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FINE-SCALE ACTIVITY, DISTRIBUTION, AND HABITAT UTILIZATION OF ATLANTIC COD (*Gadus morhua*) ON THE IPSWICH BAY SPAWNING GROUND

BY

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B.A., Oberlin College, 2001

THESIS

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DEDICATION

I dedicate this thesis to my parents, for fostering my obsession with all the strange and misunderstood creatures of the past, present, land and sea.

I also dedicate this to anyone who has ever been patient with me.

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ABSTRACT

FINE-SCALE ACTIVITY, DISTRIBUTION, AND HABITAT UTILIZATION OF ATLANTIC COD (*Gadus morhua*) ON THE IPSWICH BAY SPAWNING GROUND

by

Laughlin Siceloff

University of New Hampshire, May, 2009

Advisor: W. Huntting Howell

Data storage tags (DSTs) and acoustic telemetry were applied to examine cod spawning habitat utilization in Ipswich Bay and compare seasonal activity patterns. I tagged 200 spawning cod in Ipswich Bay during April – May 2006 with DSTs recording depth and temperature. Twenty-six cod were also implanted with acoustic transmitters and relocated manually and with stationary listening stations during May and June. Twenty-five DSTs were returned, showing that most cod departed the spawning ground during May and June and dispersed throughout the western Gulf of Maine. Cod shared a low vertical activity pattern in Ipswich Bay, but adopted various site-specific vertical behaviors after leaving. Spawning activity was concentrated in a ~35 km^2 area where cod aggregated alongside particular bathymetric features. These fine-scale movement and spawning data have implications for area closures, defining Essential Fish Habitat, and identifying cod population structure in the Gulf of Maine.

CHAPTER I

INTRODUCTION

Rationale for study

The goals of this study were to describe the seasonal migration of Atlantic cod in and out of Ipswich Bay, and examine their spawning behavior and spatial distribution during their residence there. Both migratory and spawning behaviors of Atlantic cod have been studied in other regions across the north Atlantic, but not in Ipswich Bay. Understanding these aspects of cod ecology is critical to distinguish separate stocks, define population structure (Svedang et al. 2007), and protect essential habitat (Lough 2004).

The Atlantic cod (*Gadus morhua*) historically represents one of the most valuable marine resources of the entire northern Atlantic. Despite well-documented exploitation and depletion since the 1960s, cod support significant commercial and recreational fisheries in the Gulf of Maine. Cod continue to have economic value to New England, and play a prominent role in local marine ecosystems, prompting extensive studies of their life history throughout their range, and concerted effort to improve their management and conservation.

Atlantic cod in US waters are currently managed as two separate stocks, belonging to the Gulf of Maine and Georges Bank (Mayo et al. 2006). Multiple strategies have been implemented to regulate and restore U.S. cod populations in recent years, yet both stocks are still overfished. Cod show not only a decline in abundance, but significant decreases in size at maturity over the past three decades in the Gulf of Maine (O'Brien 1998; Barot et al. 2004). Cod management dilemmas reflect widespread concerns over many species' depletion in recent years. One emerging avenue for population restoration is the identification and protection of Essential Fish Habitat (EFH). Recognizing the "the long term viability of living marine resources depends on protection of their habitat" (National Marine Fisheries Service Strategic Plan for Fishery Research), Congress defined the concept of EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity." Consequently, the Sustainable Fisheries Act of 1996 required regional fishery management councils to describe and identify EFH in their regions, and take actions to conserve and enhance EFH, particularly by minimizing damaging effects of fishing (Lough 2004).

Despite these mandates, there is little data to characterize cod activity at Gulf of Maine spawning grounds. Cod distribution in the northeastern U.S. is well-documented, and the locations of spawning sites have been established (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. 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 et al. 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 in adult cod within US waters. Furthermore, it is unknown how spawning and migratory behavior 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 in spawning grounds, and the sequence of events that comprise reproduction.

Fishery managers have divided the western Gulf of Maine into a grid of management areas along latitude/longitude coordinates, with each area comprising a 30 x 30-minute square (48 km x 48 km). The commercial cod fishery in the western Gulf of Maine is currently managed with rolling time/area closures of these management areas (New England Fishery Management Council 1998). In an effort to protect seasonal aggregations, each area is closed to commercial fishing during certain months of the year when cod biomass is believed to be highest. Ipswich Bay, the study site of my research, is located within Area 133, which also encompasses Cape Ann and the northern Massachusetts coast (Fig.1a).

The foundation for my 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 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 indicate two temporal peaks in biomass within Area 133, and associated seasonal movements. Adult, pre-spawning cod assemble offshore of Area 133 in April, to the east on Scantum Basin and Jeffreys Ledge (Area 132). They move inshore into Ipswich Bay in Area 133 during April and May to spawn. Cod appear to gradually disperse from Ipswich Bay and move offshore throughout June and July. A similar pattern occurs again in the winter, when fish assemble and move inshore from October through December, and disperse from Area 133 in February after spawning (Howell et al. 2008).

Most recaptures came from the same management areas where the cod were tagged. In Area 133, cod dispersed in all directions after spawning periods, but most movement was directly offshore to the east. Depending on the month they were released, the cod tagged in Area 133 traveled mean distances ranging from 17 – 63 km between release and recapture (Howell et al. 2008). Furthermore, recapture data indicate that although many cod in Ipswich Bay disperse offshore after both the winter and spring spawning seasons, they exhibit high site fidelity and return to the same spawning grounds each year, as reported in other coastal populations (Lawson et al. 2000b; Wright et al. 2006a; Howell et al. 2008).

Although recent tagging work has begun to indicate general movement patterns around Ipswich Bay, several fundamental questions remain. Additional movement data are needed to better understand where these aggregations arrive from, and migrate to after leaving. 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.

Although the winter spawning component in Ipswich Bay was historically large and vital to the commercial fishing community (Ames 2004), it has dwindled in recent years and is no longer a productive winter fishing ground (D. Goethel & C. Bouchard, pers. comm.). Abundance, density, spawning activity and mean fish length are greater during the spring spawning season (Howell et al. 2008). Particle transport models predict the spring component also has greater larval transport success to both Ipswich and Massachusetts Bay nursery grounds than the winter component (J. Runge, unpublished data). The rolling closure for Area 133 currently restricts commercial fishing activity from April through June to protect spring spawning activity, but the area is open throughout the winter. Due to the spring component's greater apparent significance to the Gulf of Maine stock, high density, site fidelity and reproductive isolation, as well as reduced fishing interference of fieldwork in the spring, I chose this component for my study.

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 et al. 1998; Godo et al. 2000; Green et al. 2000; Robichaud et al. 2001; Stensholt 2001;

Righton et al. 2002; Palsson et al. 2003; Robichaud et al. 2003; Cote et al. 2004; Espeland et al. 2007; Lindholm et al. 2007; Svedang et al. 2007). To my knowledge, however, no studies have integrated both data storage tags and acoustic tags to study the activity and distribution of cod relative to their habitat. The use of both electronic tag types enabled me to construct profiles of ambient temperature, vertical movement in the water column, and horizontal movement across the spawning area for individual cod, and ultimately address the following hypotheses:

Scientific 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, I 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.

Background

The goals of this study are to describe the seasonal migration of Atlantic cod into and out of Ipswich Bay, and examine their spawning behavior and spatial distribution during their residence there. Both migratory and spawning behaviors have been studied in other regions across the north Atlantic. Understanding these aspects of cod ecology is critical to distinguish separate stocks, define population structure (Svedang et al. 2007), and protect essential habitat (Lough 2004). In this section I will briefly review key aspects of cod behavior relevant to my research: 1) migration and homing behavior, 2) vertical distribution and movement, 3) spawning behavior, and 4) habitat utilization and preference.

1. Migration and homing behavior

Most cod populations undergo some type of seasonal migration on varying spatial scales, which are usually characterized as movements between spawning and feeding grounds (Wright et al. 2006b). Robichaud and Rose (2004) reviewed past cod movement studies and attempted to assign all discrete cod groups in the north Atlantic to one of four migratory behaviors: 1) sedentary or resident cod, that exhibit year-round site fidelity and only small-scale migrations; 2) dispersers, which utilize vast home ranges with no clear fidelity, pattern or direction to their movement; 3) accurate homers, which undertake long-distance seasonal movements (hundreds of kilometers) but return to the same locations each year; and 4) inaccurate homers that make seasonal migrations but do not consistently return to the same site. The majority of known cod population units are resident, yet populations in the three more mobile categories are larger in biomass (Robichaud et al. 2004).

Regardless of the extent of their movements, many cod populations either exhibit year-round site fidelity, or leave but make return migrations to the same general spawning area each year (Thorsteinsson et al. 1998; Green et al. 2000; Lawson et al. 2000b; Robichaud et al. 2001; Wright et al. 2006a). Some degree of larval retention on a spawning ground is a common phenomenon that promotes successful recruitment (Espeland et al. 2007; Huret et al. 2007), but cod larvae may also be transported considerable distances before recruitment, and may grow to maturity far from their spawning origin (Begg et al. 2000). Spawning migrations may be driven in part by instincts in cod to return to their natal grounds for spawning (Svedang et al. 2007).

Identifying the mechanisms by which cod groups are able to seasonally navigate and return to general areas, or specific habitat features, is important in understanding migratory behavior. To date, studies of homing mechanisms have largely been conducted on Newfoundland populations, where homing over long distances to inshore spawning grounds has been documented over multiple years (Robichaud et al. 2001). Cod follow migratory pathways along deep, warm-water currents (Rose 1993), and experiments have shown that cod transplanted from spawning grounds have more success homing back to their capture location when they are released along those pathways (Robichaud et al. 2002a; Windle et al. 2005). Northeast Arctic cod have also been reported to migrate along stable thermal pathways, and may use temperature to follow a current and maintain course (Stensholt 2001). In addition to currents and temperature gradients, other cues may be used to recognize routes and destinations, including spatial memory of bathymetric features, or distinctive sound emitted from a destination (Fahay et al. 1999; Robichaud et al. 2002a; Cote et al. 2004; Robichaud et al. 2004; Windle et al. 2005). Cod often migrate with advancing currents, making olfactory cues from their destination unlikely in these instances (Robichaud et al. 2001; Windle et al. 2005).

There is evidence of younger cod acquiring familiarity with migration routes and destinations by traveling in large aggregations that follow older, larger "scouts" that direct movement (Rose 1993). Cod may therefore learn migratory behavior through experience and imitation of older individuals. This learning process is known to exist in other fish. In herring, for example, migratory routes are imprinted at an early age by young fish following older individuals (Corten 2001). Evidence that this mechanism may also be true for cod is found in the observation that juvenile cod participate in spawning migration, along with the adults, before they are reproductively mature (Svedang et al. 2007). Some juveniles were found to successfully home back to spawning grounds after being transplanted away from them, suggesting that the migratory learning process is complete before cod are sexually mature (Windle et al. 2005).

The majority of cod tagged in Ipswich Bay and the western Gulf of Maine by Howell et al. (2008) appear to migrate relatively short distances, and meet the criteria for the sedentary/resident population type. Few other movement studies have been published for the Gulf of Maine and Georges Bank populations, and they suggest that these cod are largely resident and exhibit limited migrations (Robichaud et al. 2004). Tagging studies on Georges Bank indicate that there are seasonal post-spawning dispersals and significant movement between Georges and Browns Bank, but the mean distance traveled from most release areas was <75 km (Hunt et al. 1999). Ames (2004) suggested that cod in the Gulf of Maine tend to make seasonal inshore migrations between spawning grounds and nearby feeding grounds, and that in the past, the subpopulation that wintered in Ipswich Bay may have moved with a herring population.

Acoustic tracking studies on Stellwagen Bank in Massachusetts Bay found that one-third of tagged cod had high site fidelity to complex gravel or boulder reef habitats where they were tagged, while the rest appeared to be transients that passed through the area without returning (Lindholm et al. 2003; Lindholm et al. 2007). Groger et al. (2007) constructed tidal geolocations of cod tagged on Stellwagen Bank using data storage tag (DST) data, and reported different migratory behaviors. Many remained resident to Massachusetts Bay; others made seasonal migrations around Cape Cod to Nantucket Shoals or Georges Bank; and some exhibited rapid movements back and forth between Massachusetts Bay and these areas. These estimates suggest some cod in the Gulf of Maine make migrations of several hundred kilometers that are not observed in other tagging studies, and that greater connectivity may exist between Gulf of Maine and Georges Bank stocks than typically reported.

2. Vertical distribution and movement

On a broad temporal scale, most cod populations show significant seasonal changes in the mean depth they occupy. This is in part a product of their semi-demersal behavior, and seasonal migrations that inevitably bring cod to areas of different depth. Seasonal depth change is also driven by environmental factors, primarily temperature preference and prey availability (Wigley et al. 1992; Swain et al. 1998; Stensholt et al. 2002; Palsson et al. 2003).

Cod also demonstrate considerable short-term variation in depth and distance from the bottom. Vertical activity is defined here as the degree to which cod exploit and move between a range of depths above the seafloor, and is often measured by the number of ascents and descents made and the maximum vertical range utilized over a given time period. Vertical movements are constrained by cod swimbladder physiology and ability to regulate buoyancy (Arnold et al. 1992; van der Kooij et al. 2007). As physoclistous fish, they must secrete gas into their swimbladder to increase buoyancy at a given depth, and resorb gas to reduce buoyancy. The secretion and resorption rates are slow processes, however, and require hours to re-establish neutral buoyancy after minor depth changes (Jones et al. 1985). Electronic tagging studies of cod have demonstrated that the range, speed, and frequency of their vertical activity exceed cod's capacity to adjust their buoyancy in response. Typical vertical activity necessitates that cod remain negatively buoyant at most occupied depths, and only reach neutral buoyancy at the top of their vertical range (Godo et al. 2000; Stensholt et al. 2002; van der Kooij et al. 2007).

Atlantic cod have a close association to the seafloor, and spend much of the year within a few meters of it (Fahay et al. 1999; Lawson et al. 1999; Turner et al. 2002).

Nevertheless, cod often exhibit wide-ranging vertical movement in the water column totaling hundreds of meters per day, make rapid ascents of up to ~80 m in less than 10 minutes, and can adopt a pelagic swimming mode for extended periods (Stensholt 2001; Righton et al. 2002). Most vertical movements are reversed within hours, however, so that an ascent is quickly followed by a descent of equal magnitude and vice versa, and the net change in mean depth from day to day is often negligible (Godo et al. 2000; Stensholt 2001). Vertical activity is associated with various environmental variables, including depth, temperature, light, and currents (Arnold et al. 1994; Michalsen et al. 1996; Aglen et al. 1999; Stensholt 2001; Palsson et al. 2003). The underlying mechanisms that drive both long-term and short-term vertical movements, however, are believed to be migratory and feeding behaviors (Neilson et al. 1990; Turner et al. 2002).

Trawl catchability studies, acoustic surveys, and electronic tagging studies have demonstrated that cod exhibit diel vertical migration (DVM). Most often, the DVM pattern entails cod remaining close to the bottom by day, and rising tens of meters at night (Engas et al. 1992; Fahay et al. 1999; McQuinn et al. 2005). The application of data storage tags (DSTs), however, which record individual depth over extended periods, has revealed greater complexity to vertical movement rhythms. The majority of cod display DVM during some period of the year. However, cod only exhibit DVM seasonally, for short-term periods, and with high individual variation, indicating that DVM is a facultative behavior employed only in particular circumstances (Neilson et al. 1990; Godo et al. 2000; Stensholt 2001; Neat et al. 2006).

Other temporal patterns are seen in cod vertical activity. Different individuals from the same population can display diel, two-week, and monthly vertical migration rhythms, corresponding to light, tidal, and lunar cycles, respectively (Neat et al. 2006). Cod also show semi-diel migrations that correspond to daily tides (Arnold et al. 1994; Aglen et al. 1999). A reversed DVM pattern was observed in Newfoundland and Barents Sea populations, where cod are active by day and descend to the bottom at night (Lawson et al. 1999; Stensholt 2001).

Vertical activity varies greatly between populations, and is shaped by different environments and prey communities (Neilson et al. 1990; Righton et al. 2001). Little is known about adult cod vertical activity in the Gulf of Maine. Cod throughout the Gulf of Maine and Georges Bank show seasonal changes in depth, possibly in association with temperature preference (Wigley et al. 1992; Lough 2004). Groger et al. (2007) reported that cod equipped with DSTs occupied a narrow vertical range when dispersing from Massachusetts Bay. It is believed that adult cod in the Gulf of Maine exhibit DVM patterns similar to those documented in Canadian waters (Fahay et al. 1999).

3. Spawning behavior

Seasonal timing and duration

Cod spawning events can be found year-round across the north Atlantic, but peak spawning times are in winter and spring in most regions. Spawning peaks occur from February through April in the North Sea, the Icelandic coast, the Norwegian coast and Barents Sea, and areas of the Newfoundland coast, Bay of Fundy, and Georges and Browns Banks. Spawning occurs from January through June or July in the western Gulf of Maine and Nantucket Shoals, and from May through July on the Grand and St. Pierre Banks, Newfoundland Shelf, and other sites along the Newfoundland coast (Colton et al.

1979; Hutchings et al. 1994; Smedbol et al. 1997; Fordham et al. 1999; Begg et al. 2000; Green et al. 2000; Lough 2004; Wright et al. 2006a; Knutsen et al. 2007; Windle et al. 2007).

The winter-spring spawning trend may be an adaptation to time spawning with food availability for cod larvae, as summarized by Cushing's investigations of the match-mismatch hypothesis (1984; 1990). Cod spawning in winter and spring roughly precedes or coincides with spring phytoplankton blooms and subsequent peaks in zooplankton biomass. Past recruitment data in the North Sea suggest that the strongest year classes for cod were produced when zooplankton biomass peaks were closely timed with larvae's need for zooplankton food. The magnitude of cod recruitment is thus affected by the timing of seasonal zooplankton abundance, and winter-spring may be the most favorable period for larval survival in the temperate and sub-Arctic waters cod occupy. The temporal relationship between cod recruitment and zooplankton biomass is supported by evidence from local populations in the North Sea and coastal Norway (Brawn 1961c; Beaugrand et al. 2003).

