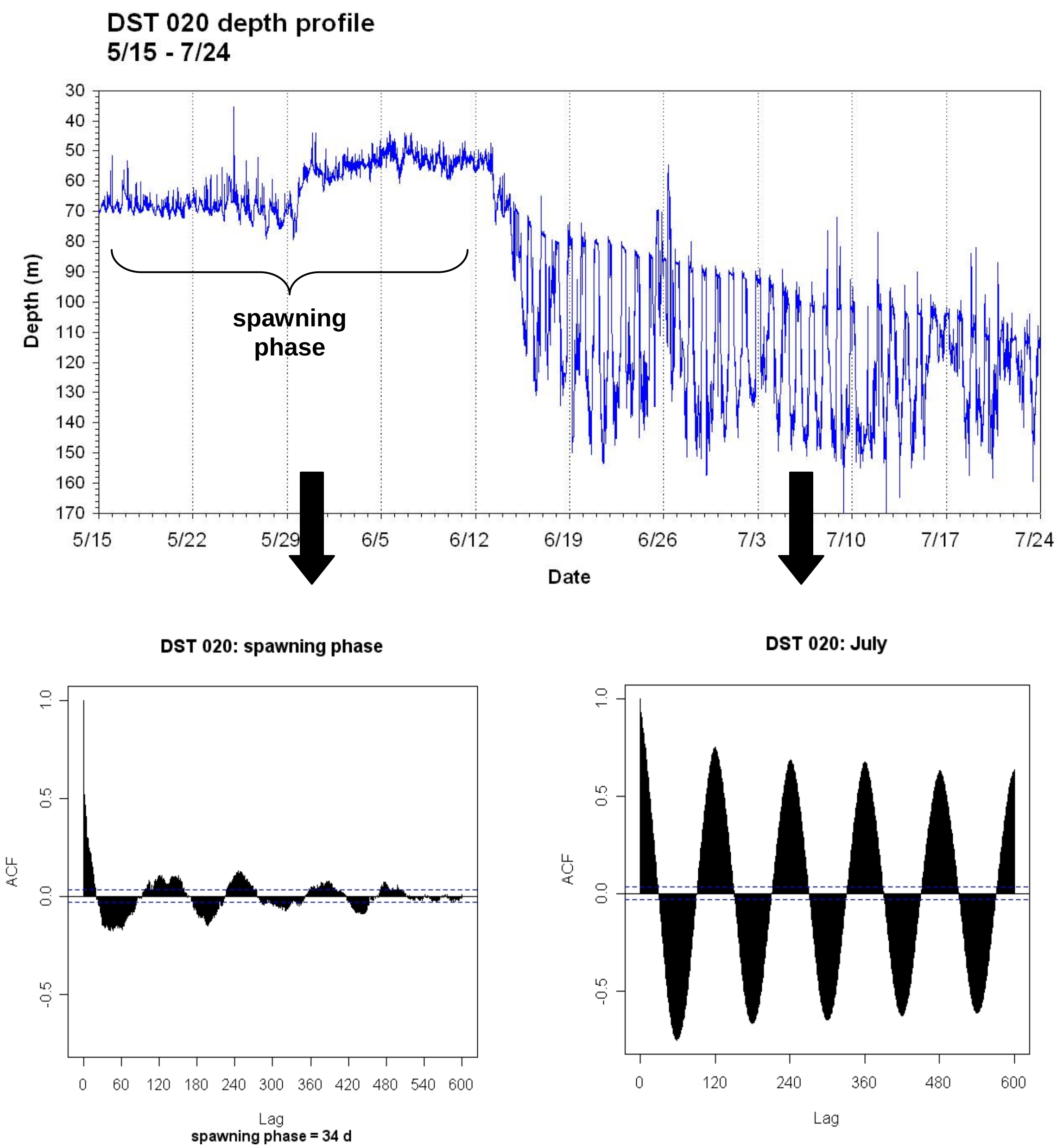

Fig. 16. Depth profile for DST 020 and corresponding ACF plots for its spawning phase and the month of July (post-spawning phase). Like several others, this cod transitioned from a faint diel rhythm during its spawning phase to a strong, consistent DVM pattern offshore.

B. Acoustic tracking results

The four continuous transmitters proved to be problematic, because the VR100 registered any ambient noise on their individual channels as a ping from a tag. Hundreds of false detections were recorded on each channel, and as a result we excluded all continuous transmitter data. Of the 26 cod equipped with coded transmitters, we excluded two that were potential mortalities due to lack of movement (T67 & T53). In total, we analyzed 24 acoustic tracks (12 males, 12 females) from coded transmitters using data from the VR100 manual hydrophone and six stationary VR2 receivers. Summaries of individual detection data are given in Table 8. Each cod was relocated by boat or VR2 on 2 – 34 separate days, averaging 16 days (~30%) of the 55-day study period. Cod were relocated an average of eight days by boat and nine days by VR2s, and cod were detected at three different VR2 sites on average.

The last detection date for each cod was used as a proxy for departure date (Table 8). For the 21 cod that left the spawning ground during the study, departures ranged from May 14 – June 15, with a mean departure of June 4. Only three cod (T65, T66, & T69) were still present when the study ended June 30. Although limited by a small sample size, there was an apparent trend of females leaving earlier than males: mean departure for females was May 29, while males left during a narrow window of June 1 – 15 with an average departure of June 11.

B1. Home range analysis

Manual tracking data (by boat) and VR2 data (by stationary receiver) were kept separate for analysis, in part because the selective placement of VR2s near elevated features could bias home range estimation. The two data sets were also difficult to integrate because the boat-mounted hydrophone recorded only a few detections at a site before moving on, while a stationary VR2 could accumulate hundreds of detections when a tag was in range.

Manual tracking data from all cod were pooled together to characterize activity and distribution of the group. A minimum convex polygon (MCP) derived from this data encompasses the area where fish were found by boat, and was approximately 60 km^2 in size (Fig. 19). VR2s detected cod several kilometers outside of this area, but only briefly as cod passed those receivers during excursions or departures.

Table 8. Acoustic transmitter data summaries (n=24 cod). Last Detection date is a proxy for departure date, except for three cod (transmitters T65, T66, T69) that were still present when the study ended. Known Residence Time is the difference between Release and Last Detection. Total Detection Days include the number of distinct days in which the cod was relocated by any means, and is divided into manual tracking and VR2 detection days. The number of VR2s each cod was detected by is also shown.