While the duration of a population's spawning season is often only broadly estimated, individual spawning periods have been studied with more precision in captivity. Female cod are partial batch spawners, releasing only a portion of their total egg mass in a spawning event. Females have been observed to release 4 – 21 batches throughout a spawning period, and spawning intervals, defined as the rest periods between batch releases, typically last 2 – 8 days (Kjesbu 1989; Chambers et al. 1996; Kjesbu et al. 1996). Overall, an individual female's spawning period varies, but often lasts 3 – 6 weeks (Kjesbu 1989; Chambers et al. 1996; Kjesbu et al. 1996; Rowe et al.

2006). There is also high individual variation in spawning start date for females (Kjesbu 1994). Less attention has been paid to males' spawning period, but they are reported to spawn significantly longer than females (Hutchings et al. 1993).

Effects of temperature

Temperature plays a significant role in cod behavior and physiology, but its effects on spawning activity remain unclear. Water temperature is positively correlated with gonadal development, and temperature decreases during early oocyte development can delay female spawning time (Kjesbu 1994). Since warmer years result in earlier phytoplankton blooms and zooplankton abundance, earlier spawning would be an advantageous response to high temperatures and increase larval recruitment in accordance with the match-mismatch hypothesis (Hutchings et al. 1994; Kjesbu et al. 1996).

The relationship between annual water temperature and an aggregation's spawning period is complicated and unpredictable. Lawson & Rose (2000) found that spawning time was not associated with specific temperatures. Hutchings & Myers (1994) found that inter-annual spawning time varied significantly with bottom temperature at spawning grounds, but the relationship varied with location. Warmer years were associated with earlier spawning times for one aggregation, but an aggregation at a different site spawned earlier in colder years. They postulated that because this aggregation overwintered in deep continental slope waters, a sharp thermocline in cold years caused these cod to spend more time at depth in warm water, in turn accelerating their gonad development. The relationship between annual temperature and spawning time may therefore be intertwined with depth, migration routes, and local geography, and preclude generalizations about the effect of temperature alone.

Movement and behavior on spawning grounds

Male and female cod show different activity when on spawning grounds, in both spatial distribution and the timing of small-scale spawning migrations. Catch data suggest that mature males arrive at spawning sites early and are followed by females and juveniles (Morgan et al. 1996; Lawson et al. 2000a). Most studies found a significant shift in sex ratios on spawning grounds as the spawning season progresses, but there is no consensus on the differences between male and female residence time. Robichaud & Rose (2003) found that acoustically tracked males emigrated from the area earlier than females. Others report that spawning males not only arrive earlier but also stay later than females and juveniles, which agrees with evidence that males remain in spawning condition longer (Hutchings et al. 1993; Morgan et al. 1996; Lawson et al. 2000a).

In instances where cod move to shallow areas to spawn, the shallowest sites have significantly male-skewed sex ratios, as well as a high proportion of both males and females in spawning condition. The deeper sites occupied by the same population are characterized by even sex ratios, and a higher proportion of spent females and immature fish (Morgan et al. 1996; Windle et al. 2007). It is believed that male-skewed, shallow sites are the focal point of spawning activity. Females, in turn, reside for most of the spawning period in deeper locations, move into the shallow sites when ready to spawn, and return to the deeper sites when they are spent (Morgan et al. 1996; Windle et al. 2007). This hypothesis is supported by acoustic tracking at a Newfoundland spawning ground, where females were more mobile and difficult to relocate than males, suggesting they move in and out of spawning sites (Robichaud et al. 2003). Sound production by males is frequent during spawning, and may create a chorus of mating calls from spawning sites that enable females to locate them from a distance (Rowe et al. 2004; Rowe et al. 2006).

Individual spawning interactions and courtship rituals have been observed in captivity. Spawning males aggressively compete to establish territories that they defend from competitors (Brawn 1961b). Females, less competitive males, and immature fish all reside in peripheral areas near these territories. A male waits for females to enter its territory, and then initiates a series of physical displays and grunts while circling the female (Brawn 1961b; Hutchings et al. 1999). If the female settles in the territory, signaling willingness to spawn, the male will attempt to ventrally mount the female to initiate spawning, and use its pelvic fins to grasp the female and align their genital pores, followed by gamete release. There are some reports that pairs make a vertical ascent after mounting, and spawn at a shallower depth above the aggregation (Brawn 1961b). The majority of males' spawning attempts are unsuccessful, and end when the female abruptly vacates the male's territory at varying stages of the courtship process. These rejections, coupled with the extended circling and fin displays by males to entice females to spawn, indicate that females control spawning events and choose mates (Brawn 1961b; Hutchings et al. 1999). Differences exist in various studies' descriptions of courtship displays and spawning events, and may indicate that the nuances of spawning behavior are population-specific (Nordeide et al. 2000).

Physical characteristics affecting spawning

Size has a notable influence on reproductive success in cod. The male dominance hierarchies that govern spatial distribution and access to females are usually size-based. The largest males in captivity are typically able to claim and defend the largest spawning territories. Dominant males are observed to spawn more often, and are often the only males that engage in spawning events in captivity (Brawn 1961b; Hutchings et al. 1999).

Genetic analyses of embryo paternity underscore the selective advantages of size. The number of offspring produced significantly increases with male body size (Bekkevold et al. 2002). Dominant males, who are typically larger than competitors, spawn more frequently and have greater fertilization success (Hutchings et al. 1999). Male body size not only helps gain access to females, but may also influence females' mate selection. Dominance hierarchies, advantages conferred by size, and female choice demonstrate that male competition and sexual selection are important determinants of cod reproductive output (Hutchings et al. 1999).

Size and age are not only related to fecundity and mating success, but also contribute to larval recruitment. Earlier spawning is often reported for older males and females, and their offspring may better match the timing of zooplankton abundance in some regions (Kjesbu et al. 1996; Lawson et al. 2000a). Older females produce larger eggs and larvae, and larval survival is believed to increase with size (Kjesbu et al. 1996). The increase in individual spawning duration with age also improves recruitment, by minimizing the effects of weather on total batch dispersal, and increasing the chances that larval production is concurrent with peaks in zooplankton biomass (Hutchings et al. 1993; Byers et al. 2006).

There is evidence that spawning is assortative by age and size, and cod tend to spawn with individuals of comparable size through temporal and spatial segregation of size classes. The relationship between age and spawning start date found in many areas may increase the probability of similar-sized cod spawning together (Hutchings et al. 1993). Spatial segregation by size was clearly noted on an Icelandic spawning ground, where larger cod were concentrated at inshore sites favoring local retention and transport success, and smaller size classes were relegated to offshore areas (Marteinsdottir et al. 2000). Size is a generally a proxy for fecundity and batch size, and spawning between individuals of comparable reproductive capacity may be optimal for fertilization. Cod of both sexes were found to have greater reproductive success when mating with an individual of comparable or larger size (Bekkevold et al. 2002; Rowe et al. 2007).

Cod use specialized drumming muscles surrounding the swimbladder to produce grunts and other sounds for various purposes, but sound production peaks during spawning (Nordeide et al. 1999). Males employ acoustic communication as a key component in attracting and stimulating females to spawn (Brawn 1961c; Rowe et al. 2004; Rowe et al. 2006). Drumming musculature reflects sexual selection: musculature is larger in males than females, seasonally increases in size before spawning, and is positively associated with size and fertilization potential (Rowe et al. 2004). One study found that male drumming muscle size was the single most significant predictor of mating success (Rowe et al. 2008). Larger drumming muscles produce sound at a higher rate, and possibly of a greater intensity (Brawn 1961c; Rowe et al. 2004; Rowe et al. 2006). Therefore, the individual qualities of a male's acoustic communication may communicate information about its reproductive fitness to selective females. In addition, sound production was found to be characteristically different between populations, and may enable females to identify males from their own population and maintain local reproductive isolation (Rowe et al. 2006).

Lekking behavior

The hypothesis that cod exhibit lekking behavior during spawning has been discussed in various studies (Nordeide et al. 2000; Windle et al. 2007). Lekking is a mating system found in other groups of vertebrates and some teleosts, characterized by clustered mating arenas (leks) formed by males, and mobile females that maintain discrete areas outside leks, but enter these arenas to mate. Reproduction is governed by female mate choice, and male competition and displays to attract females. Leks appear to exist for cod, as males create individual, contiguous territories in captivity where spawning events occur. In the wild, males arrive first on spawning grounds, and establish male-dominated sites where active spawning appears most concentrated. In captivity, female cod temporarily move into male territories to spawn, but occupy defined zones with non-spawning cod outside of these territories.

There is substantial evidence for lekking in cod derived from detailed observations of spawning events in captivity, and catch data suggesting spatial distribution on spawning grounds. Yet spawning events have only been observed in confined spaces and shallow depths (<5 m). Individual movements in and out of spawning arenas and behavioral variation between sexes that constitute lekking have neither been observed in a natural habitat, nor on the spatial scale of a spawning ground. Variation in sex ratios at different sites across a coastline may not be related to the sexual segregation observed inside a tank. Individual tracking has the potential to demonstrate lekking on spawning grounds, but previous attempts at this have been inconclusive. In one study, tracked males were easier to relocate, and thus appeared to be more resident at the spawning site and less mobile than females – yet departed the spawning ground earlier than females (Robichaud 2004). At another area, tracked males were wide-ranging and did not center their activity at the male-dominated sites, and females were equally unpredictable and difficult to relocate (Windle & Rose 2007).

Spawning in the Gulf of Maine

Peak spawning periods for Gulf of Maine and Georges Bank cod are winter and spring, although there is enough variation in spawning time that there are eggs present in the region's waters year-round (Colton et al. 1979; Berrien et al. 1999; Lough et al. 2006). Principal spawning locations for both stocks have also been identified (Page et al. 1999; Ames 2004). Cold winters delay annual spawning times, and warm winters stimulate earlier spawning (Lough 2004).

Studies of egg and larval dispersal and recruitment for the Gulf of Maine and Georges Bank stocks have shed light on the preservation of local population structure. Circulation patterns on Georges Bank promote local retention of eggs and larvae, and the location and timing of peak spawning also maximize the probability of retention (Page et al. 1999; Lough et al. 2006). In comparison, Huret et al. (2007) modeled larval dispersal from several spawning grounds in the western Gulf of Maine, including Ipswich Bay, and found less local retention. A high proportion of larvae from all spawning grounds were found to travel south and settle within Massachusetts Bay, Cape Cod Bay, and Nantucket

Shoals, demonstrating significant connectivity between spawning sites. Survival and successful recruitment were linked to local retention, and both rates were higher the farther south a spawning ground was located. Nevertheless, dispersal modeling also indicated Ipswich Bay retained a sufficient proportion of its larval output to maintain a local population (Huret et al. 2007).

The results of Howell et al. (2008) established that Area 133, and Ipswich Bay in particular, is the center of cod biomass and spawning activity across the six 30 x 30-minute rolling closures surveyed (Fig. 1a), and one of the most significant spawning grounds in the western Gulf of Maine. Spawning conditions of tagged fish revealed two peak spawning periods within Area 133, one from December-January and the other from May-June. Both spawning periods show corresponding peaks in biomass, as cod seasonally move inshore to Ipswich Bay to spawn during these times.

Ames (2004) suggested the Gulf of Maine stock may be composed of 3-4 distinct subpopulations. The findings of Howell et al. (2008) and Wirgin et al. (2007) confirmed historical evidence and beliefs that Ipswich Bay attracts two distinct spawning components at different times of year (Klein-MacPhee 2002; Ames 2004). Wirgin et al. (2007) conducted a genetic analysis of adult cod at spawning locations throughout the Gulf of Maine and Georges Bank, and discovered that the Ipswich Bay spring spawning component is genetically distinct from the winter aggregation and fish from other winter spawning locales. Preliminary results from the continuation of this analysis indicate that the Ipswich spring component may not be genetically distinct from other spring spawning sites in Massachusetts Bay and coastal Maine, but these spring components are different from all winter components and from the Georges Bank stock (Breton 2008). Therefore, the coastal spring spawning components from Cape Cod to northern Maine, including Ipswich Bay, appear to constitute a reproductively isolated subpopulation in the Gulf of Maine stock. Its isolation is likely achieved through some combination of temporal segregation, local retention of larvae, and the return of juveniles and sub-adults that are dispersed as eggs and larvae (Huret et al. 2007; Svedang et al. 2007).

4. Habitat preference and utilization

Little is known about the habitat preferences of cod, particularly among adults. Juvenile cod prefer complex substrates that provide refuge, such as uneven rock, boulders, and kelp (Cote et al. 2003; Cote et al. 2004). In some locations, adult cod are also associated with elevated bathymetry (Thorsteinsson et al. 1998; Lindholm et al. 2007). Although diel rhythms vary by population and season, adult cod move over a variety of habitat types during active periods of the day and show little preference, but seek out complex substrate for cover during rest periods (Clark et al. 1990; Lawson et al. 1999).

Coastal spawning areas are often found where the configuration of land masses, bathymetry, and currents promotes local retention of eggs and larvae, which may be a fundamental mechanism to preserve local population structure (Lawson et al. 2000a; Espeland et al. 2007; Knutsen et al. 2007). If larval retention enables a spawning component to thrive and persist over time, then the confluence of environmental factors that produce retention must be incorporated into our definition of critical habitat for cod (Byers et al. 2006). The conditions of shallow, inshore spawning grounds are

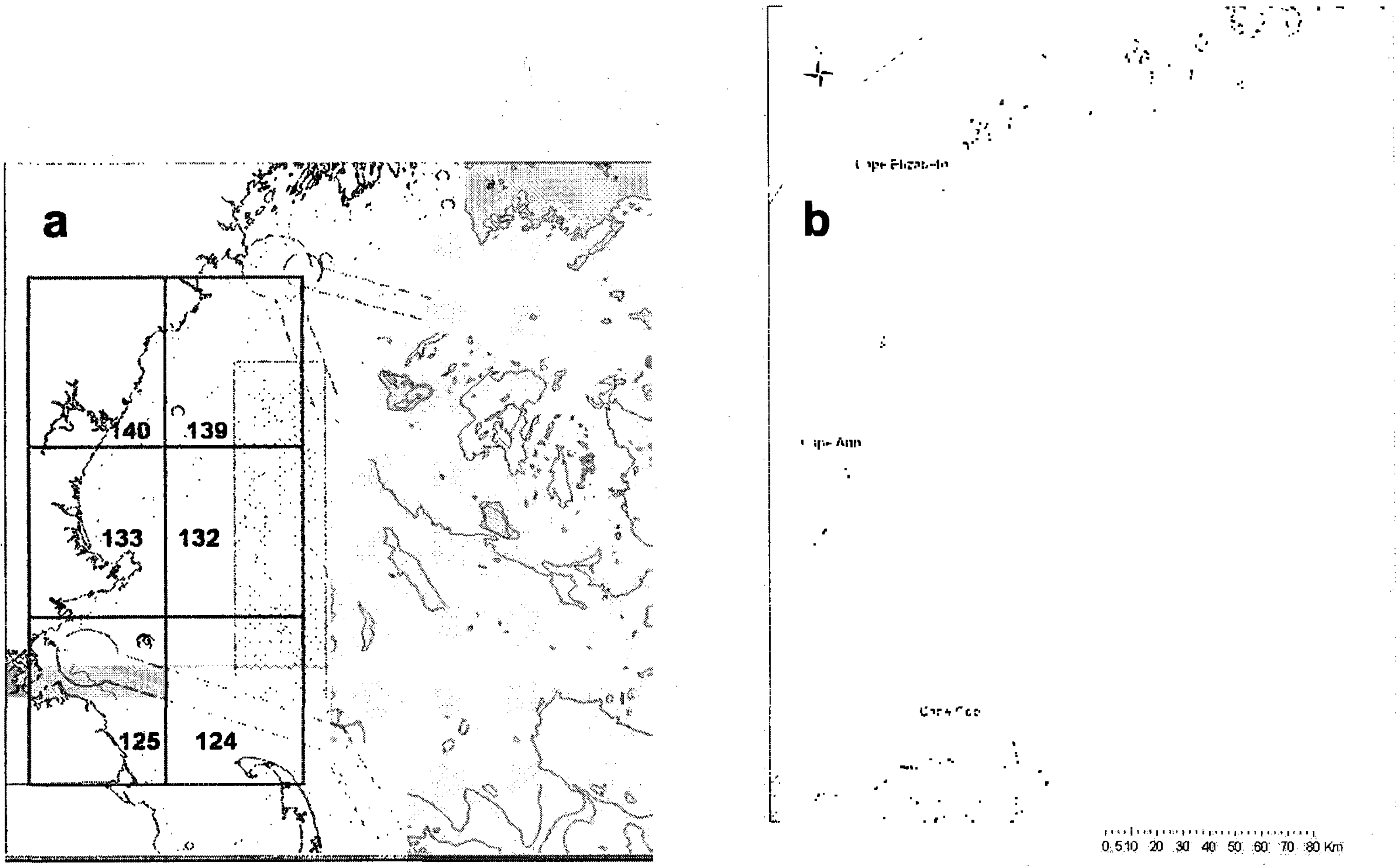

Fig. 1. Western Gulf of Maine. a). Grid of rolling closure areas where cod were tagged by Howell et al. (2008). Ipswich Bay is in Area 133. Gray area indicates Western Gulf of Maine Closure Area, where fishing is prohibited year-round. b). Location of study area, outlined in red.

favorable for larval retention, and appear to represent optimal spawning habitat for some populations (Hutchings et al. 1993; Marteinsdottir et al. 2000). Elevated bathymetry may be important for spawning activity, either by aiding retention or serving as landmarks for aggregation. An Icelandic population was documented to form spawning aggregations around specific seamounts, and spawn alongside or above them (Thorsteinsson et al. 1998).

Limited data suggest Atlantic cod in the Gulf of Maine are more commonly found over substrates of gravel, shells, or other hard bottom, coarse-grain sediment (Klein-MacPhee 2002; Lindholm et al. 2003). Post-larval settlement in Georges Bank is concentrated over complex gravel areas (Lough 2004). Newly settled juveniles on the Massachusetts coast do not show a substrate preference, but are concentrated in near-shore areas in depths < 30 m (Howe et al. 2002). Older juvenile cod in the Gulf of Maine prefer complex, rocky substrates that provide shelter, and show higher survivorship in these habitats than open areas and fine-grain sediments (Lindholm et al. 1999; Lindholm et al. 2001). Ipswich Bay and Massachusetts Bay were designated as suitable nursery habitats for juvenile cod, and contain relatively high juvenile abundances (Howe et al. 2002; Lough 2004). Complex substrate may also be significant to mature cod; some resident adults in Massachusetts Bay show fidelity to boulder reefs (Lindholm et al. 2007).