Transmitter	Sex	Release	Last Detection	Known Residence Time (days)	Total Detection Days*	Manual Days*	VR2 Days	No. VR2s
T51	M	May 6	June 10	35	20	12	9	3
T52	M	May 6	June 14	39	24	19	8	6
T54	M	May 6	June 13	38	22	11	14	4
T55	F	May 6	May 22	16	10	3	7	4
T56	M	May 6	June 9	34	19	9	12	1
T57	F	May 6	May 30	24	9	2	7	4
T58	F	May 6	May 14	8	2	1	1	1
T59	M	May 6	June 15	40	22	15	12	5
T60	F	May 17	June 1	15	9	4	6	4
T61	M	May 6	June 12	37	21	8	15	2
T62	M	May 6	June 9	34	18	11	8	4
T63	F	May 17	June 2	16	5	5	0	0
T64	M	May 6	June 6	31	21	12	11	3
T65	M	May 6	*June 29*	54	22	18	4	3
T66	F	May 6	*June 28*	53	34	7	30	2
T68	F	May 17	June 14	28	15	13	4	3
T69	F	May 6	*June 28*	53	18	4	14	5
T70	F	May 17	June 6	20	12	2	11	3
T71	F	May 6	May 31	25	11	7	4	3
T72	F	May 6	May 18	12	7	3	4	4
T73	M	May 6	June 9	34	19	8	12	3
T74	M	May 6	June 2	27	14	8	7	5
T75	M	May 6	June 11	36	23	13	12	3
T76	F	May 17	May 28	11	7	3	5	3

* includes release day

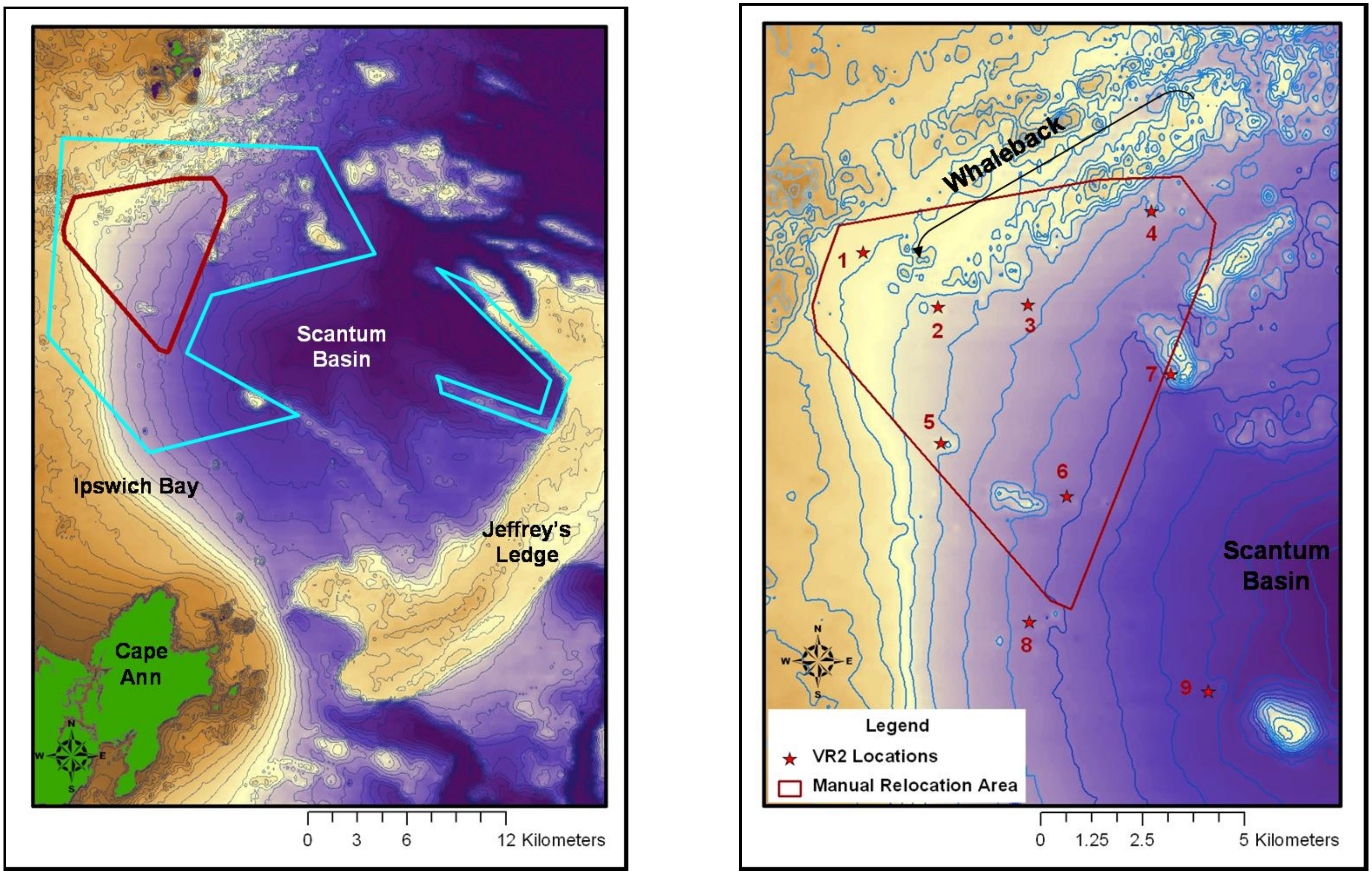

Fig. 19. a). Bathymetric map of manual tracking areas: light blue outlines the areas searched by boat, and red outlines the area in which cod were actually relocated. b). Close-up of the manual relocation area. Fish were also detected at all VR2 positions (numbered stars). Map highlights elevated bathymetric features including "Whaleback," a series of humps running southwest to northeast that borders a shallow shelf and the Isles of Shoals to the north.

Table 9. Summary data for each VR2, including deployment dates, number of transmitters detected, and total detections logged for each. Last row gives data for VR2 that went missing and was later relocated.

VR2 No.	Name	Lat.	Lon.	Deployment Dates	No. Days	No. transmitters detected	Total detections	Mean detections/ transmitter	Mean detections/ day	Mean no. transmitters/ day
1	30-Fath Edge	42.902	70.684	June 12-22	10	1	294	294.0	29.40	0.10
2	Stacy's	42.890	70.662	May 8-June 22	45	19	10,119	532.6	224.87	0.42
3	The 164 East	42.890	70.635	June 22-28	6	1	111	111.0	18.50	0.17
4	Whaleback	42.910	70.598	June 12-28	16	4	1586	396.5	99.13	0.25
5	The Rock	42.860	70.661	May 8-June 28	51	16	2,241	140.1	43.94	0.31
6	The Sisters	42.848	70.624	May 8-June 12	35	13	753	57.9	21.51	0.37
7	SW Hump	42.874	70.592	May 8-June 28	51	13	2,752	211.7	53.96	0.25
8	The 236	42.820	70.635	May 8-June 12 / June 22-28	41	8	569	71.1	13.88	0.20
9	Halfway Hump	42.804	70.582	May 8-27	19	2	61	30.5	3.21	0.11
10	Dragged VR2	42.738	70.595	June 6-28	24	2*	49*	24.5*	2.04*	0.08*

* VR2 #10 was confirmed to be missing on June 6 from its original site (Halfway Hump), and found with anchors attached at its “dragged” location on June 28. Detections it recorded after June 6 were assumed to be from the recovery location