Only broad generalizations about Gulf of Maine spawning habitat are known: depths <100 m, 3-10 mile distance from shore, and a temperature range of 0-9°C (Berrien et al. 1999; Klein-MacPhee 2002; Ames 2004). Ames (2004) concluded that cod spawning areas are typically in channels or basins in close proximity to shallower feeding grounds. In contrast to reports that cod generally prefer rocky substrate, Ames found that spawning habitat was characterized by sandy gravel, sand, or mud. The majority of currently active spawning grounds in the Gulf of Maine are shallow and near-shore (Wirgin et al. 2007). The spawning grounds closer to shore and enclosed by land features have proportionally greater local retention and successful recruitment, and thus proximity to land may in part define critical spawning habitat (Huret et al. 2007).

CHAPTER II

MATERIALS AND METHODS

Adult cod were tagged, released, and acoustically tracked during the spring and summer of 2006 in 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 size, 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.

Electronic tags were attached to adult cod to record data about their behavior and track their movements. Two types of electronic tags were employed: external data storage tags, 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 11 g. All tagged fish weighed >1 kg, thus the combined tag weight was well under the maximum 2% of fish body weight recommended for aquatic organisms (Winter 1983).

Data storage tags

Data storage tags (DSTs) recorded pressure (depth), ambient water temperature, and time. The DSTs used, (Star-Oddi DST milli) weighed 5 g in water, and were 15 x 46 mm 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 6 g 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 at a 69 kHz frequency 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. "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. I 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, I 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 et al. 2005; Sakaris et al. 2005). The wax coating was composed of a 70:30% paraffin/beeswax mixture to achieve optimal consistency (M. Shane, pers. comm.).

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 12 h 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 I 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 60 cm 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 sex. Gonadal biopsy was performed using a small-diameter rubber tube inserted through the genital pore and into the oviduct to retrieve an egg sample. I tagged only ripening females, using the criteria defined by Kjesbu (1994), and spermiating males. Sex 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 a fish. An incision 3 cm in length 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 to be robust and physically recovered from the effects of surgery and anesthesia were released with tags attached. Following the recommendation of Mulcahy (2003), I 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 April 21 and May 17, 2006. This period was chosen because I 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, I 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. I 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. I implanted all acoustic transmitters on May 6 & 17 (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 700 m (~0.4 nautical miles) for the VR100 and 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

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

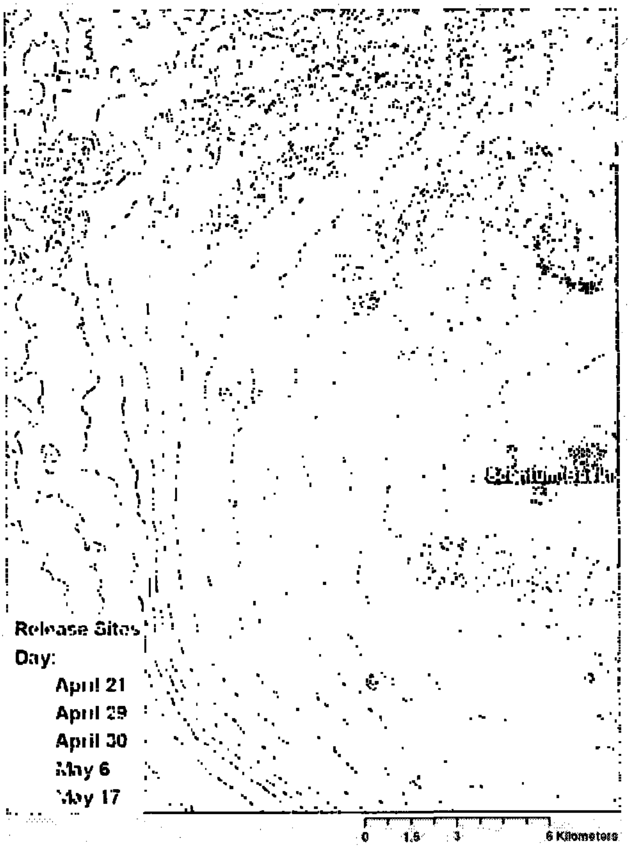

Fig. 2. Release sites (n=18) in Ipswich Bay for all 5 days that cod were caught and tagged. Symbols correspond to different tagging dates. Acoustic tags were released May 6 & 17.

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

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 – 12 h excursion for one of the four commercial fishing vessels involved in the project. On each day I attempted to relocate as many of the 30 acoustic transmitters in the study area as possible. Eight of these tracking days were extended over 24 h to determine if cod behavior varied throughout a 24 h period.

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 km²) 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 et al. 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, I applied the methods of Neat et al. (2006) to de-trend the depth profiles and apply autocorrelation functions on residual data. First, I 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 produced a smoothed curve that best fit the data and represented the trend of the time series (Neat et al. 2006). I 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). I then subtracted that smoothed trend from the time series and extracted the residuals, which represented de-trended depth data. Next, I 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). I again subtracted this best-fit curve from the time series. Finally, I applied an autocorrelation function (ACF) to this twice de-trended depth data to reveal short-term temporal rhythms.

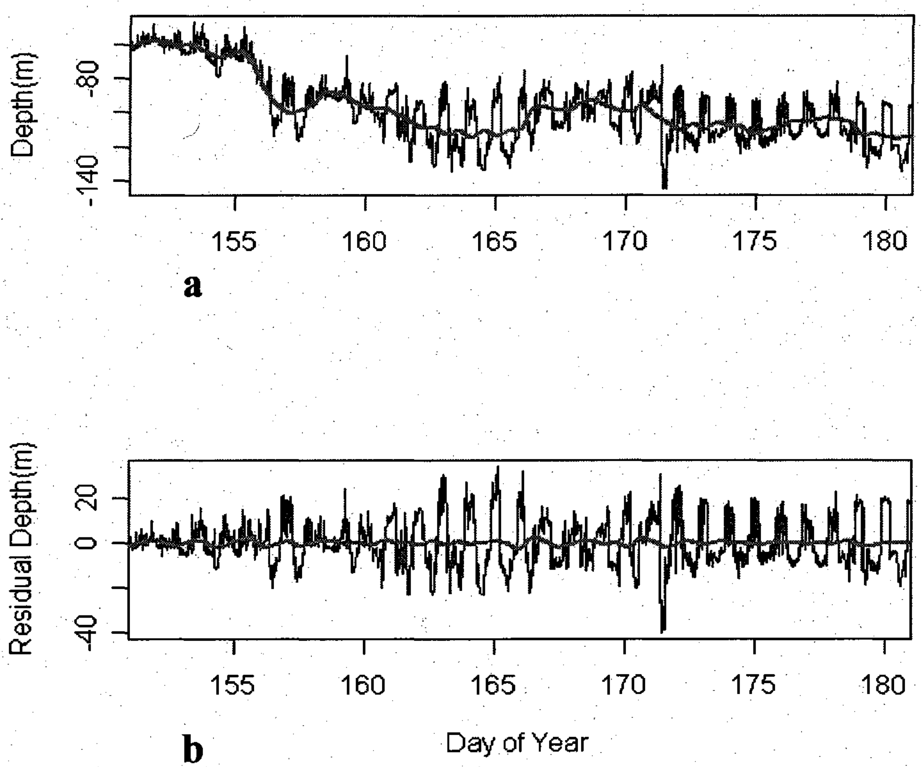

Fig. 4. Example of the smoothing and de-trending steps applied to depth time series. a). Raw depth profile for DST 056 throughout June, overlaid with a best-fit curve produced with loess smoothing (span width=1/10). b). Same depth data and time frame, but with trend in (a) subtracted from time series. 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.

CHAPTER III

DST DATA RESULTS

1. 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 each DST is hereafter referred to by a 3-digit ID number. 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 Jeffreys Ledge, directly east of Ipswich Bay. Four cod (13%) were caught on Stellwagen Bank, south of Cape Ann. Finally, one

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**= Jeffreys 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	

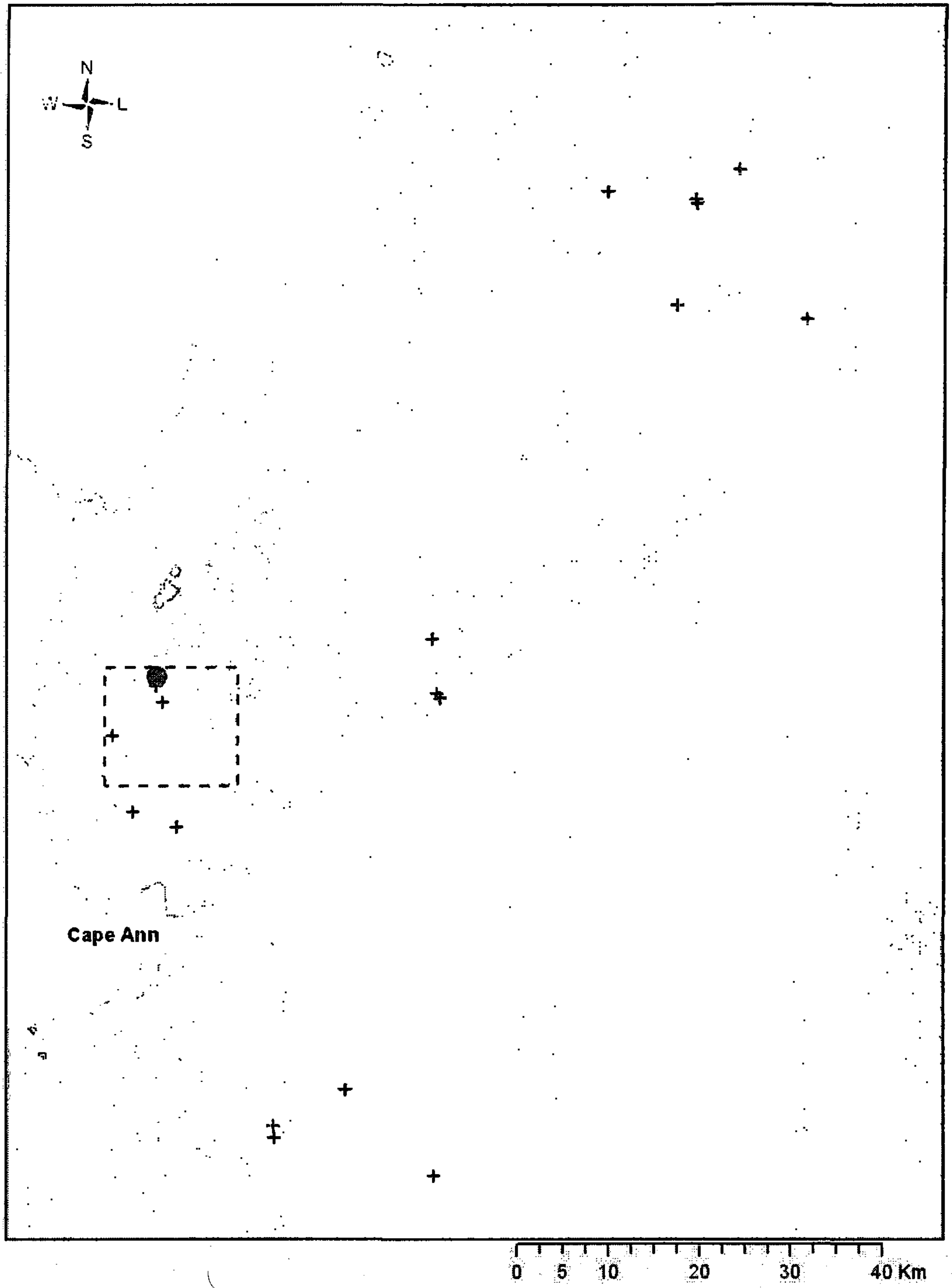

Fig. 5. Recapture locations for cod equipped with DSTs with known position coordinates (n=22). Cod recaptured off Cape Cod not shown. Circle shows location of Massachusetts Division of Marine Fisheries survey tow where four DST equipped cod were recaptured. Tag and release area indicated by dashed square.

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). I 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 (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, I utilized 26 DSTs for vertical movement analysis.

2. Tagging Recovery Phase

All 26 cod displayed several days of behavior immediately after tagging that was 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 I 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). I 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 et al. 2000; Heffernan et al. 2004), and described as recuperation or equilibration behavior after release (Nichol et al. 2006; van der Kooij et al. 2007). This pattern often followed Behavior 1 or 2. In Behavior 3, the cod made a gradual descent

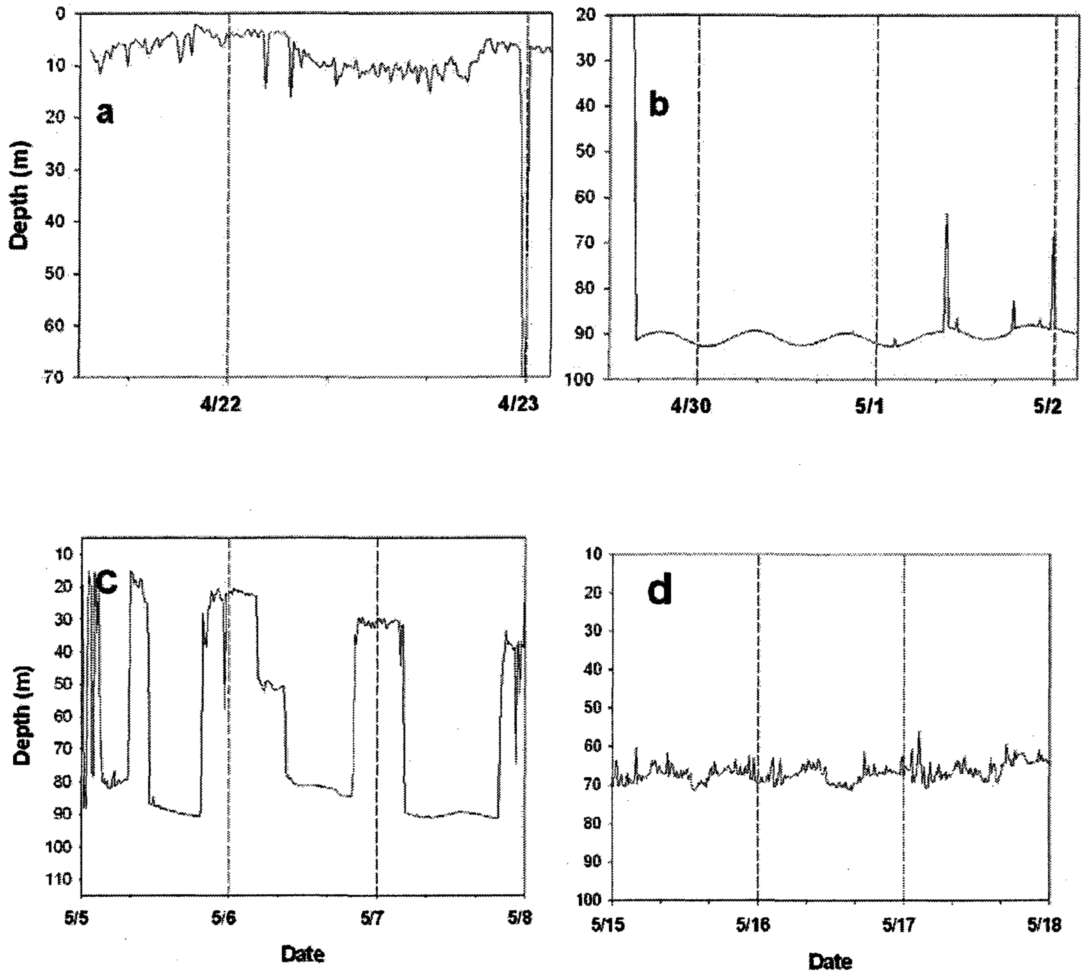

Fig. 6. Tagging recovery phase behaviors and typical subsequent spawning phase activity. a). Shallow period after release during recovery phase. b). Escape dive and sedentary period during recovery phase. c). Oscillatory descent behavior during recovery: deep by day, gradually decreasing ascents at night.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

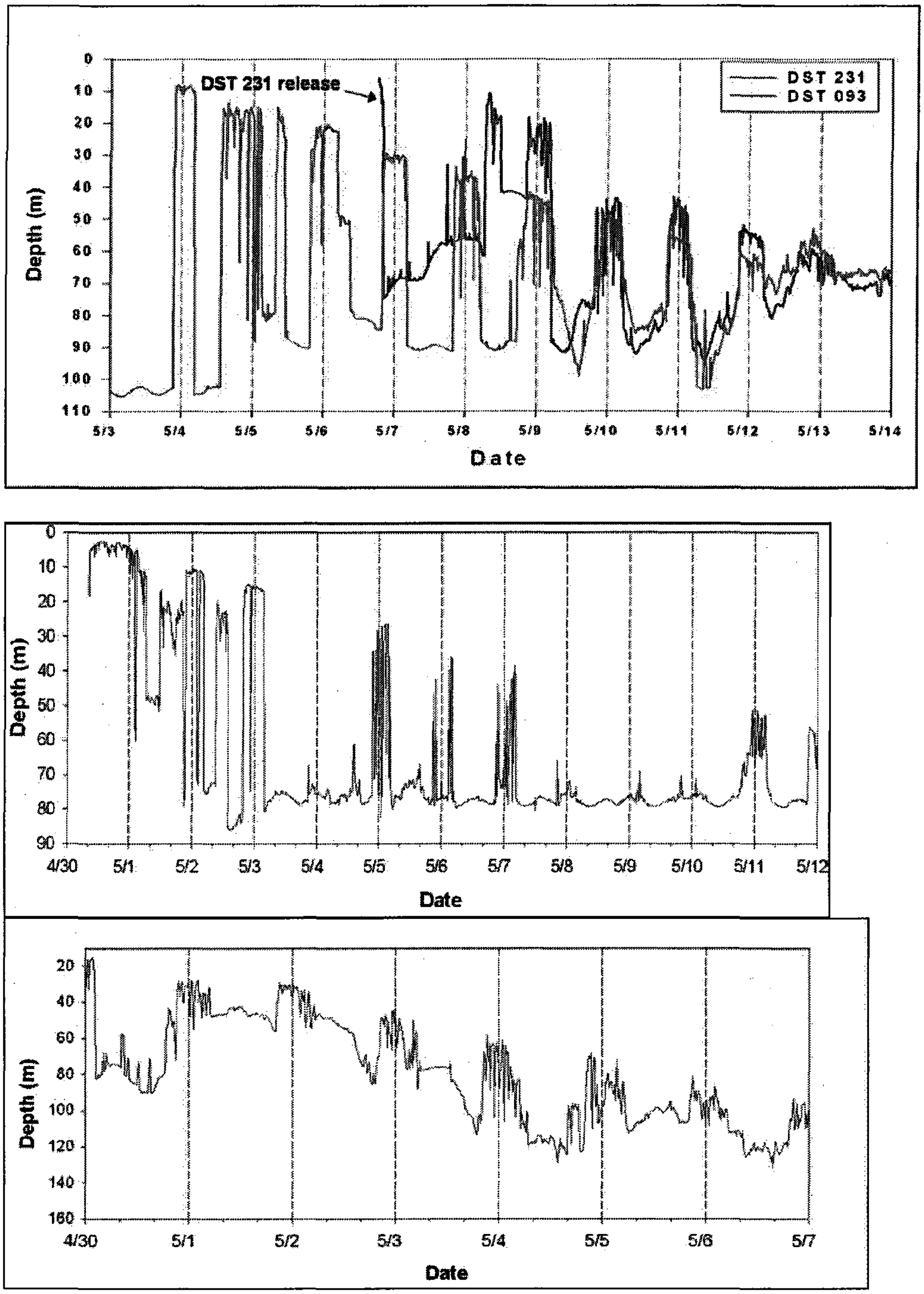

Fig. 7. Oscillatory descent behavior during the recovery phase. Dotted gridlines indicate 12:00am on successive days. Top plot shows overlapping recovery phases of two DSTs. The first was tagged a week earlier and displayed an initial bottom interval. Both adopted diel oscillations that diminished in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

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).