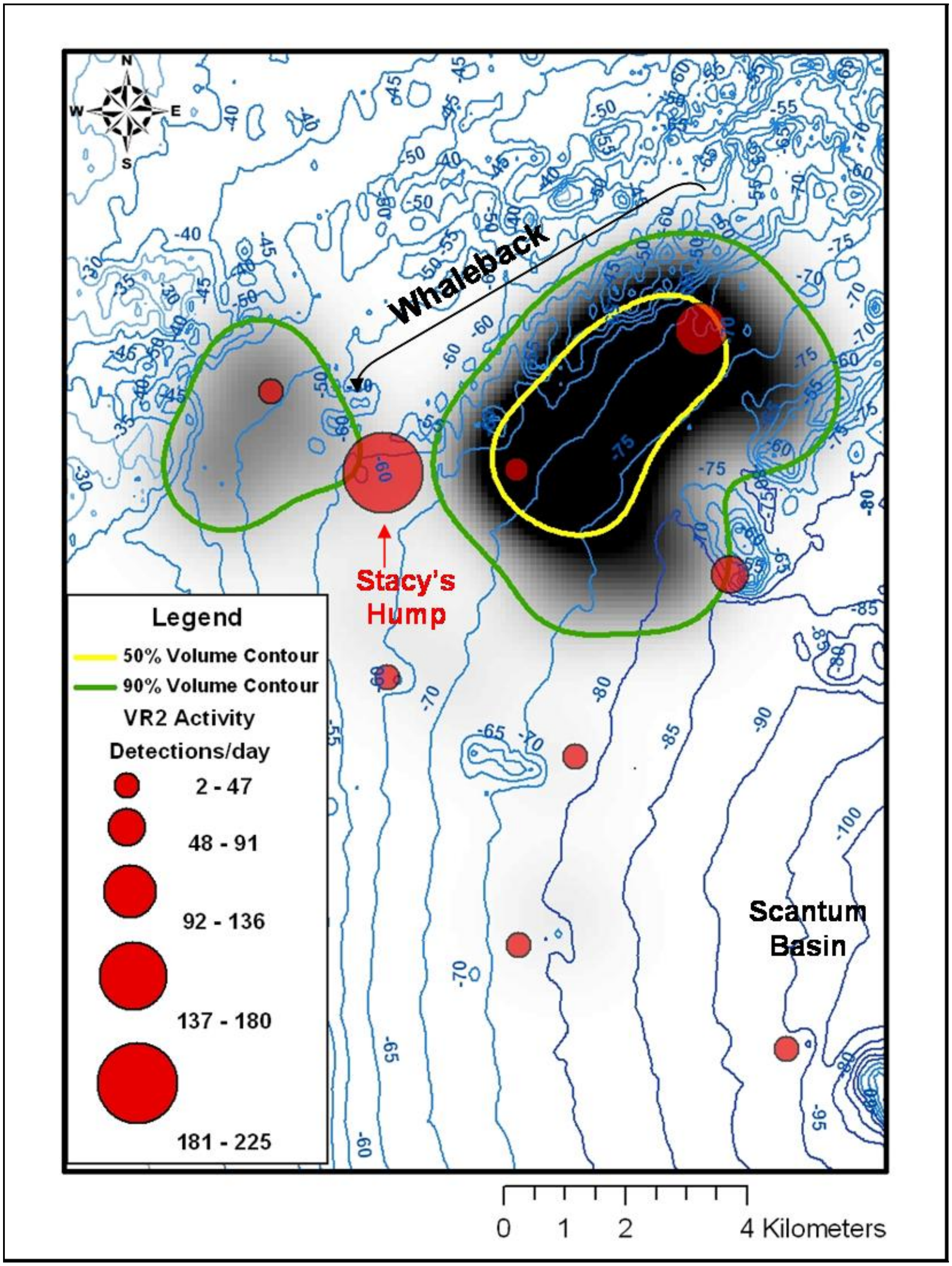

Fig. 20. Kernel Distribution Estimation (KDE) derived from pooled manual tracking data for all fish. Dark areas indicate where probable activity for the group was most concentrated, based on manual tracking. Green and yellow contours contain 90% and 50% of activity, respectively. Relative VR2 activity is illustrated by graduated circles. Tracking effort using a directional hydrophone suggested fish were not directly over Whaleback but on its gradual slopes and the muddy bottom representing the mean number of tag detections (pings) per day at each site. Depth contours are labeled in meters.

A kernel distribution estimation (KDE) was also calculated from pooled manual tracking data to visualize the probable activity area for the group (Fig. 20). Cod aggregated around a large bathymetric feature known as “Whaleback,” a series of rocky humps running southwest to northeast that framed the northern border of the spawning ground. The shallowest part of this ridge was 40 m deep; about 30 m shallower than the muddy flats south of it. Cod activity was clustered alongside its southern edge and inshore adjacent to it. Fifty percent of the group’s activity was estimated to be within a ~ 6 km^2 area alongside the eastern half of Whaleback, and 95% of all activity was in a ~35km^2 area alongside the length of Whaleback and the inshore slope west of it (Fig. 20).

VR2 activity is displayed with the group kernel distribution to illustrate the relative number of detections/day at each VR2 site (Fig. 20). Most activity occurred on the east and west ends of Whaleback, particularly at VR2 #2, a small hump called “Stacy’s” on the west end rising ~ 4 m above the bottom. The majority of cod (n=19, 74%) moved to this hump at some point regardless of release site, and most were detected there over several days. There were two separate weeks during the two-month study when the majority of cod converged on this aggregation ‘hot-spot.’ VR2 #2 received on average more than twice as many detections per day as any other VR2 (Table 9). There was a ~3.5 km distance between this ‘hot-spot’ and the centers of activity estimated from manual tracking (Fig. 20) that we attribute to timing inconsistencies. Activity peaked at VR2 #2 on days when manual tracking did not occur due to adverse weather or scheduling. Manual tracking, however, found high activity on Whaleback to both the west and east of VR2 #2 in May, but VR2s were not deployed to those areas there until June.

An individual KDE was also calculated for each fish that was manually relocated on at least seven separate days, to approximate home range during its Ipswich Bay residence (n=14 fish). From these we extracted volume contours that enclosed 90% of each cod’s probable activity (Fig. 21). Volume contours overlapped in an area stretching 10 km from east to west, and individuals were primarily active in areas < 8 km^2 in size. Individual analyses further show cod predominantly along the southern margin and west end of Whaleback. Activity was distributed along a rough V-shaped “corridor” bounded by elevated bottom features: Whaleback along the north, several distinct humps to the south, and rising slopes and inshore boulder formations to the west (Fig. 21).