3. 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, I 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 I 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

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.

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, Jeffreys Basin, or the trenches east of Cape Ann. I 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 Jeffreys 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 I chose the mean date of

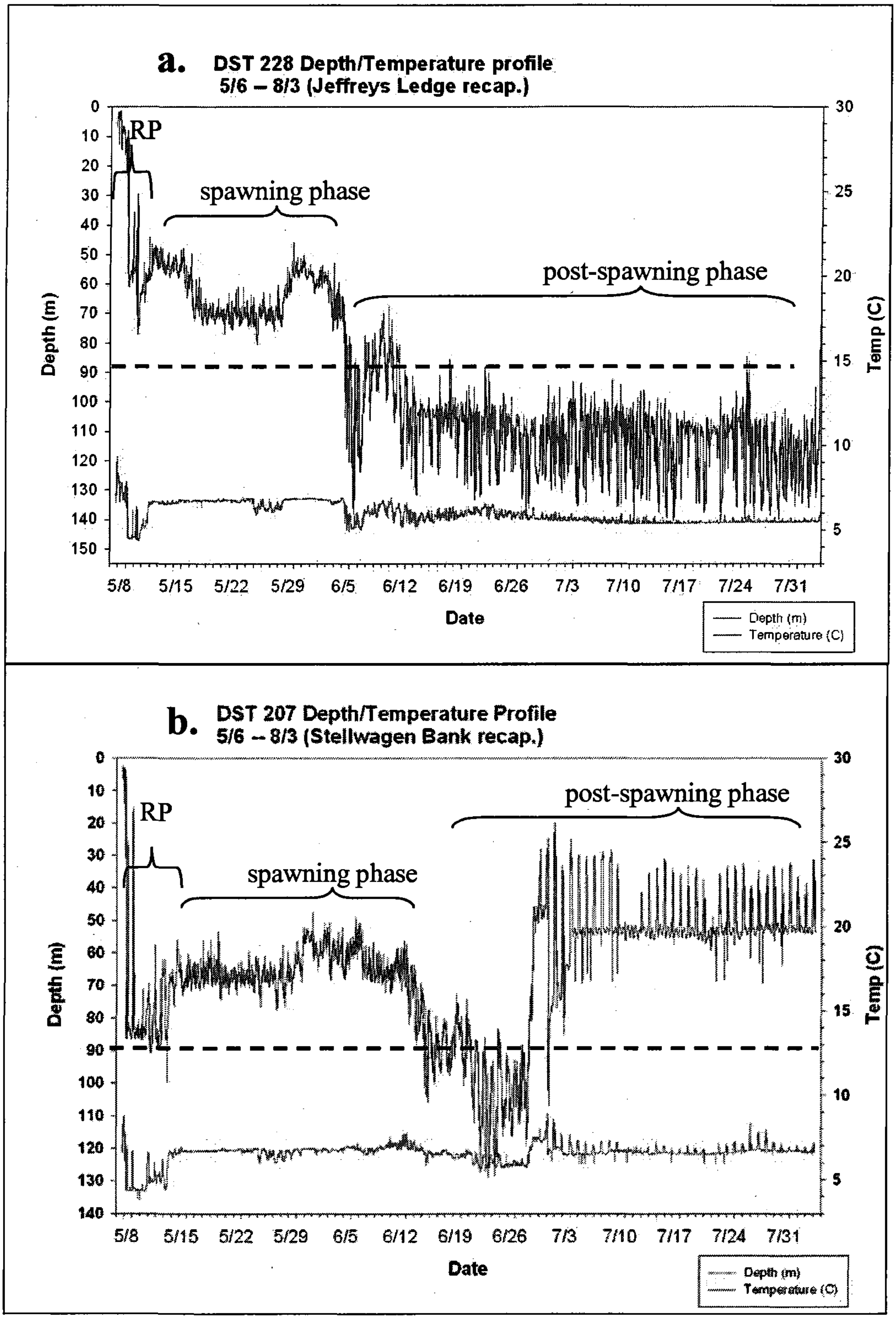

Fig. 8. DST depth & temperature profiles, illustrating recovery phase (RP), spawning phase, offshore descent in June, and post-spawning phase. Dotted line indicates maximum depth in Ipswich Bay. One DST shows consistent deep-water activity after the spawning phase, while the other ascended to a bank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

offshore descent, June 8, as a rough estimate for the end of their spawning phase.

4. 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.

5. Trends in DST data

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.

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

Cod/ DST	Sex	Size (cm)	Time Period					
			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) for cod equipped with DSTs 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) for cod equipped with DSTs 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

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).

Vertical range

I 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).

Cod 086

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

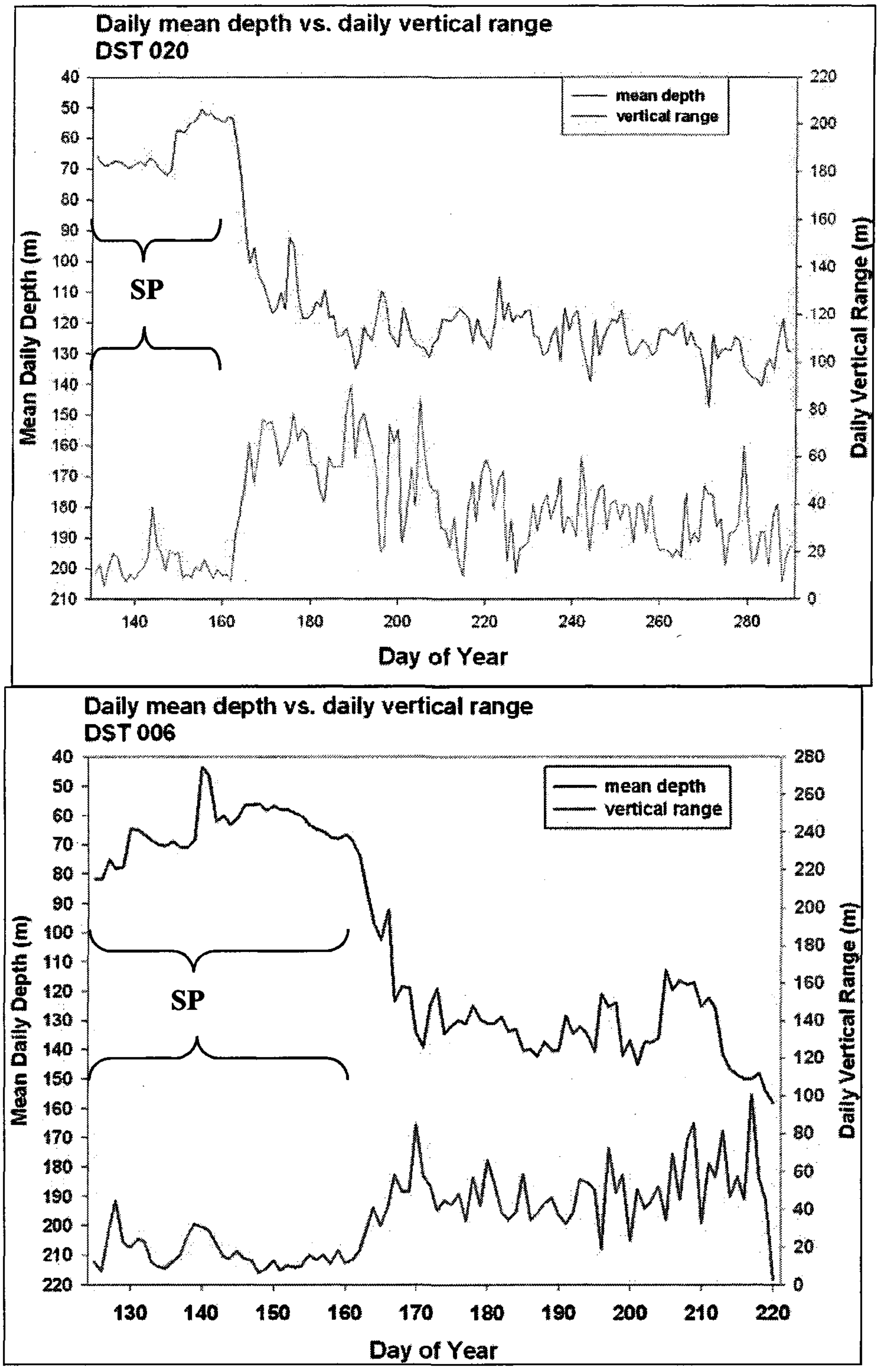

Fig. 9. Examples of the positive relationship between depth and vertical range. For each DST, daily mean depth and daily vertical range are plotted together. Spawning phases (SP) are indicated.

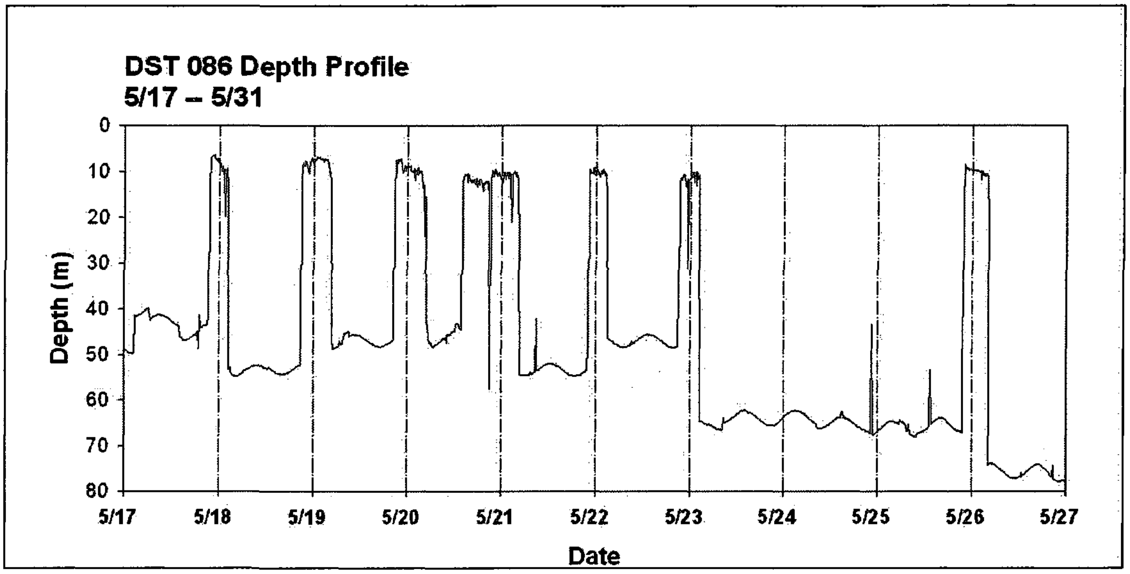

Fig. 10. Depth profile of DST 086, illustrating a series of unusual nocturnal ascents in May during its spawning phase that do not appear to be equilibration behavior. A second series during its spawning phase occurred in June.

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 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).

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

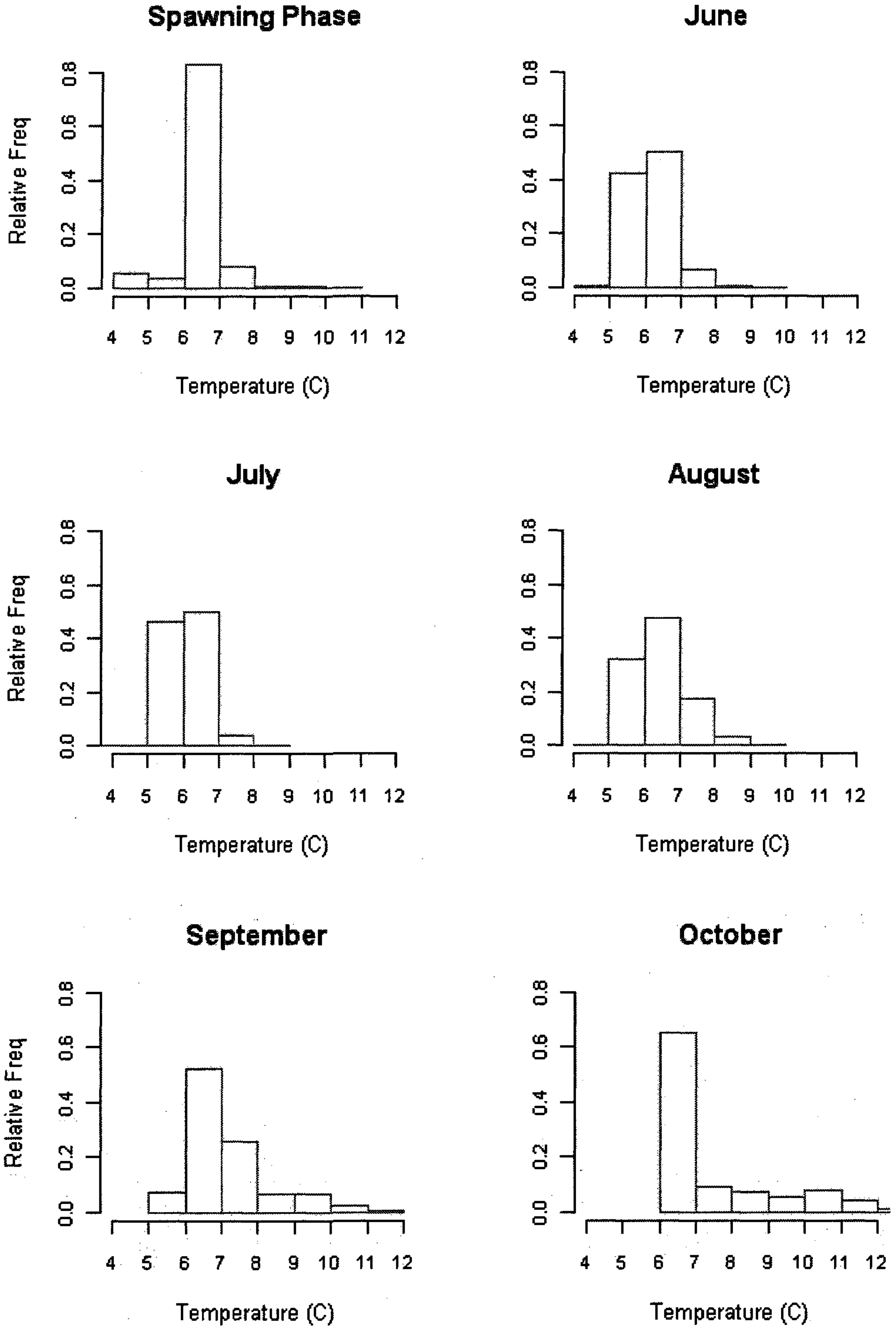

Fig. 11. Relative frequency distribution histograms of temperature (°C) using pooled data from all DSTs. Distributions are divided into spawning phase and post-spawning months.

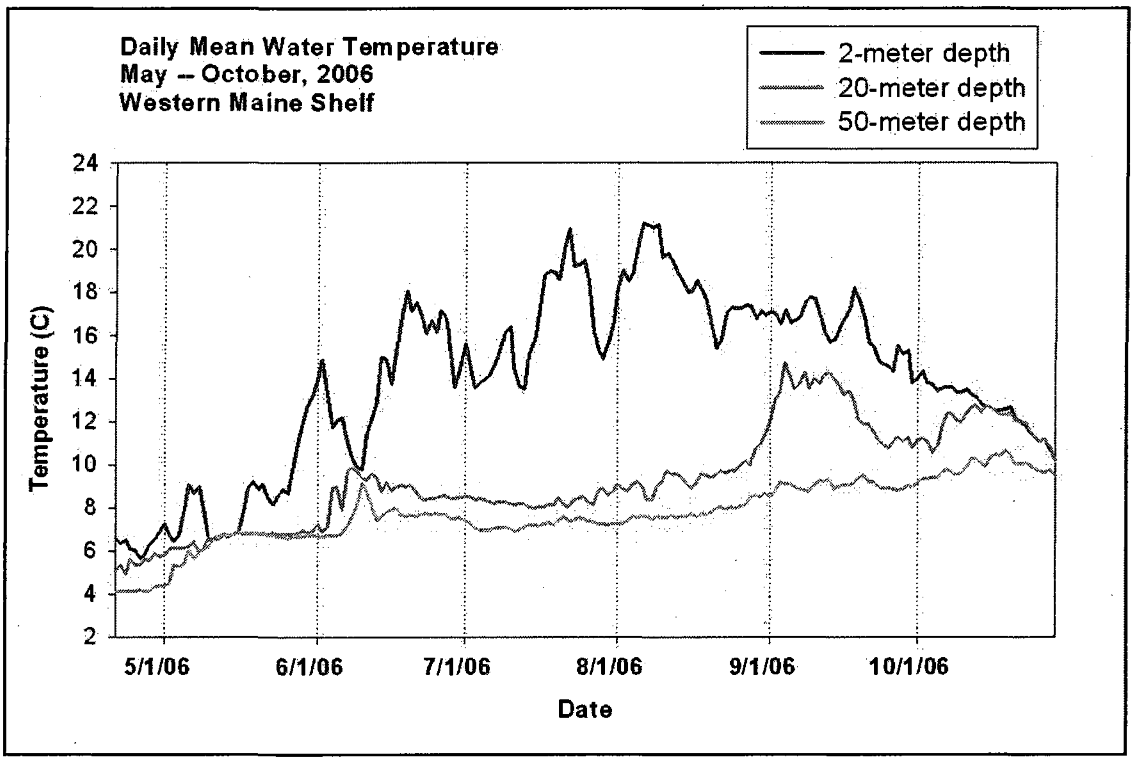

Fig. 12. Mean daily water temperature profile at 2 m, 20 m, and 50 m depths on southwestern Maine shelf during study period. Data obtained from GoMOOS buoy B01. Bottom temperature gradually increases throughout the study period. A small increase in temperature occurs in early June, just preceding the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

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 demonstrate that water temperature at 20 m and 50 m gradually increased through mid-October (Fig. 12, GoMOOS Western Maine Shelf Buoy B).