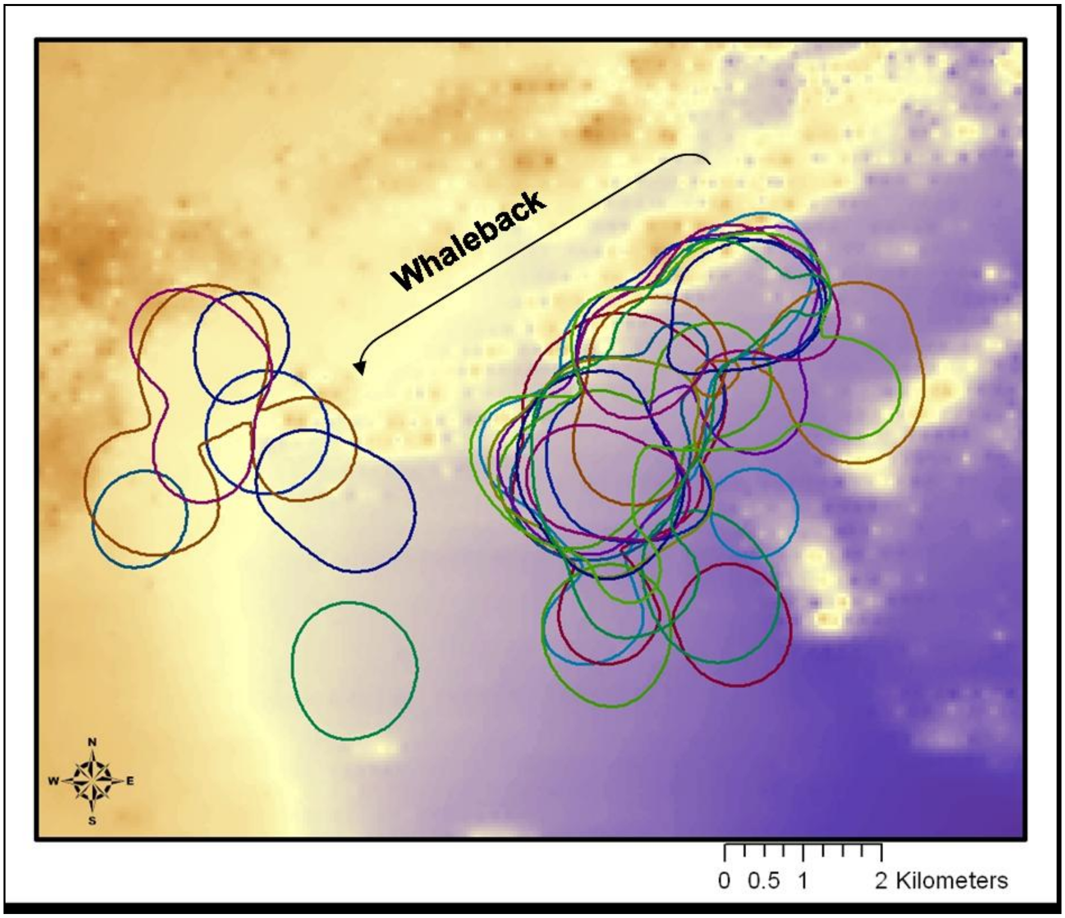

Fig. 21. Map of northern half of the study area displaying 90% volume contours from the individual kernel distribution estimations (KDEs) of 14 cod. Individual activity was distributed alongside of Whaleback, additional prominent humps, and the inshore slope and elevated bathymetry to the west.

B2. Movement trends on the spawning ground

Although individual tracks were unique, the majority of cod assembled at the same fine-scale locations around specific dates, creating a general circuit of movement across the spawning ground. Although cod gradually left the area throughout the study, most followed several segments of this circuit before leaving.

The majority of the cod were tagged May 6 near VR2 #7 (Fig. 22A), and many (49%) clustered around this area for the first few days after release. Heavy storms throughout the Gulf of Maine prevented manual tracking from May 9 – 16. During this weather event, VR2s tracked 68% of the cod moving south across the study site into deeper water, past southern VR2s (#6, 8, & 9) up to 6 km south of their release. Just as quickly they reversed direction and moved north, and most (74%) arrived at the west end of Whaleback (VR2 #2) between May 12 and May 15 as storms subsided (Fig. 22A). From this point on, the spawning ground circuit was characterized by group shifts between the east and west ends of Whaleback from May 17 – June 15 (Fig. 22B-D) until most cod departed. The three cod remaining after June 15 (one male and two females) each settled around a different bathymetric feature and displayed little activity thereafter.

In addition to the gradual shifts along the side of Whaleback, we observed finer-scale patterns oriented around bathymetric features. During late May – early June, seven cod (a third of those present) adopted temporary shuttling patterns between different pairs of elevated features on the west end. These rapid back-and-forth patterns lasted only a few days at a time, and occurred between humps and slopes < 3 km apart (Fig. 22B).

There was no evidence of a difference between nocturnal and diurnal location. Most of the manual tracking at night was in mid-June when cod were leaving the area, and yielded little data. Detections from VR2 receivers were split relatively evenly between day and night (55% at night), suggesting that cod's proximity to humps did not vary with time of day.

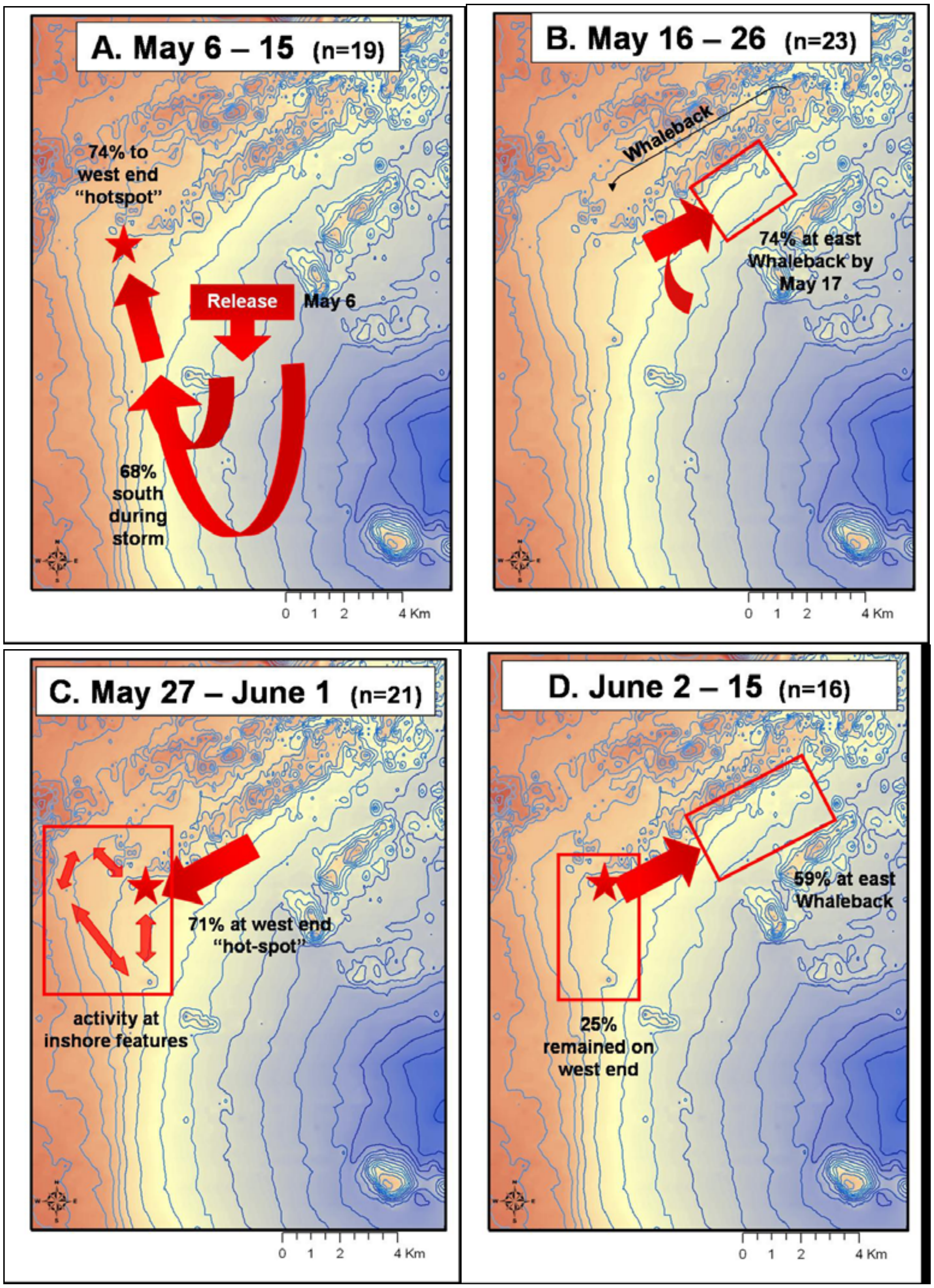

Fig. 22. Circuit of movement across the spawning ground. Percentages are of total cod present during given time period. a) After release, the majority moved south then north during storms, and appeared at the west end of Whaleback by mid-May. b) Most shifted to the east side of Whaleback by May 17th for several days, and five more cod were tagged there. c) Majority moved to west end in late May. Shuttling movements observed between features around west end. d) Majority returned to east end until departure. Only three cod remained after June 15th.