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 were pooled, all July data were pooled, etc.). The overall distribution of depth, daily vertical range, and temperature for each time period was calculated and illustrated in Figure 13. These boxplots 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).

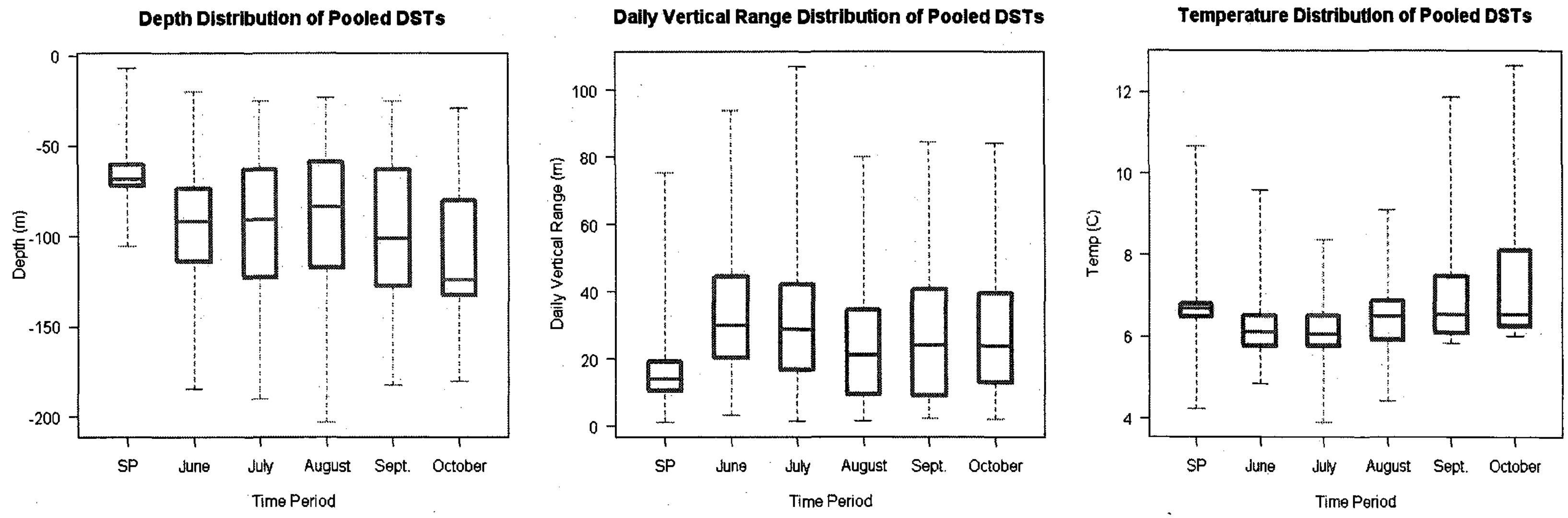

Fig. 13. Boxplots of depth, daily vertical range, and temperature distribution by time period for all DST data combined. Whiskers extend to data extremes. SP = spawning phase.

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).

6. Temporal rhythms of depth data

I 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 at 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 24 h apart (120 depth readings) were consistently similar. If the peak repeats at multiples of 120 on the lag axis, depths values at 48 h, 72 h, 96 h, etc. apart were also correlated. Negative peaks at a lag of 60 indicate depths were consistently different when only 12 h apart. A pattern of positive peaks at 24 h intervals ,and negative at 12 h intervals, indicates there was a diel rhythm to vertical movement, particularly if 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 5-day maximum (Fig. 14).

Three types of fine-scale movement rhythms are given in Table 7. "Semidiel" indicates a pattern of positive correlation at 12 h and 24 h apart, and negative correlation at 6 and 18 h 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

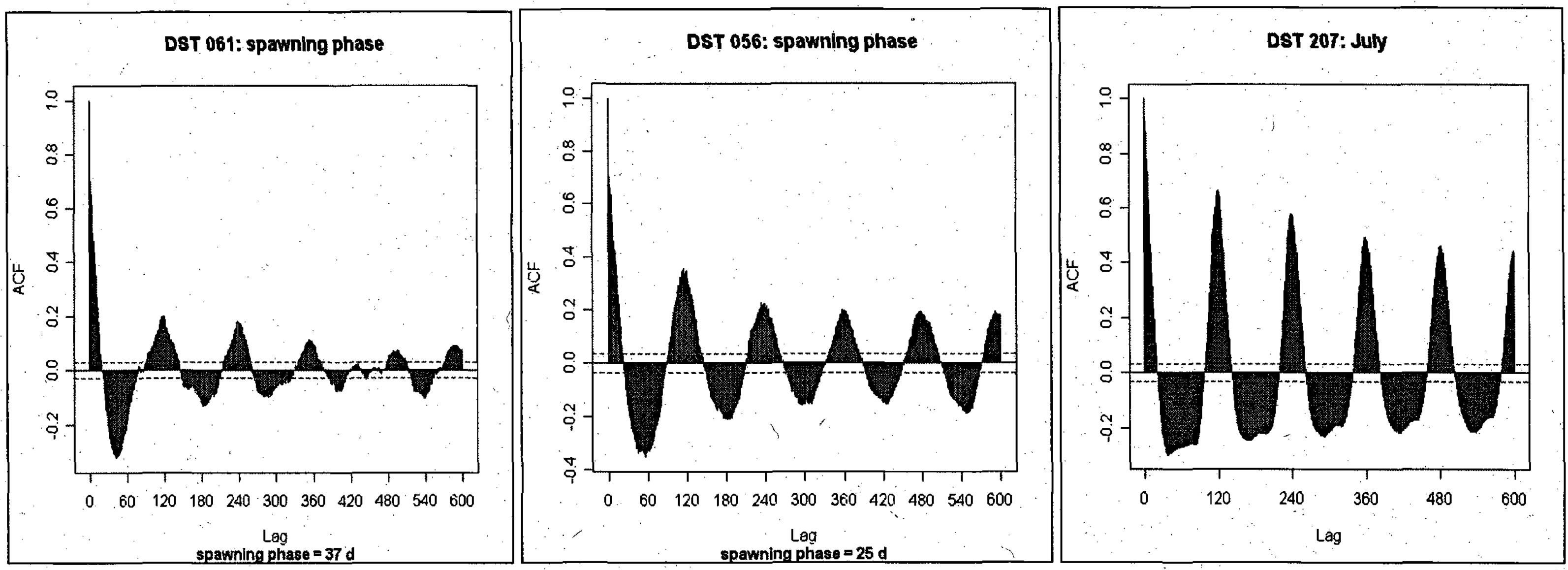

Fig. 14. Three ACF plots that provide examples (left to right) of weak, moderate, and strong ACF signals. Plots are from different DSTs and time periods. All are examples of a diel pattern of vertical movement, where depths are consistently similar 24 hrs. apart and consistently different 12 hrs. apart. 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 equipped 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.

(e.g. fish 060 & 981 in Fig. 15a). I 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 24 h movement pattern was observed in the depth profile, the pattern was classified simply as "diel" in Table 7.

Tidal adjustment

One concern when applying ACF to depth profiles was the potential effect of the tide on any observed temporal patterns. I attempted to address this potential bias by removing the tidal signature from depth data. I 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), I 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. I 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.

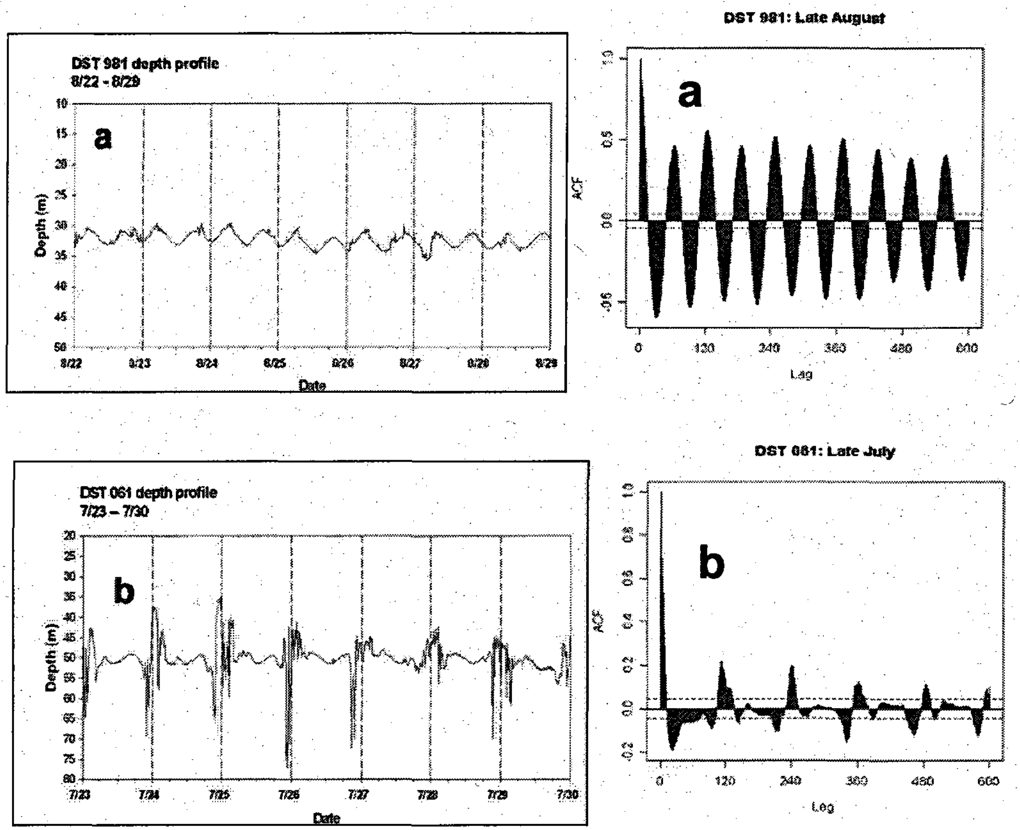

Fig. 15. Examples of fully sedentary and partially sedentary depth profiles and their corresponding ACF plots. Gridlines indicate 12 a.m. on successive days. a). Fully sedentary behavior at constant depth and a smooth, sinusoidal tidal signature (location unknown). A strong semidiel ACF signal results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

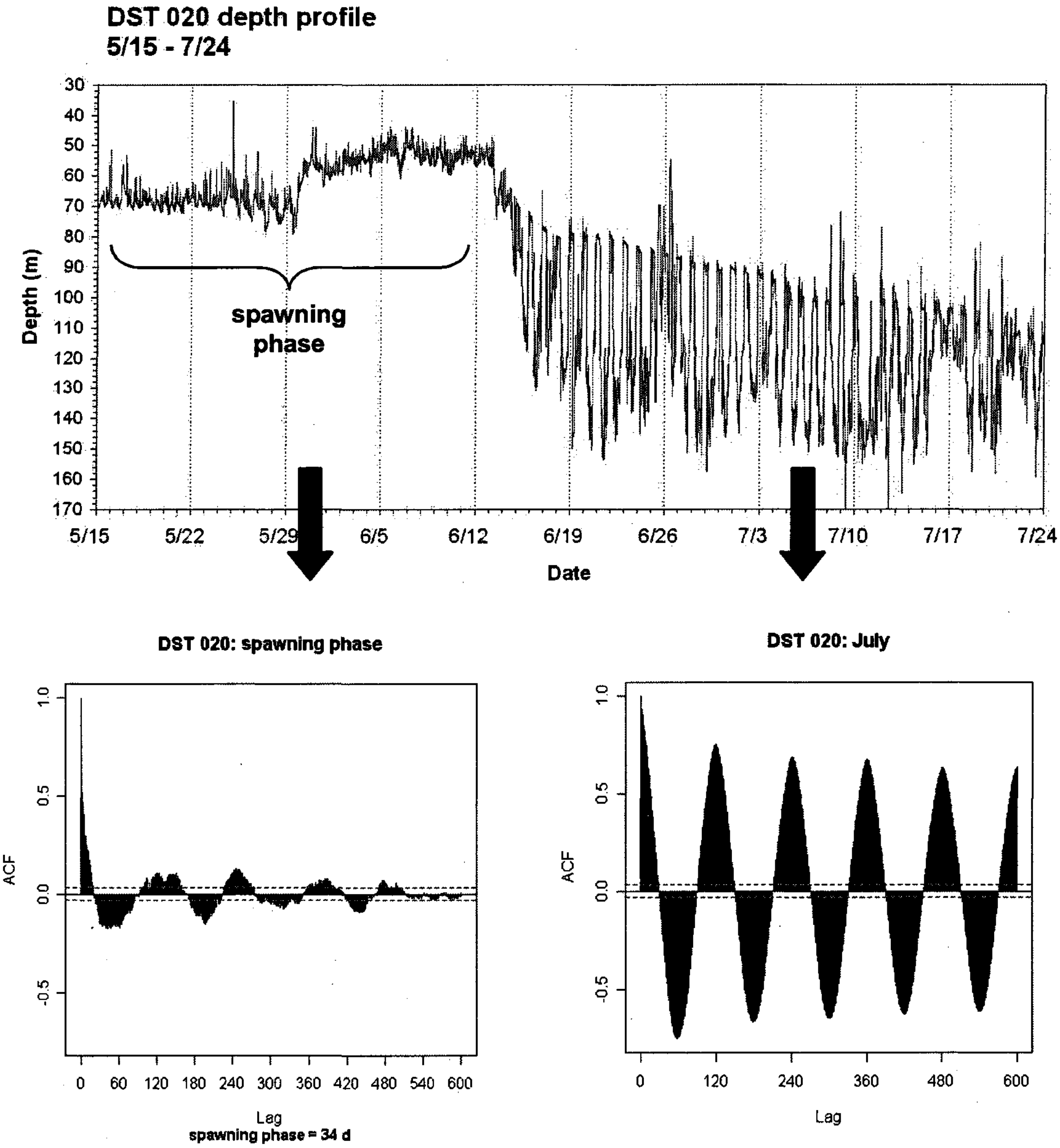

Fig. 16. Depth profile for DST 020 and corresponding ACF plots for its spawning phase and the month of July (post-spawning phase). Like several others, this cod transitioned from a faint diel rhythm during its spawning phase to a strong, consistent DVM pattern offshore.

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 I 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.

CHAPTER IV

DST DATA DISCUSSION

1. Recovery behavior

The behavioral patterns seen in the tagging recovery phase typically lasted from 2–14d, as in previous DST studies (Godo et al. 2000; Nichol et al. 2006). The bottom interval of low activity following an escape dive in many profiles may be a recuperative period. Both the speed of escape dives and a comparatively slow swimbladder gas secretion rate should have caused cod to be negatively buoyant when they reached the seafloor, and they may have remained so for days (Arnold et al. 1992; Godo et al. 2000; van der Kooij et al. 2007).

The repetitive depth fluctuations (Behavior 3) seen in many cod are a direct result of buoyancy change after a significant ascent (Nichol et al. 2006; van der Kooij et al. 2007). Given the swimbladder's resorption rate, and the minimum speed at which a bottom trawl is raised, cod swimbladders are believed to usually rupture during capture, but can remain partially functional and rapidly seal off (Godo et al. 2000; Nichol et al. 2006). Although many cod that survive trawl capture sustain severe barotrauma and cannot swim or submerge, the cod tagged with DSTs in most studies are a healthy sub-sample that appears neutrally buoyant, apparently due to gas resorption. If neutrally buoyant at the surface, these cod must become negatively buoyant when they return to their capture depth. Gas secretion is a much slower process than resorption, and re-inflating their swim bladder to achieve neutral buoyancy at their preferred depth may take days or weeks (Arnold et al. 1992; Heffernan et al. 2004).

Behavior 3, or equilibration behavior, may be an effort to compensate for temporary negative buoyancy at the preferred depth. Van der Kooij et al. (2007) proposed that continuous negative buoyancy at depth during this re-inflation process is energetically costly due to compensatory swimming. Depth fluctuations may represent a compromise between a cod's desire to maintain demersal behavior at the maximum depth of their oscillations, and conserve energy at a shallower, neutrally buoyant depth, corresponding to the peaks of their oscillations. As the swimbladder re-inflates over the recovery phase, the neutrally buoyant depth increases. As a result, mean daily depth progressively increases during equilibration and oscillation peaks follow a gradual, linear descent dictated by secretion rate that ends when neutral buoyancy is achieved at the target depth (Nichol et al. 2006).

Similar patterns have been shown to occur long after release and recovery when a cod makes a significant shift to greater depth, suggesting this is a natural behavior not caused by capture stress or injury (van der Kooij et al. 2007). Mid-record oscillations were indeed spotted in this study's DST records during some offshore descents, but never in such regular and linear fashion as the recovery phase.

A distinctive feature of the recovery phase equilibration behavior was a clear diel pattern to most oscillations, which previous studies have not reported. During the recovery phase, cod were usually observed to make ascents at night during their recovery phase, and return to the seafloor by day. On the other hand, the mid-record equilibrations in DST records did not always conform to a diel rhythm. Sunlight may play a pivotal role in shaping this behavior. Ipswich Bay is a relatively shallow site, and cod's equilibration ascents brought most of them closer to the surface (sometimes <10 m) than any other point in their DST records. These cod may have shunned intense light during the day, and light avoidance may thus be partially responsible for the regimented oscillatory patterns during the recovery phase.

2. Vertical activity during the spawning phase

Reports of vertical activity on spawning grounds have been inconclusive and conflicting, and activity may be influenced by location-specific features. Captive studies and trawl catch data suggest that spawning cod spend most of their time within a few meters of the seafloor, and male spawning territories are closely associated with the bottom. In captivity, individual spawning events sometimes culminated in a paired vertical ascent to the surface (Brawn 1961b), but since laboratory tanks are only a few meters deep, it is unknown what the magnitude or appearance of these ascents would be in a natural habitat. However, acoustic surveys over Newfoundland spawning grounds documented occasional spawning columns, characterized by narrow formations of pairs or small groups rising above a more widespread aggregation on the bottom (Rose 1993). These columns, which may reflect spawning ascents, extend up to 40 m above the seafloor and as shallow as 15 m below the surface at coastal sites (Lawson et al. 2000a). A more recent study at a Norwegian spawning ground, however, found wide-ranging vertical activity and strong DVM. It was hypothesized that cod preferred conditions at depth for rest and maturation during the day, and made nocturnal ascents to spawn near the surface in order to maximize egg dispersal (Michalsen et al. 2006).

As a whole, Ipswich Bay cod did not make vertical movements in the spawning phase that reached the height of ascents or columns seen at other sites. Small, brief ascents were frequent during the spawning phase, but they appeared no different from similar movement in the post-spawning phase. DSTs are not the optimal tools to identify spawning ascents of the magnitude seen in captive studies (<5 m), or to detect spawning columns. The sole exception to typical spawning phase activity was cod 086. Its dramatic ascent sequences may have constituted spawning events where eggs were released high in the water column, as Michalsen et al. (2006) proposed for one spawning component, but nothing comparable was observed in other Ipswich Bay cod. This female's greater size (and presumably age) may be related to its unique behavior.

Most cod in Ipswich Bay displayed reduced vertical activity, which has also been seen in cod on Icelandic and some Norwegian spawning grounds (Thorsteinsson et al. 1998; Stensholt 2001). Spawning activity is distinguished not by conspicuous patterns or singular events, but by a consistent depth range and controlled movement. Ipswich Bay cod were in a constant state of motion and rarely adopted a completely sedentary mode, yet maintained a narrow depth range of ~ 10 m and remained largely within several meters of the seafloor. The consistency of day-to-day behavior, the small yet active vertical range, and the similarity between individuals were not seen again after the spawning phase.

Observations in captivity help to explain these patterns – male cod may maintain minimal vertical movement close to the bottom in order to defend benthic territories and attract females, and females may show similar movement as they inspect these territories and interact with males (Brawn 1961b; Hutchings et al. 1999). Moreover, survey data show cod are densely concentrated during May and June in Ipswich Bay (Hoffman et al. 2006; Howell et al. 2008), which is similar to other spawning grounds (Rose 1993; Ouellet et al. 1997; Lawson et al. 2000a). It is possible that this mode of reduced vertical activity reflects not just spawning behavior, but aggregation behavior, and cod control their vertical movement to maintain cohesive shoaling structure in a crowded area. Higher vertical activity in the post-spawning phase may be permitted by more diffuse, mobile aggregations or a lack of aggregations altogether.

I found little evidence to suggest a 24-hour cycle to spawning for Ipswich Bay cod. Cod in Ipswich Bay showed only weak or moderate diel rhythms, probably due in part to their narrow vertical range. Cod were slightly more shallow at night overall, but DVM was inconsistent, and non-spawning cod are also known to inhabit shallower depths at night in captivity (Claireaux et al. 1995). Cod have been found to spawn at all hours of the day in captivity, but it is believed the majority of spawning occurs at night (Brawn 1961b; Hutchings et al. 1999; Klein-MacPhee 2002). This claim is supported by high egg densities found in tanks at dawn coupled with comparatively few spawning events observed in daylight. Furthermore, there is increased sound production at night, which suggests either that courtships are more frequent, or male suitors utilize sound to enable females to locate them in darkness (Rowe et al. 2006). Researchers have been unable to observe spawning events at night, however, because artificial light disrupts their spawning behavior, and so their nocturnal activity during spawning remains poorly understood.

Feeding during the spawning phase

No studies have examined feeding during spawning in the Gulf of Maine and Georges Bank, and the behavior of Ipswich Bay spawning cod remains a curiosity. The relationship between feeding and spawning in captivity has received limited attention. At least one study observed cod to eat readily while spawning (Brawn 1961b), but it is most often reported that feeding is greatly reduced or nonexistent during spawning periods (Chambers et al. 1996). Fordham & Trippel (1999) found that in experimental conditions, both sexes fasted through most of the pre-spawning and spawning periods. They displayed an intensive resumption in feeding, however, towards the close of the spawning period, but before they ceased spawning altogether. In Ipswich Bay, small vertical range, weak diel rhythms, and demersal depth suggest that during the spawning phase, cod were not actively pursuing prey with pronounced DVM patterns or pelagic activity, such as herring or shrimp. Their behavior indicates benthic feeding or fasting. Anecdotal evidence indicates otherwise – herring were historically abundant in the area during the winter spawning period (Ames 2004), and cod caught during pre-spawning and spawning times in the spring often contain recently consumed shrimp or herring (pers. obs., D. Goethel & C. Bouchard, pers. comm.). Ipswich Bay also supports a thriving recreational hook and line fishery for adult cod during the spring spawning season, implying they readily consume bait.

Nonetheless, these reports do not necessarily contradict the standard assumption that cod rarely feed while spawning. Cod may not invest energy in foraging during their spawning period but still accept bait placed before them. In addition, other studies demonstrate individual variation in spawning timing and duration, rapid turnover at a spawning ground, resumption of feeding prior to the completion of spawning, and the presence of immature fish in spawning aggregations (Kjesbu 1994; Fordham et al. 1999; Robichaud et al. 2002b; Windle et al. 2005). Given these factors, there could be many cod ready to eat at any given time within a spawning aggregation, even if each individual fasts through most of its spawning period.

3. Spawning time and residence period

The scarcity of cod in the Ipswich Bay spawning ground on the first day of tagging (April 21) and abundance in subsequent weeks supports previous evidence that cod arrive on Ipswich Bay in late April and early May (Howell et al. 2008). Fifteen recaptured cod were tagged on the western edge of Scantum Basin in late April. Almost all of these (>90%) moved into depths shallower than their capture site in May and entered a spawning phase, and 50% were actually recaptured on the Ipswich Bay spawning ground, 7-11 km northwest of their release, during May and June. These recaptures strongly suggest that many spawning cod initially assemble in Scantum Basin or traverse it to reach the inshore spawning ground. Timing of migration may vary according to sex, and there is evidence that male cod undertake spawning migrations prior to females (Morgan et al. 1996; Lawson et al. 2000a). All catches in April were skewed towards males (3:2 ratio), and it is possible males are abundant in Ipswich Bay before females.

Catch data in Ipswich Bay suggest when cod began to arrive, and offshore descents in DST records roughly approximate when most individuals left. DST-tagged cod resided on the spawning ground for at least three weeks, and some may have been present for two months or more. Although the specific duration of an individual's spawning period cannot be identified from tag data, females often spawn from 3 – 6 weeks in captivity (Kjesbu 1989; Chambers et al. 1996; Kjesbu et al. 1996; Rowe et al. 2006) High individual variation in spawning time, combined with batch release behavior, results in a protracted spawning season for cod aggregations that can last up to several months (Chambers et al. 1996). Robichaud & Rose (2002) estimated that although cod abundance on a spawning ground remained constant over a two month period in Newfoundland, <10% of the fish surveyed early in the spawning period were present a month later. This suggests a high turnover rate on spawning grounds. It also implies that individual spawning period may be far briefer than the spawning season of the aggregation, and that spawning activity is staggered. An extended spawning season can be an adaptive phenomenon that increases larval retention to a local population, by minimizing the impact of brief weather events on overall dispersal (Byers et al. 2006).

Reproductive condition of recaptures is known only for the four cod recaptured by the Massachusetts Division of Marine Fisheries' Industry-Based Survey on the spawning ground on May 19. Two were found to be spent and two were still in pre-spawning condition. Just as offshore descents were spread through May and June, individual spawning activity is also likely staggered in Ipswich Bay. Furthermore, the window of time to arrive on the spawning ground is unclear. Cod may continue to appear throughout the spawning season as others depart, in which case I may have tagged only an initial wave of spawners.

The timing of offshore descents in depth profiles support previous evidence that cod leave the spawning ground beginning in late May and continuing through June. Nevertheless, the intensive fishing effort in this area when the rolling closure is lifted each year demonstrates fish remain abundant in July. Moreover, some acoustically tagged cod were still present when tracking ended on June 30, and I observed distinct shoals of fish believed to be cod during multibeam acoustic surveys of the spawning ground in late June 2008. Not all migrations involve mass aggregations; in some cod populations, the variation in migration start date among individuals suggests solitary or small group movements (Comeau et al. 2002b). Post-spawning migrations from Ipswich Bay may therefore be spread out over several months and continue gradually throughout summer.

In this and other cod spawning studies, it is assumed that the timing of spawning ground departure is closely related to individual spawning timing and duration. However, cod may reside for variable lengths of time on the spawning ground after their spawning period is over, and other cues may initiate their departure. The initiation of seasonal migration is thought to be linked to temperature change, photoperiod, prey availability and lipid reserves, and cues from older individuals (Comeau et al. 2002a). Shoaling cod may wait for the onset of favorable currents before initiating directed movement (Wroblewski et al. 2000). Temperature is one possible stimulus in Ipswich Bay: ambient water temperature measurements on the coast show a spike over 1 degree in early June, just preceding the majority of offshore descents (Fig. 12, GoMOOS Western Maine Shelf Buoy B). Although it may act as a signal, it is doubtful that warming temperatures made the spawning ground inhospitable, as several traveled south to sites in Massachusetts Bay that were shallower and warmer by several degrees (Table 6).

The majority of recaptures were in the 65 – 85 cm range, and many of the larger individuals were caught in Ipswich Bay soon after release. I found no relationship between size and spawning phase duration, but a larger sample size with more complete size and sex distribution might shed light on the mechanisms for variation in spawning period and residence time. Older and larger females spawn longer than younger fish, as might be expected from their higher fecundities coupled with longer intervals between spawning events (Hutchings et al. 1993; Kjesbu et al. 1996; Lawson et al. 2000a). Male spawning duration also increases with age (Hutchings et al. 1993).

Hutchings and Myers (1993) proposed that the association between age and spawning time may produce size-specific spawning patterns that match individuals of comparable age and fecundity throughout the spawning season. There have been conflicting reports, however, as to whether older or younger cod spawn first, and patterns may vary by population (Kjesbu 1994; Chambers et al. 1996; Ouellet et al. 1997; Lawson et al. 2000a). Spatial segregation by size and possibly age also exist on spawning grounds (Marteinsdottir et al. 2000), but was not apparent from my catch data. If size- and age-specific temporal segregations exist in Ipswich Bay, then tagging in late May or early June might yield a different sample composition from what I found in April and early May.

DST profiles reveal that three cod moved offshore within a week of tagging into Scantum or Jeffreys Basin, only to return west into Ipswich Bay days or weeks later where they were recaptured (cod 074, 976, & 241). The depth profile of cod 241 suggests it may have left and returned twice before recapture. All three cod were females. Their behavior may be explained by reports that female cod are more mobile than males; they make inshore forays to spawn in male territories, but return to the deeper end of the spawning ground between batch releases or when they are spent (Morgan et al. 1996; Robichaud et al. 2003; Windle et al. 2007). If this scenario exists in Ipswich Bay, and some females spend portions of the spawning season in deeper waters such as Scantum Basin, then our definition of the spawning ground should be expanded to encompass the total area utilized.

4. Post-spawning migration and homing

Recapture distances support previous findings that the Gulf of Maine cod stock are largely resident and make short seasonal migrations, and that cod spawning from Maine to Massachusetts Bay remain predominantly inshore and move along the New England coastal shelf (Ames 2004; Howell et al. 2008; Tallack 2008). Although there is often significant variation in the extent of individual migrations, and reports that older, larger cod travel farther than smaller individuals (Templeman 1974; Lawson et al. 2000b), I found no trends in migration distance or direction according to size or sex in this study.

The clustering of recapture locations in Ipswich Bay, Bigelow Bight/coastal Maine, Jeffreys Ledge, and Stellwagen Bank is biased by the geographic distribution of commercial fishing effort. However, much of the Gulf of Maine is open to commercial activity in late summer and fall, and fishing activity is often a strong indicator of where the cod are most abundant during this period. These recapture areas may support recent findings, based on genetic data, that spring spawning cod from Ipswich Bay, coastal Maine, and Massachusetts Bay constitute a genetically homogeneous complex, which infers at least a small degree of mixing between areas (Breton 2008). I found that Ipswich Bay spawners move to other areas of this genetic complex in summer and fall and it is plausible that some Ipswich Bay cod might remain in these areas into spring, and spawn with local components instead of making return migrations to Ipswich Bay.

The Western Gulf of Maine Closure Area (WGMCA), which is closed to commercial fishing year-round and encompasses much of Jeffreys Ledge to the east of the study site (Fig. 1a), was an obstacle to complete migration analysis. Because I depended on commercial fishermen to recapture DSTs, it represented a geographic void for tag returns. Previous tagging and survey trawls in the closure found little exchange of cod between the closure and the spawning ground, but results may be affected by limited fishing and survey effort in the closure (Howell et al. 2008; Tallack 2008). No tagging or surveys were conducted during winter, and so it is unknown whether pre-spawning cod aggregate or pass through the WGMCA before arriving at Area 132 (Scantum Basin) in April and continuing west to Ipswich Bay (Howell et al. 2008). During the post-spawning phase, likely migration tracks from my data indicate Bigelow Bight recaptures passed through the northern portion of the WGMCA during their migration. And since cod were recaptured along its north, east, and south borders, it is possible that other Ipswich Bay cod took up residence within it boundaries.

Although all DSTs stopped recording before the end of October 2006, recaptures show some evidence of interannual site fidelity to the spawning ground. Cod 147 & 017 were the only two recaptured during the spawning season of subsequent years (Table 2).

Depth profiles show both made clear offshore descents and left the spawning ground in the summer of 2006. Cod 147 was recaptured in May 2007, a year after tagging, while 017 was recaptured in May 2008. Both were recaptured on the Ipswich Bay spawning ground, less than 10 km from where they were tagged, demonstrating that these cod made return migrations to Ipswich Bay over multiple years, as has been documented by Howell et al. (2008) It is unknown whether cod homing to Ipswich Bay also travel to the same post-spawning destination each year, but there is evidence that homing cod are familiar with a specific migratory circuit that they follow from year to year (Robichaud et al. 2001; Windle et al. 2005).

Although migratory pathways for cod have been identified thus far on a larger spatial scale than the "resident" movements seen here, comparable processes may be at work. It is unknown whether pre-spawning cod in the Gulf of Maine follow currents or thermal gradients leading inshore, or if the spawning ground itself possesses physical properties that attract cod or facilitate navigation to it. Although DSTs document the narrow thermal range cod occupy on the spawning ground, a comprehensive data set of ambient temperature at depth (>50 m) throughout the coastal GOM is needed to identify unique properties in Ipswich Bay.

5. Vertical activity during the post-spawning phase

In addition to the mean depth shifts that occurred when cod moved offshore, two vertical activity patterns were evident after cod left Ipswich Bay that distinguished the post-spawning phase from the spawning phase. The first was the adoption of sedentary behavior at post-spawning sites, where vertical activity appeared to cease altogether. The second, more frequent pattern was increased vertical activity in the post-spawning phase, featuring strong DVMs with daily vertical ranges much greater than those of the spawning phase.

Sedentary behavior

On one hand, the majority of sedentary behavior was observed during the post-spawning phase at depths < 80 m, usually when cod migrated onto elevated banks. There appears to be a relationship between these banks and inactivity, which may reflect recuperation and rest after spawning and migration, or a local abundance of benthic prey. Similar "rest periods" at shallow sites following post-spawning migrations have been observed in other populations, and both DSTs and telemetry suggest little movement of any kind during such periods (Righton et al. 2001). Cod 981 became sedentary for three months at a constant depth of 35 m, which was far longer and shallower than any other cod (Fig. 15a). As a result it produced the smallest mean vertical range in the post-spawning phase, and experienced the highest temperatures of any fish (Tables 5 & 6). Its location is unknown during this time, but its depth suggests it may have settled on top of Stellwagen or Jeffreys Ledge. Vertical activity can be greatly reduced during known residency periods (Righton et al. 2001). In shallow North Sea waters, for example, cod spend ~55% of the year within 5 m of the bottom on average, and spend extended periods completely sedentary on the seafloor with no vertical movement (Turner et al. 2002; Hobson et al. 2007). Sedentary periods at constant depth suggest residency at specific sites and small home ranges, similar to Ipswich Bay behavior, but without the activity associated with searching for mates and engaging in spawning.

High vertical activity

Increased vertical range and frequent diel vertical migration in the post-spawning phase were likely due to the interconnected influences of migration, depth, and feeding behavior. Vertical activity frequently increases in association with migrations (Thorsteinsson et al. 1998; Hobson et al. 2007). A North Sea population exhibited its highest vertical activity of the year during migrations from a spawning ground to a summer resting area, and some populations make seasonal shifts from demersal to pelagic living for extended periods during migrations (Righton et al. 2001; Righton et al. 2002; Stensholt et al. 2002). Cod migration speed is associated with distance from the seafloor, and the most rapid horizontal migration movements coincide with the greatest ascents off the bottom. Cod are typically negatively buoyant on the seafloor, and rising to shallower depths increases buoyancy and reduces energy expenditures, while giving them better access to advancing currents (Rose et al. 1995). Some cod vertically migrate with tides to utilize tidal streams for migration, (Arnold et al. 1994; Michalsen et al. 1996; Aglen et al. 1999), but no active Ipswich Bay cod displayed semi-diel rhythms that would suggest this behavior.

In addition to high vertical ranges in the post-spawning phase, many cod showed a decrease in depth at the end of their spawning phase for several days prior to their offshore descent, and it appears to signal the start of their migrations. It may reflect cod moving over elevated bathymetric features that border the spawning ground to the north and east, but also suggests these cod may rise above the bottom when actively migrating.

Vertical activity is consistently found to increase with location depth, and is often observed when individual cod make seasonal shifts to greater depths (Stensholt 2001;

Palsson et al. 2003). Pelagic living is also more frequent over deeper areas (Stensholt et al. 2002). The relationship between depth and vertical movements is also evident when comparing separate populations occupying different depths year-round. Deep-water populations show dramatically higher vertical activity levels and movement rates (Righton et al. 2001; Heffernan et al. 2004).