B3. Exit tracks

Departure pathways from the spawning ground are unknown for most of the tagged cod, however the most common movement immediately before departure was an appearance at the east end of Whaleback (42% of cod), often lasting several days before the fish left. Seven cod (29%), however, were tracked making rapid movements across the spawning ground before leaving (T59, T60, T68, T70, T71, T75, & T76). These cod passed by multiple VR2s in < 24 h before disappearing, providing an indication of their initial headings out of the spawning ground to the south and east (Fig. 23). Two fish passed the VR2 that had been lost and dragged south while it was missing. Because it was eventually found with all moorings attached, it was likely moved in one swift event by a passing boat. For this reason, we believe it detected these cod at the location where it was found in late June, > 15 km south of Whaleback (Fig. 23).

B4. Combining tracking and DST data for individuals

Three acoustically tracked cod were recaptured after leaving Ipswich Bay (T61, T73, & T76), and their DSTs (207, 228, & 241) were downloaded. For these we compared data from both tags, which gave both vertical and horizontal positions at certain times on the spawning ground, and provided a more comprehensive understanding of their spawning activity.

The first of these cod (T76/DST 241) remained in the post-tagging recovery phase for the two weeks it spent in Ipswich Bay. This cod made east-west movements between different humps while displaying a vertical equilibration pattern. However, it was only detected by VR2s at these elevated features during its cyclic nocturnal ascents, peaking at 20 – 50 m in depth (Fig. 24). During the day it was manually relocated at depths of 65 – 90 m, on the flat bottom > 1 km from these sites.

Two cod (T61/DST 207 and T73/DST 228) were tracked shifting back and forth between the west and east ends of Whaleback. They were constantly active within a 55 – 70 m depth range, and occasionally rose several meters shallower near the west end. This combined data suggests the cod were close to the bottom and slope of Whaleback on the east end but may have either ascended small humps on the west end, or been active above the bottom while farther inshore.

Data from all three cod show concurrence between last detections and deep-water shifts. Each cod began moving into deeper water <24 h after their last detection, and dropped below 100 m about 48 h after last detection (Fig. 25). For the last cod (T73/DST 228), a comparison of both tags suggested back and forth movement between the spawning ground and Scantum Basin. This cod passed a VR2 on the edge of Scantum Basin just before its first deep-water descent, but moved back to shallower water and reappeared at the same VR2 five days later. Soon after this detection it descended once more to deeper waters and remained there.

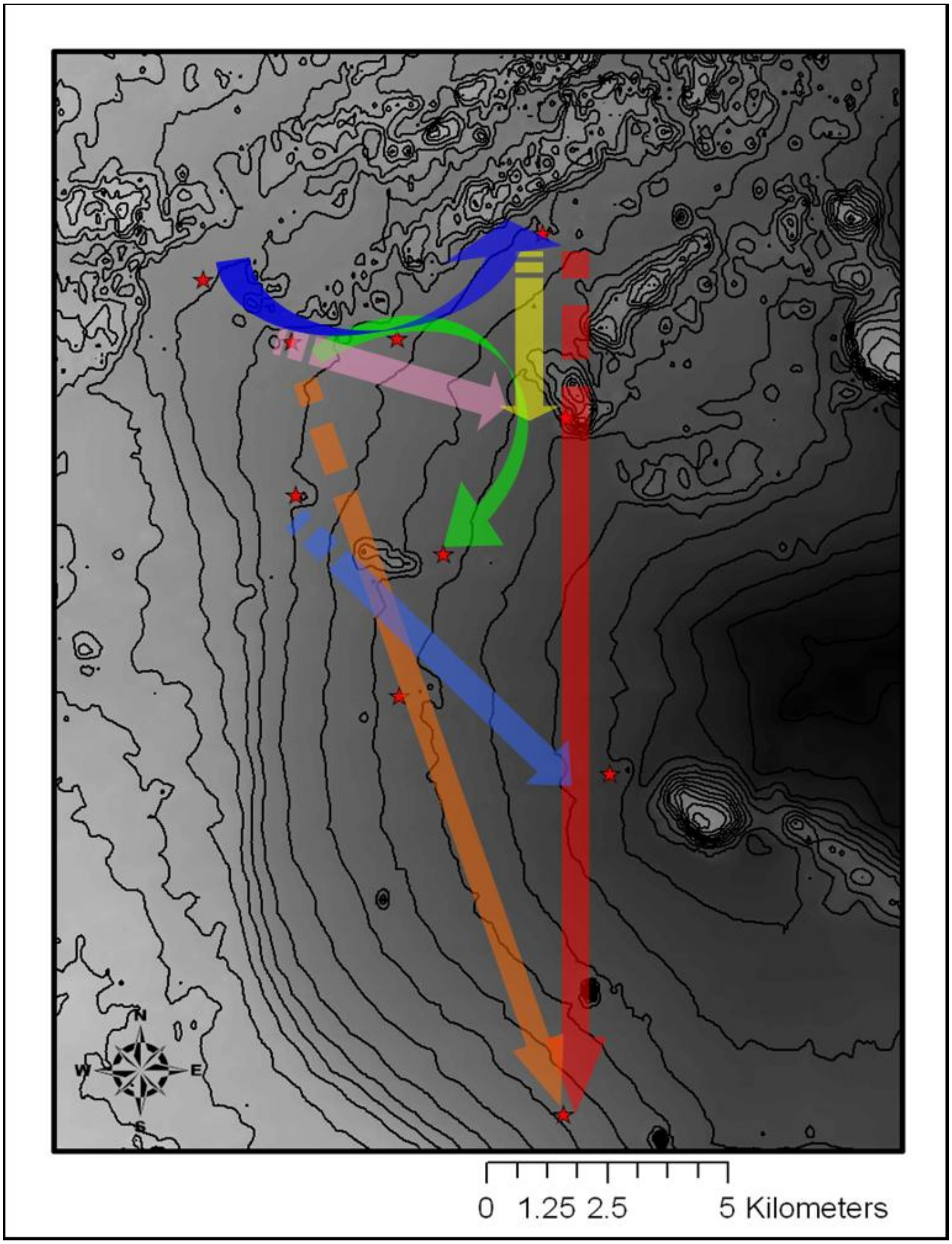

Fig. 23. Exit tracks for seven cod tracked moving past multiple VR2 receivers in < 24 h before disappearing from the spawning ground. Receiver locations are indicated by red stars. Southernmost location indicates VR2 that was dragged south and detected fish while it was missing.