Stensholt et al. (2002) attributed these trends to the effect of depth on feeding activity. In deeper water, cod may spread out over a wider depth distribution to reduce competition for food. In addition, pelagic prey species may congregate in near-surface waters, necessitating that cod in deeper areas stray farther from the seafloor to access preferred food. Physiology also plays a role. A cod's free vertical range is the space it can ascend and descend within without significant effects on swimbladder volume, and the size of the free vertical range increases with depth. Cod may therefore show greater vertical activity at depth because their swimbladder physiology permits it (Arnold et al. 1992; Palsson et al. 2003).

The characteristic spawning phase pattern (constant but reduced activity and small vertical range) was not seen during the post-spawning phase of any cod, even at comparable depths. Many cod migrated to even shallower areas and still maintained high vertical ranges. Post-spawning data support the notion that the constrained vertical activity in Ipswich Bay was not simply a function of depth, but also reflected spawning and aggregation behavior specific to the site.

High vertical ranges in the post-spawning phase may represent active foraging, that often accompanies migration (Godo et al. 2000; Palsson et al. 2003). Ascents and descents may be associated with searching for both pelagic and benthic prey (Godo et al.

2000). Cod are known to migrate with pelagic prey species in several regions, and migrating shoals of cod have been observed to temporarily disperse and pursue prey encountered en route (Rose 1993; Rose et al. 1995; Stensholt 2001).

Diel rhythms

Diel vertical migration was frequent in the post-spawning phase. This behavior may confer several benefits to cod, but because it is usually most prevalent during known feeding periods (Neilson et al. 1990; Neat et al. 2006; Strand et al. 2007), it is attributed to improved foraging. Many of cod's dominant prey species, including capelin, herring, shrimp, krill, and amphipods, exhibit seasonal DVM and ascend to shallower depths at night. The seasonal timing of cod DVM corresponds to DVM timing in cod's preferred prey species, and to the time of year when cod populations spatially overlap with those same species (Stensholt 2001; Stensholt et al. 2002). Godo & Michalsen (2000) reported intermittent DVM, and suggested that when pursuing large, energy-rich prey such as capelin, cod may only adopt DVM patterns long enough to acquire a meal, then cease foraging during digestion periods lasting several days.

Other instincts may drive DVM besides foraging. Clark & Green (1990; Clark et al. 1991) proposed an additional energetic basis for DVM when cod are active in thermally stratified waters. If cod move up into the warm waters above a thermocline to feed, their return to deeper, cooler waters during non-feeding times may conserve energy and optimize growth. In another Newfoundland location, juvenile cod seasonally switch DVM from nocturnal to diurnal activity, possibly reflecting changes in predator threats or prey availability (Clark et al. 1990).

6. Site-specific activity patterns

Just as cod shared a general behavioral pattern while in Ipswich Bay, cod recaptured in the same geographic area in the post-spawning phase exhibited strikingly similar vertical patterns that were specific to that area. Cod from the same population may show different vertical patterns when they are separated by only a few kilometers, but when present at the same fine-scale site, such as a specific bathymetric feature they may display nearly identical behavior (Thorsteinsson 1995; Neat et al. 2006). Similarities in the behavior at the same site often vanish when cod disperse (Palsson et al. 2003). This suggests the influence that fine-scale habitat features such as bathymetry and thermal regimes may have on vertical activity (Thorsteinsson 1995; Neat et al. 2006).

Recaptures illustrate that cod dispersed in every direction from Ipswich Bay, but were found in one of three general areas outside of the spawning ground (excluding a single recapture east of Cape Cod). For those cod caught before their DSTs stopped recording (n=21), knowledge of their release and recapture locations and their intervening depth ranges allowed me to make informed hypotheses about where they traveled before recapture.

Bigelow Bight recaptures (offshore Maine)

Four cod recovered from the offshore Bigelow Bight area in the summer of 2006 all showed similar highly active vertical patterns after their deep-water descent, characterized by cyclical, wide-ranging movement in water between 100 – 180 m deep (Cod 010, 014, 140, & 006). This behavior is shown in Fig. 17a. All maintained mean depths > 120 m and had daily vertical ranges > 40 m until recapture (e.g. cod 006 in Fig.

9). Mean temperatures for each fish were within 0.2°C of one another for all months, and all exhibited obvious diel vertical migration patterns, usually associated with strong ACF signals. These cod maintained high activity and displayed little sedentary behavior, suggesting they remained some distance from the seafloor. Two recaptures (cod 006 & 014) adopted deep sedentary modes at the end of their DST records, but were caught within days of settling on the bottom.

I believe these diel patterns occurring in conjunction with high vertical range reflect feeding behavior, especially given that cod intensively resume feeding when spawning ends (Fordham et al. 1999). Cod in this area may have adopted foraging modes for active, pelagic prey such as herring, mackerel or squid that also display DVM. High activity also suggests horizontal movement, and cod were likely migrating north during these active periods or patrolling large areas in Bigelow Bight and Jeffreys Basin.

The occupied depth ranges closely match the uneven bottom terrain of Jeffreys Basin and the area northwest of Platts Bank where they were caught. Jeffreys Ledge, which bounds Scantum and Jeffreys Basin to the east, reaches an elevation throughout its length comparable to the highest bathymetric features that fish aggregated around on the spawning ground (40 – 50 m). It appears that none of these northern recaptures ever moved shallow enough to have crossed Jeffreys Ledge, and therefore the most likely northerly migration pathway was through Jeffreys Basin (Fig. 18a).

Stellwagen Bank recaptures

The four cod recaptured near Stellwagen Bank in 2006 show strong similarities in depths and vertical activity patterns (cod 033, 060, 061, & 207). Although one (061)

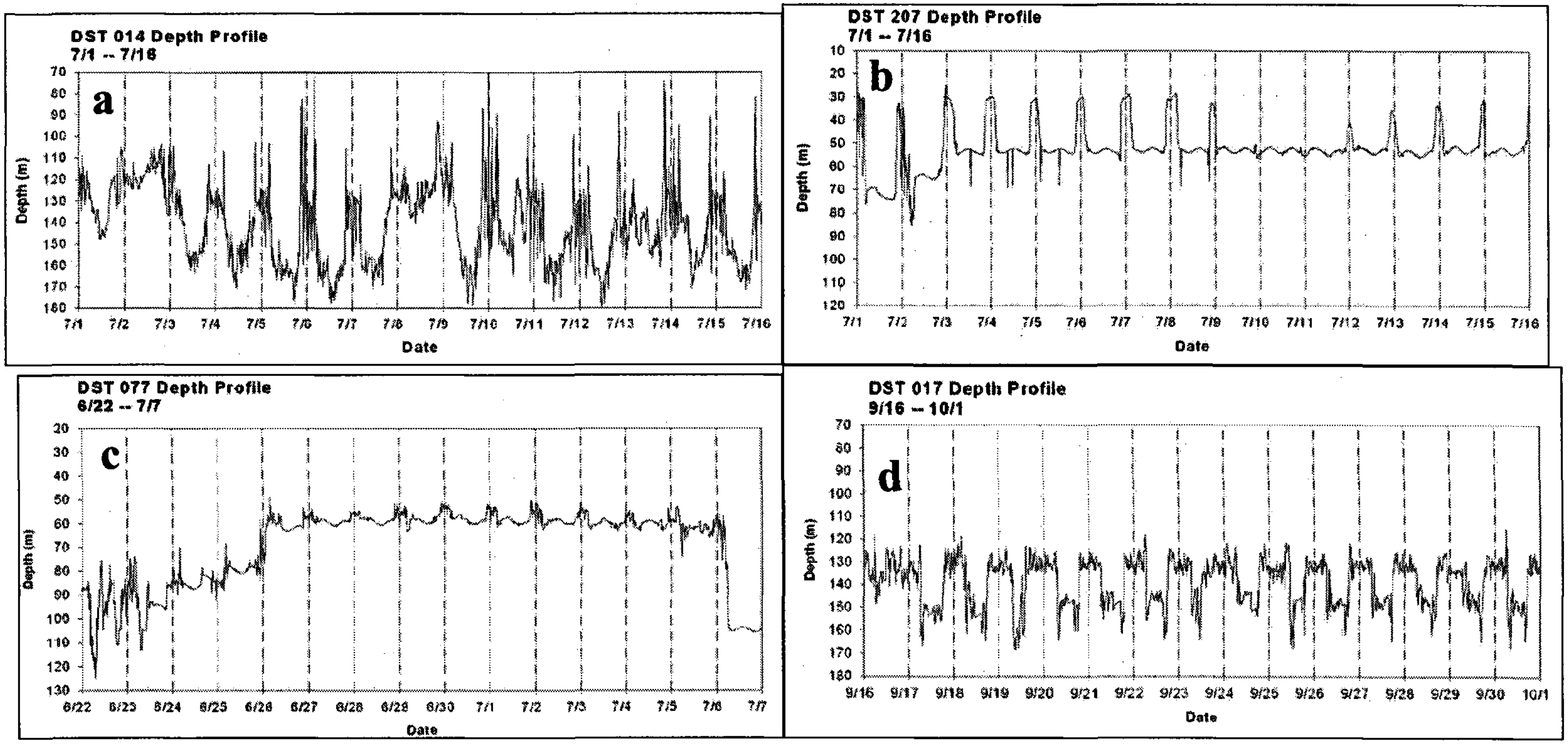

Fig. 17. Characteristic vertical activity at different recapture areas. Note the different depth ranges. Gridlines indicate 12 a.m. on successive days. a) Bigelow Bight: constant high activity, DVM until recapture. b). Stellwagen Bank: sedentary by day on shallow slope; ascents at night. c). Jeffreys Ledge: became sedentary on shallow site before moving down slope where recaptured. d). One of several later recaptures with unknown whereabouts, but deep activity and DVM suggest Bigelow Bight or Jeffreys Basin.

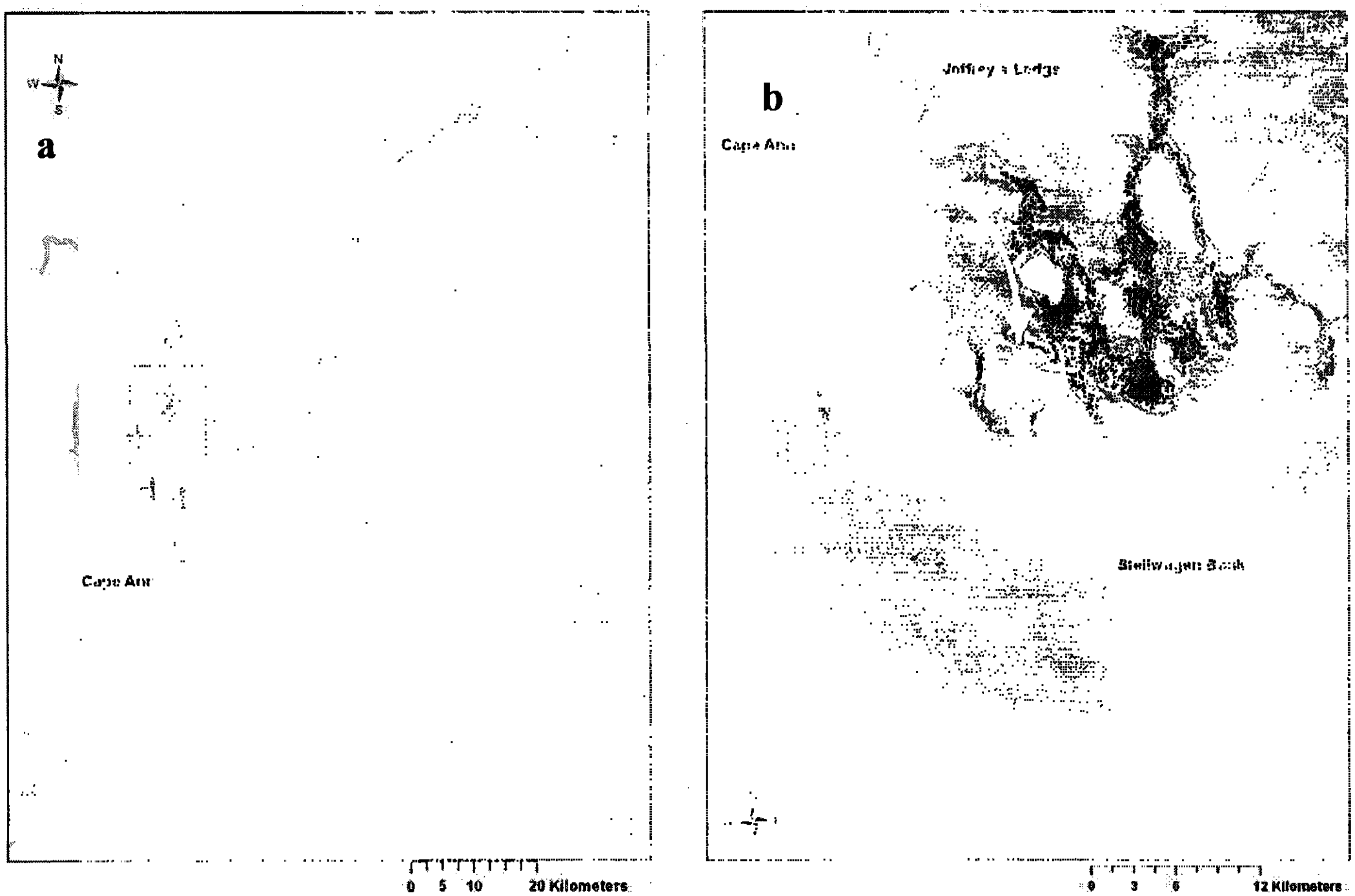

Fig. 18. a). DST recapture locations (+) with potential migration pathways based on depth profiles. Study area is indicated by red square. Ipswich recaptures are shown in red, Jeffreys Ledge recaptures in yellow, Bigelow Bight in blue, and Stellwagen Bank in green. b). Close-up of Stellwagen recaptures on a multibeam bathymetry map. Trenches running between Jeffreys Ledge and Stellwagen Bank are shown in black.

never displayed a deep-water shift, the others exhibited increased vertical ranges and regular forays to >130 m in June and early July. Eventually, however, all ascended to shallower depths and adopted a distinctive diel rhythm in those months (Fig. 8b). Each fish became sedentary at a fixed depth of 50 – 60 m during daylight hours, and displayed almost no vertical movement during this period. At night, these fish made smooth ascents or descents up to 35 m above or below their daytime resting depth before returning to their sedentary depth before dawn (Fig. 17b). Given their recapture locations and daytime depth, it appears all settled on the northern slope of Stellwagen Bank by day, and likely made nightly excursions to the top of the bank or further down the slope to deeper waters.

North Sea cod were observed to make nocturnal foraging excursions from the seafloor each night (Turner et al. 2002). In this study, nocturnal activity varied between ascents, descents, combined ascents and descents within each night, and completely sedentary periods. Because nocturnal activity varied in form, some exhibited strong DVM in their ACF plots while others produced weak diel signals despite clear rhythms of activity/inactivity (Fig. 15b). No clear trends were apparent from Tables 4-6, although all Stellwagen recaptures maintained shallower mean depths and smaller vertical ranges (< 100 m and < 40 m, respectively) than Maine recaptures.

I believe that the observed diurnal or 24h sedentary behaviors indicate inactive rest periods, while nocturnal activity reflects site-specific and prey-specific foraging behavior that was considerably different from deep-water cod to the north. Cod in this shallow, and therefore more brightly illuminated area, may have waited until dark to search for benthic invertebrates, sand lance and/or other demersal fish occurring on the slope of Stellwagen Bank.

Prior to their distinctive diel patterns on the Stellwagen slope, it does not appear that these cod were ever shallow enough to have crossed over Jeffreys Ledge. Therefore, a narrow channel (< 5 km wide) between Cape Ann the southern edge of Jeffreys Ledge is the most direct and logical avenue for migration between Ipswich Bay and Stellwagen (Fig. 18a). Just south of Jeffreys Ledge are a series of narrow basins as deep as 180 m interspersed with small banks that stretch to Stellwagen Bank (Fig. 18b). This is the only area deeper than 90 m between Scantum and Stellwagen, and it appears three out of four cod made repeated forays into these trenches before adopting their shallow diel pattern.

There is evidence that post-spawning migrations to Stellwagen Bank may be influenced by environmental cues. Both the Western Maine Coastal Current and Gulf of Maine Coastal Plume travel southward along the Gulf of Maine coastline (Lynch et al. 1997; Keafer et al. 2005; Huret et al. 2007). Their paths correspond to the probable movement track of Stellwagen recaptures from Ipswich Bay into Massachusetts Bay. Furthermore, deep trenches frame a direct course from Cape Ann and Jeffreys Ledge to northern Stellwagen Bank where cod were caught, and their apparent movements in and out of these trenches suggest they may utilize these channels as guides to reach the slope of Stellwagen.

Jeffreys Ledge and other recaptures

The three fish recaptured due east of Ipswich Bay on the western side of Jeffreys Ledge show a mixture of Bigelow Bight and Stellwagen Bank behavioral patterns that correspond to their variable recapture depths (cod 004, 077 & 228). Two showed shallow sedentary behavior at 60 m, with minor nocturnal activity and forays to deeper water < 100 m, suggesting concentrated movement on the slope of Jeffreys Ledge (Fig. 17c). They may have traveled close to elevated features surrounding Scantum Basin when they left Ipswich Bay (Fig. 18a). The third (cod 228) behaved similarly to northern recaptures by staying between 90 – 150 m and maintaining a high vertical range, but was recaptured in Jeffreys Basin (Fig. 8a). It was at liberty two months after all Bigelow Bight recaptures, and may have roamed up and down Jeffreys Basin until it became sedentary and was caught a few days later.

Four of the analyzed DSTs were from cod that remained at liberty after their DST memory reached capacity (usually in October 2006), and were recaptured between March 2007 and May 2008. I can only speculate where these fish were located for the bulk of their data record. One (cod 147) showed a strong diel pattern of shallow and sedentary by day and active at night for several months, similar to Stellwagen and Jeffreys Ledge recaptures. Two others (cod 020 & 017) exhibited the same continuous movement, high vertical range, DVM, and 100-180 m depth range after their offshore descent as seen in Bigelow Bight recaptures (Fig. 17d). Cod 981, which was previously discussed, was sedentary for several months, and considering its survival through this vulnerable period and unusually shallow depth, may have settled on a bank protected from fishing such as Jeffreys Ledge in the WGMCA.