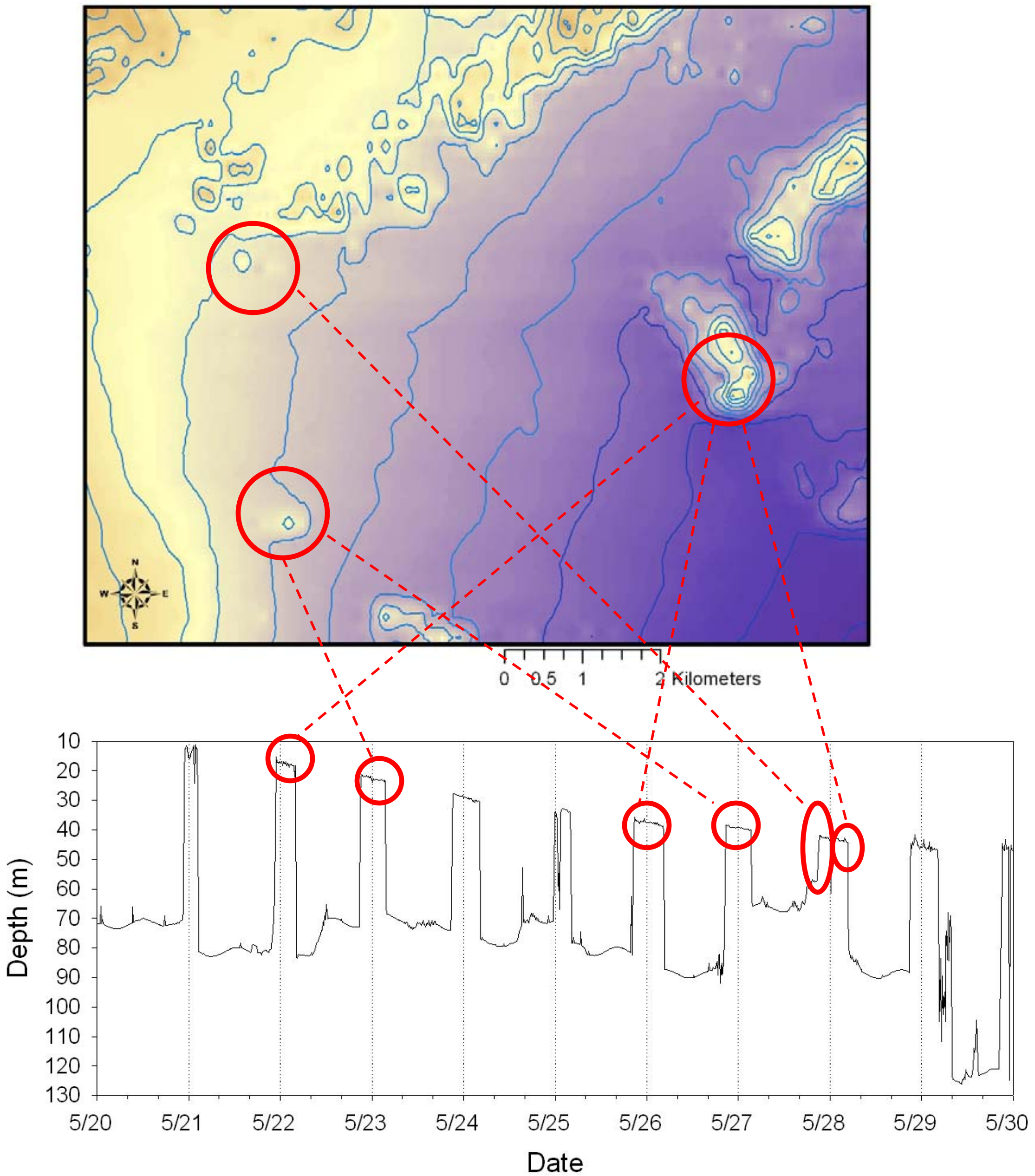

Fig. 24. Comparison of DST depth profile and tracking positions from same fish (DST 241 & transmitter T76). During its recovery phase, this cod exhibited an equilibration pattern and made dramatic ascents each night. It was detected by VR2s stationed at various humps only during these nocturnal ascents. By day it was out of VR2 range, but manually relocated on the flat bottom < 2 km from these features.

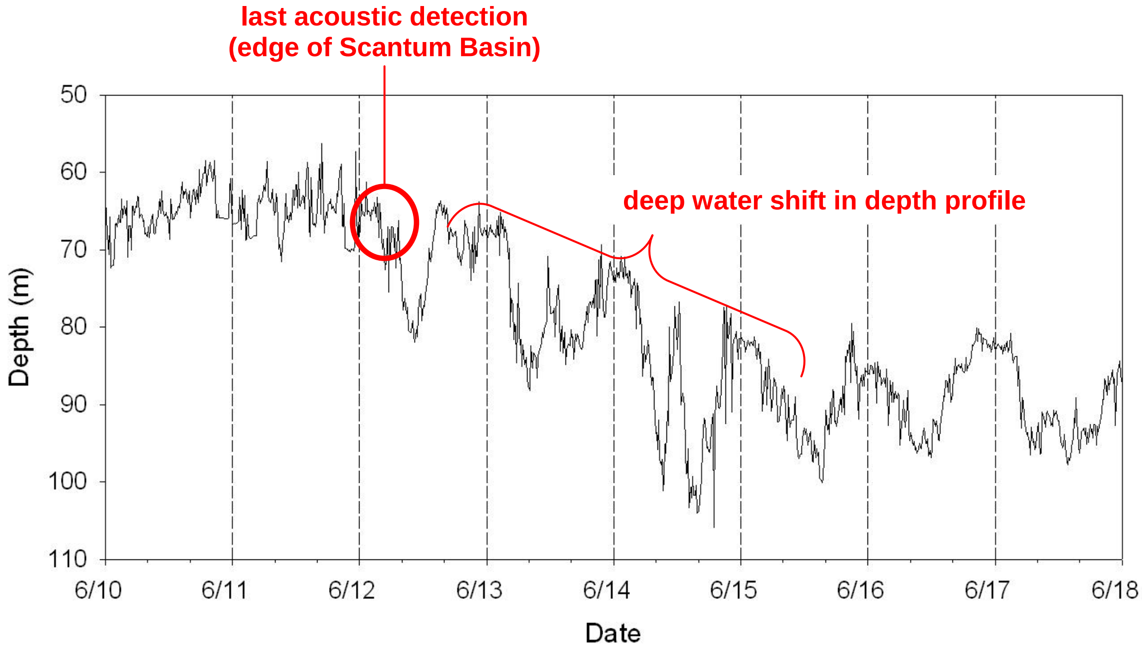

Fig. 25. Depth profile of DST 207 (transmitter T61) indicating the timing of it last acoustic detection and its shift to deep water outside of Ipswich Bay.

Partnerships:

The scientists and fishermen involved in the project worked well together. The partnerships began when all parties originally designed the project, continued through the field work, and still exists today. It is fair to say the scientists and fishermen were both keenly interested in the research, that we learned a lot from one another, and that we developed mutual respect and friendship. For the most part the fishermen involved with this project were ones we had worked with in the past, and we have continued to work with them on new projects.

Impacts and applications:

This was the first ever study of the fine scale temporal and spatial distribution of cod in the western Atlantic. Although the study was limited to only a few months, the timing encompassed the weeks prior to, during, and immediately after the spawning season. During this time the fish are aggregated, and thus most vulnerable to capture. Moreover, it is likely there are important reproductive behaviors occurring in these aggregations, and fishing activity could disrupt these. Thus while we acknowledge the study has its limitations, we are confident that we chose a critical period to explore. We are also confident that we chose an important location. Although we cannot know how representative of other locations the Ipswich Bay spring spawning cod may be, this group is probably the largest spawning group left in the western Atlantic, so it was an important group to study.

The study revealed several aspects of cod biology that have significant implications to management. These include:

a) Confirmation of spawning site fidelity, which suggests that spring spawning Ipswich Bay cod should be treated as a discrete management unit. The discreteness of this group of fish has also been shown through genetic analysis (Tim Breton, UNH MS thesis).

b) Confirmation of residency (limited seasonal horizontal displacement) and spawning duration (timing of arrival and departure), and new information about the size of home range. All of these population attributes have implications for the size and timing of the established rolling closures.

c) New, fine scale information about cod spawning habitat. We found that Ipswich Bay cod spawned in areas adjacent to structures with some vertical relief, in mean depths between 55 and 80 m, and mean temperatures ranging from 6 to 7^{o}C.

d) Confirmation that trawl caught fish experience barotraumas upon release, characterized by uneven and sporadic vertical movements, including dramatic ascents and intervals both at the surface and on the seafloor. In general, it took 4-18 days for behavior to return to normal, i.e. occupying a more consistent depth. This data may be useful to those interested in the behavior of discarded cod, and discard mortality.

e) Characterization of the vertical movements of cod in Ipswich Bay. This is important because the patterns of vertical movements differ from area to area, and change seasonally (Righton et al. 2001). Obviously vertical movements influence cod catchability in bottom trawls, and therefore the outcome of stock assessments based on trawl surveys.

The study also revealed several aspects of cod biology that should be of interest to harvesters. These include an appreciation for the relatively small size of spawning areas, vertical movement patterns that may influence the catch during different parts of the day, the vulnerability of dense, spawning aggregations, and the importance of protecting these areas during the spawning season. The study also reinforced the concern of commercial fishers that the charter boat fleet, which is allowed to exploit these dense aggregations, may be slowing cod recovery.

Related projects:

This study arose from two cod tagging projects funded by the Northeast Consortium (NEC). The first sought to explore the temporal and spatial distribution of cod relative to the timing of rolling closures in the western Gulf of Maine. The second focused on the western Gulf of Maine Area Closure. Results of these projects were reported in Howell et al. (2008). A third related project, started with NEC development funds and subsequently the UNH Sea Grant program, seeks to develop multi-beam sonar as a fisheries tool for stock assessment and the identification of essential habitat of Atlantic cod. The field work for this project has been completed, and the data is currently being analyzed and written up as a doctoral dissertation by Chris Gurshin, a UNH graduate student.

The original tagging project also served as the stimulus for two genetic studies. Results from one of these were reported in Wirgin et al. (2007). The second formed the basis of a Masters thesis at UNH (Breton 2008).

The research reported here also stimulated a current study, designed to investigate the spawning movements and habitat use of winter flounder in the southern Gulf of Maine. It is also funded by the NEC (E. Fairchild, PI), and uses many of the same methods and commercial partners as the cod project.

Finally, a multi-investigator proposal has been submitted to the National Science Foundation. It seeks to identify the ecological mechanisms that have led to the fine scale population genetic structure of cod in the Gulf of Maine, and to determine the implications of this fine scale structure. This proposal, which would fund 4 years of research, is currently being reviewed.

Presentations:

Siceloff, L. and W.H. Howell. 2009. Vertical activity and fine scale distribution of cod on Ipswich Bay spawning ground. Workshop to identify future research priorities for cod tagging in the Gulf of Maine. Gulf of Maine Research Institute, Portland, ME. February 12, 2009.

Siceloff, L. 2009. Fine-scale activity, distribution and habitat utilization of Atlantic cod (*Gadus morhua*) on the Ipswich Bay spawning ground. UNH, Dept. of Biological Sciences seminar series. Durham, NH. May 1, 2009.

Published reports and papers:

Howell, W.H., D. Goethel. C. Bouchard, C. Felch, M. Stettner and P. He. 2008. Northeast Consotium Project Annual Progress Report 2008: Activity and distribution of cod in the Ipswich Bat spawning area (Contract number 111A22), 5p.

Siceloff, L. and W.H. Howell. 2009. Vertical activity and fine scale distribution of cod on Ipswich Bay spawning ground. *In* Tallack, S. (ed.). Proceedings from a workshop to identify future research priorities for cod tagging in the Gulf of Maine, 12 February, 2009. Northeast Fisheries Science Center. Reference Document 09-09, 76 pages.

Siceloff, L. 2009. Fine-scale activity, distribution, and habitat utilization of Atlantic cod (*Gadus morhua*) on the Ipswich Bay spawning ground. M.S. Thesis, Dept. of Zoology, Univ. of New Hampshire.

Siceloff, L. and W.H. Howell (In Prep.) Vertical and horizontal movement of spawning cod in Ipswich Bay as revealed by data storage tags.

Siceloff, L. and W.H. Howell (In Prep.) The use of acoustic telemetry to determine home range size and fine scale movements of spawning cod in Ipswich Bay.

Conclusions:

Both DSTs and acoustic tracking proved to be useful tools to determine the distribution and movements of spawning cod in Ipswich Bay, and the timing of their post-spawning movements out of Ipswich Bay. Acoustic tracking showed spawning cod were primarily distributed in an area of Ipswich Bay approximately 60 km^2 in size during May and June, with some limited movement to Scantum Basin and deeper waters. Individuals spent the majority of their residence in areas < 8 km^2, and aggregated around elevated bathymetric features during the spawning period. Both acoustic tracking and DST data demonstrated that most cod dispersed from the spawning ground during May and June. This study's findings support the current timing of rolling closures in Area 132 & 133 (Fig. 1) that appears to effectively protect the bulk of spawning cod from commercial fishing. Future tagging and long-term tracking could determine whether there may be later arrivals to the spawning ground not represented in this study, as well as the degree of inter-annual variability in arrival and departure times.

Most cod initially moved into water >90 m when they left Ipswich Bay, and traveled to diverse locations and depths. Post-spawning cod dispersed to the north, south, and east but appeared to remain within the western Gulf of Maine during the summer and fall. More data are needed to learn where these spring spawners overwinter, but there is substantial evidence that many predictably return to Ipswich Bay to spawn each year (Howell et al. 2008). The degree of movement between Ipswich Bay and the Western Gulf of Maine Closed Area to the east is still unclear, and warrants further research to understand the significance of this area to Ipswich Bay spawning components.

Cod displayed a wide spectrum of site-specific vertical activity patterns ranging from continuous vertical migration to motionless periods on the seafloor. These patterns are likely influenced by spawning and aggregation behavior, depth, bathymetry, environmental conditions, and prey availability. Most cod adopted forms of diel vertical migration after the spawning period that may reflect foraging strategies. These diverse activity patterns may impact their vulnerability to commercial fishing gear, and the accuracy of groundfish survey data at different locations and times of year.

This study found that spawning cod predictably aggregated alongside vertical relief and around specific sites. These elevated features, and the stretches of muddy bottom surrounding them, represent clear examples of Essential Fish Habitat for cod. Similar features that attract spawning cod warrant identification, documentation, and conservation throughout the Gulf of Maine as mandated by the Sustainable Fisheries Act. Identification of such fine-scale critical habitat features may allow a refinement of current management strategies, and could lead to both the creation of new protected areas and a surgical adjustment or reduction of existing closures.

This study has identified approximate spawning times, fine-scale spawning locations, bathymetric features of importance, and the vertical distribution and occupied temperature of spawning cod. These data sets can be applied to significantly improve the detail and accuracy of future larval transport and population connectivity modeling.

In conclusion, the results of this study represent significant progress in the identification and description of EFH for Atlantic cod in the western Gulf of Maine. These data characterize spawning activity, and document the variation in cod behavioral patterns according to location and season, as well as the diversity of behavior and migration pathways among cod from the same spawning component. Finally, this study details cod's utilization of a spawning ground, and provides a foundation for unraveling the significance of specific locations to cod spawning activity and population structure.

Future research:

Many questions about cod spawning behavior could not be answered with data storage tags or acoustic telemetry, including the timing and location of individual spawning events, spatial dynamics between males and females, and the nature of mating rituals among aggregations in their natural habitat. However, using the locations and times identified in this study, future research involving acoustic surveys and video could address many of these issues. Like other locations that attract migratory spawning aggregations, there are a number of possible reasons for the importance of Ipswich Bay (and specific features within it) to multiple cod spawning components. Continued exploration of environmental features of this area and the dispersal and retention of eggs and larvae may help improve our understanding.

Literature Cited:

Ames, E. P. (2004). Atlantic cod stock structure in the Gulf of Maine. Fisheries 29(2): 10-28.

Breton, T. (2008). Spawning stock identification of Atlantic cod (*Gadus morhua*) using microsatellite loci. MS Thesis, UNH Dept. of Zoology. Durham, N.H.

Byer, H. L. (2004). Hawth's Analysis Tools for ArcGIS. www.spatialecology.com

Colton, J. B., W. G. Smith, A. W. Kendall, P. L. Berrien, and M. P. Fahay. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fishery Bulletin 76(4): 911-915.

Cote, D., S. Moulton, P. Frampton, D. Scruton and R. McKinley. (2004). Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology 64(3): 665-679.

Espeland, S. H., A. F. Gundersen, E.M. Olsen, H. Knutsen, J. Gjoesaeter and N.C. Stenseth. (2007). Home range and elevated egg densities within an inshore spawning ground of coastal cod. ICES Journal of Marine Science 64(5): 920-928.

Godo, O. R. and K. Michalsen. (2000). Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. Fisheries Research 48(2): 127-140.

Green, J. M. and J. S. Wroblewski. (2000). Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. Journal of the Marine Biological Association of the United Kingdom 80(6): 1077-1085.

Heffernan, O., D. Righton and K. Michalsen. (2004). Use of data storage tags to quantify vertical movements of cod: effects on acoustic measures. ICES Journal of Marine Science 61(7): 1062-1070.

Howell, W. H., M. Morin, N. Rennels and D. Goethel. (2008). Residency of adult Atlantic cod (*Gadus morhua*) in the western Gulf of Maine. Fisheries Research 91(2-3): 123-132.

Ihaka, R. and R. Gentleman. (2008). R: A Language and Environment for Statistical Computing. Vienna, Austria, R Foundation for Statistical Computing. www.r-project.org

Kjesbu, O. S. (1994). Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. Journal of Fish Biology 45(5): 719-735.

LaVigne, H. R. (2002). An improved portable surgical table for the field and laboratory. North American Journal of Fisheries Management 22(2): 571-572.

Lindholm, J., P. J. Auster and A. Knight. (2007). Site fidelity and movement of adult Atlantic cod, *Gadus morhua,* at deep boulder reefs in the western Gulf of Maine, USA. Marine Ecology-Progress Series 342: 239-247.

Loekkeborg, S. (1998). Feeding behaviour of cod, Gadus morhua: Activity rhythm and chemically mediated food search. Animal Behaviour 56(2): 371-378.

Mayo, R. K. and L. A. Col (2006). The 2005 assessment of the Gulf of Maine Atlantic cod stock, Northeast Fisheries Science Center, Reference Document 06-02.

Meyer, C. G. and R. R. Honebrink. (2005). Transintestinal expulsion of surgically implanted dummy transmitters by bluefin trevally: Implications for long-term movement studies. Transactions of the American Fisheries Society 134(3): 602-606.

Mulcahy, D. M. (2003). Surgical implantation of transmitters into fish. J. Inst. Laboratory Animal Research 44(4): 295-306.

Neat, C.F., Wright, P.J., Zuur, A.F., Gibb, I.M., Tulett, D., Righton, D.A., Turner, R.J., 2006. Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). Mar. Biol. 148, 643-654.

Nichol, D. G. and E. A. Chilton (2006). Recuperation and behaviour of Pacific cod after barotrauma. ICES Journal of Marine Science 63(1): 83-94.

Palsson, O. K. and V. Thorsteinsson (2003). Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): Evidence from storage tag data. Canadian Journal of Fisheries and Aquatic Sciences 60(11): 1409-1423.

Pierce, D. E., and P. E. Hughes. 1979. Insight into the methodology and logic behind National Marine Fisheries Service fish stock assessments, or how did you guys come up with those numbers, anyway? Publication of the Commonwealth of Massachusetts, 17pp.

Robichaud, D. and G. A. Rose. (2001). Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Sciences 58(12): 2325-2329.

Robichaud, D. and G. A. Rose. (2003). Sex differences in cod residency on a spawning ground. Fisheries Research 60(1): 33-43.

Righton, D., J. Metcalfe and P. Connolly. 2001. Different behaviour of North and Irish Sea cod. Nature 411: 156.

Righton, D. and J. Metcalfe. (2002). Multi-torsking: simultaneous measurements of cod behaviour show differences between North Sea and Irish Sea stocks. Hydrobiologia 483(1-3): 193-200.

Righton, D., O. S. Kjesbu and J. Metcalfe. (2006). A field and experimental evaluation of the effect of data storage tags on the growth of cod. Journal of Fish Biology 68(2): 385-400.

Sakaris, P. C. and R. V. Jesien (2005). Retention of surgically implanted ultrasonic transmitters in the brown bullhead catfish. North American Journal of Fisheries Management 25(3): 822-826.

Summerfelt, R. C. and L. S. Smith (1990). Anesthesia, surgery, and related techniques. In: C. B. Schreck and P. B. Moyle (eds.) Methods for Fishery Biology. Bethesda, MD, American Fisheries Society. pp. 213-272.

Stensholt, B. K. (2001). Cod migration patterns in relation to temperature: analysis of storage tag data. ICES Journal of Marine Science 58(4): 770-793.

Svedang, H., D. Righton and P. Jonsson (2007). Migratory behaviour of Atlantic cod *Gadus morhua*: natal homing is the prime stock-separating mechanism. Marine Ecology Progress Series 345:

Thorsteinsson, V. and G. I. Eggertson (1998). Vertical migration patterns of Atlantic cod (*Gadus morhua*) in Icelandic waters, results from electronic data storage tags (DSTs). Meeting of the Int. Council for the Exploration of the Sea, Cascais (Portugal), ICES, Copenhagen (Denmark).

Turner, K., D. Righton, et al. (2002). The dispersal patterns and behaviour of North Sea cod (*Gadus morhua*) studied using electronic data storage tags. Hydrobiologia 483(1-3): 201-208.

van der Kooij, J., D. Righton, E. Strand, K. Michalsen, V. Thorsteinsson, H. Svedaeng, F. Neat and S. Neuenfeldt. (2007). Life under pressure: insights from electronic data-storage tags into cod swimbladder function. ICES Journal of Marine Science 64(7): 1293-1301.

Wagner, G. N. and S. J. Cooke (2005). Methodological approaches and opinions of researchers involved in the surgical implantation of telemetry transmitters in fish. Journal of Aquatic Animal Health 17(2): 160-169.

Winter, J.D. 1983. Underwater biotelemetry. In: L.A. Nielsen and D.L. Johnson (eds,), Fisheries Techniques. pp.555-590.