Management implications

Among the cod caught while their DSTs were recording, there was a striking relationship between sedentary behavior and recapture. Out of 14 recaptures in the post-spawning phase, 10 (71%) were sedentary when caught, even when sedentary behavior did not dominate their post-spawning phases. Many were continuously active with high vertical ranges for 2 – 4 months after leaving the spawning ground, but eventually became completely sedentary on the bottom and were quickly caught within days. Moreover, many cod were recaptured during the spawning phase, and although none were completely motionless, all were close to the bottom and showing low activity when caught.

It is intuitive that cod would be more likely to be caught by a commercial fleet of bottom trawlers and gillnetters when they were resting on the seafloor. However, these capture patterns raise interesting questions about the catchability of cod when they are not sedentary, and the implications of vertical behavior for management and conservation. Vertical distribution of cod has been shown to impact the results of abundance surveys (Engas et al. 1992; Michalsen et al. 1996; Aglen et al. 1999). If individuals or entire spawning components are highly active in the water column during certain times of year, such as during migrations, then they may be seasonally less vulnerable to demersal fishing gear and possibly undetected in trawl surveys used for population assessment. Conversely, a shift to resting behavior at a fixed location would seasonally increase their risk of capture. Demersal fishing may select for more active, migratory individuals or subpopulations. Two of the four cod recovered after more than a year at large may have had a survival advantage by maintaining constant, wide-ranging activity through the end of their records. In addition, my results show site-specific activity patterns. Cod may be more vulnerable to capture at sites characterized by sedentary or near-sedentary behavior. Cod may be caught in large quantities in Ipswich Bay not only because they are densely concentrated, but also because their vertical behavior makes them more vulnerable to capture than at other times and locations.

CHAPTER V

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 I excluded all continuous transmitter data. Of the 26 cod equipped with coded transmitters, I excluded two that were potential mortalities due to lack of movement (T67 & T53). In total, I 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

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

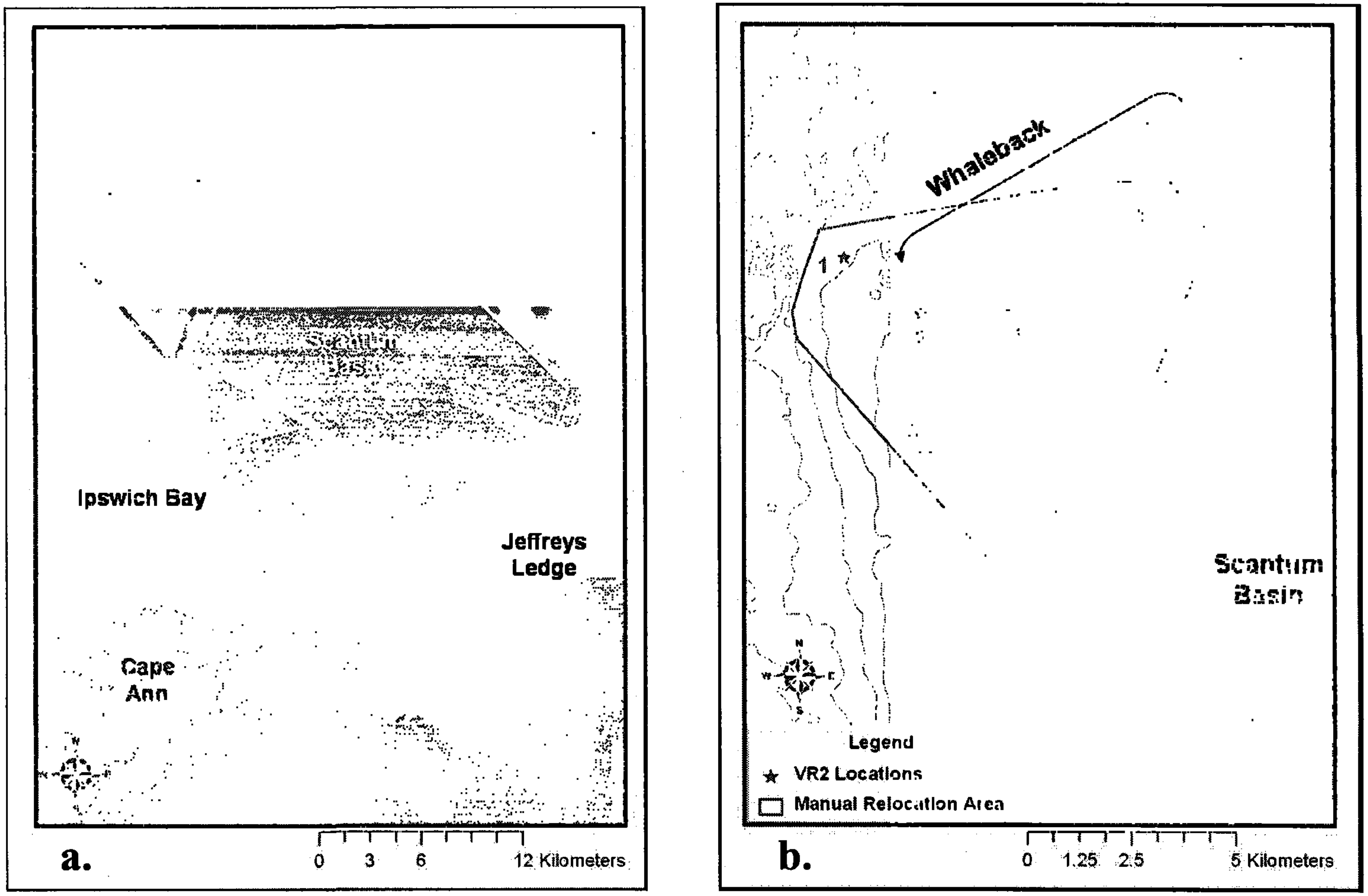

Fig. 19. a). Bathymetric map of manual tracking areas: light blue outlines the areas searched by boat, and red outlines the area in which cod were actually relocated. b). Close-up of the manual relocation area. Fish were also detected at all VR2 positions (numbered stars). Map highlights elevated bathymetric 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

for females was May 29, while males left during a narrow window of June 1 – 15 with an average departure of June 11.

1. 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.

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 and about 30 m shallower than the muddy flats south of it. Cod activity was clustered alongside its southern edge and inshore around its west end. Tracking effort using a directional hydrophone suggested fish were not directly over Whaleback but on its gradual slopes and the muddy bottom

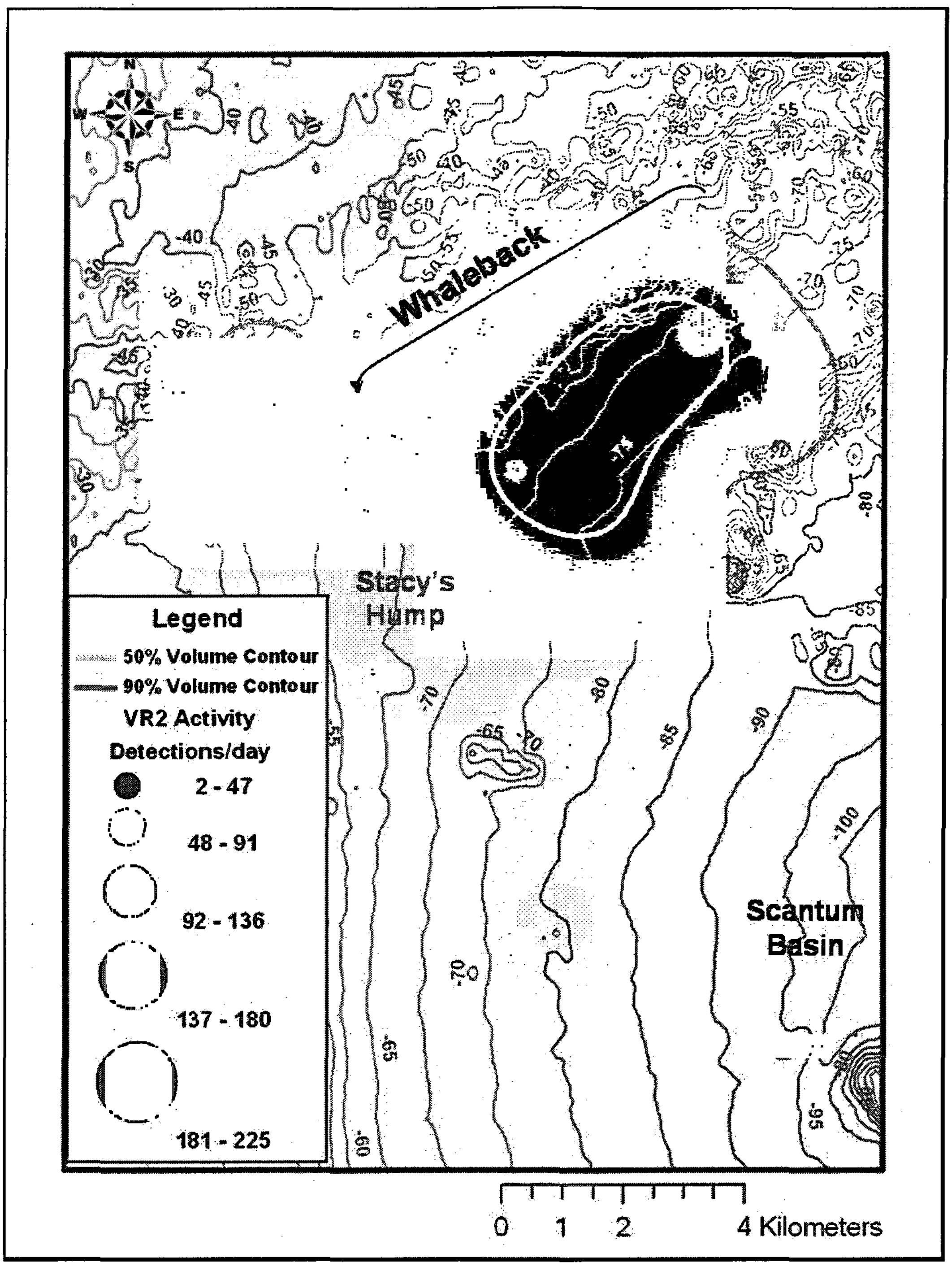

Fig. 20. Kernel Distribution Estimation (KDE) derived from pooled manual tracking data for all fish. Dark areas indicate where probable activity for the group was most concentrated, based on manual tracking. Green and yellow contours contain 90% and 50% of activity, respectively. Relative VR2 activity is illustrated by graduated circles, representing the mean number of tag detections (pings) per day at each site. Depth contours are labeled in meters.

adjacent to it. Fifty percent of the group's activity was estimated to be within a ~ 6 km² area alongside the eastern half of Whaleback, and 95% of all activity was in a ~35 km² 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 I 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 I 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 km² in size. Individual analyses further show cod predominantly along the southern margin and west

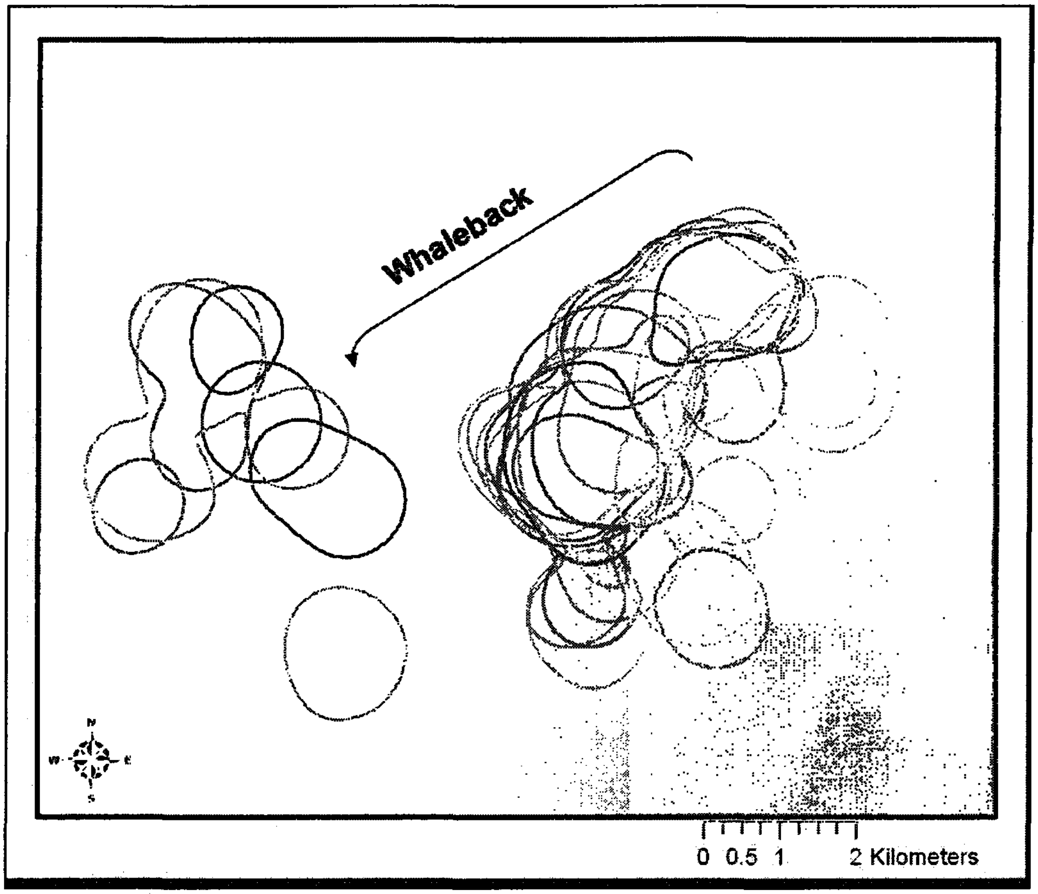

Fig. 21. Map of northern half of the study area displaying 90% volume contours from the individual kernel distribution estimations (KDEs) of 14 cod. Individual activity was distributed alongside of Whaleback, additional prominent humps, and the inshore slope and elevated bathymetry to the west.

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).

2. 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, I observed finer-scale patterns oriented around bathymetry. During late May – early June, seven cod (a third of those present) adopted temporary shuttling patterns between different pairs of

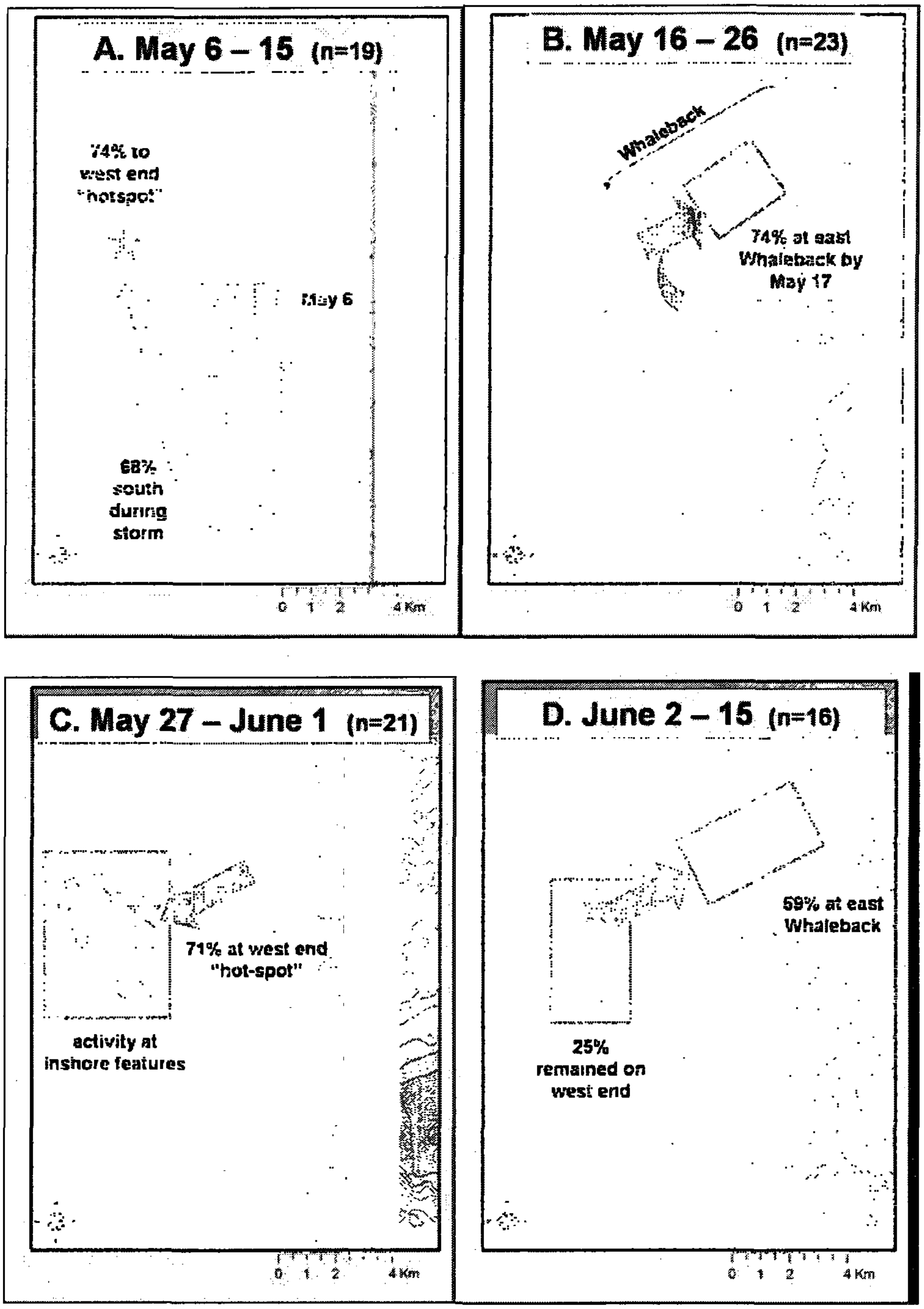

Fig. 22. Circuit of movement across the spawning ground. Percentages are of total cod present during given time period. a) After release, the majority moved south then north during storms, and appeared at the west end of Whaleback by mid-May. b) Most shifted to the east side of Whaleback by May 17th 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.

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.

3. 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, I believe it detected these cod at the location where it was found in late June, > 15 km south of Whaleback (Fig. 23).

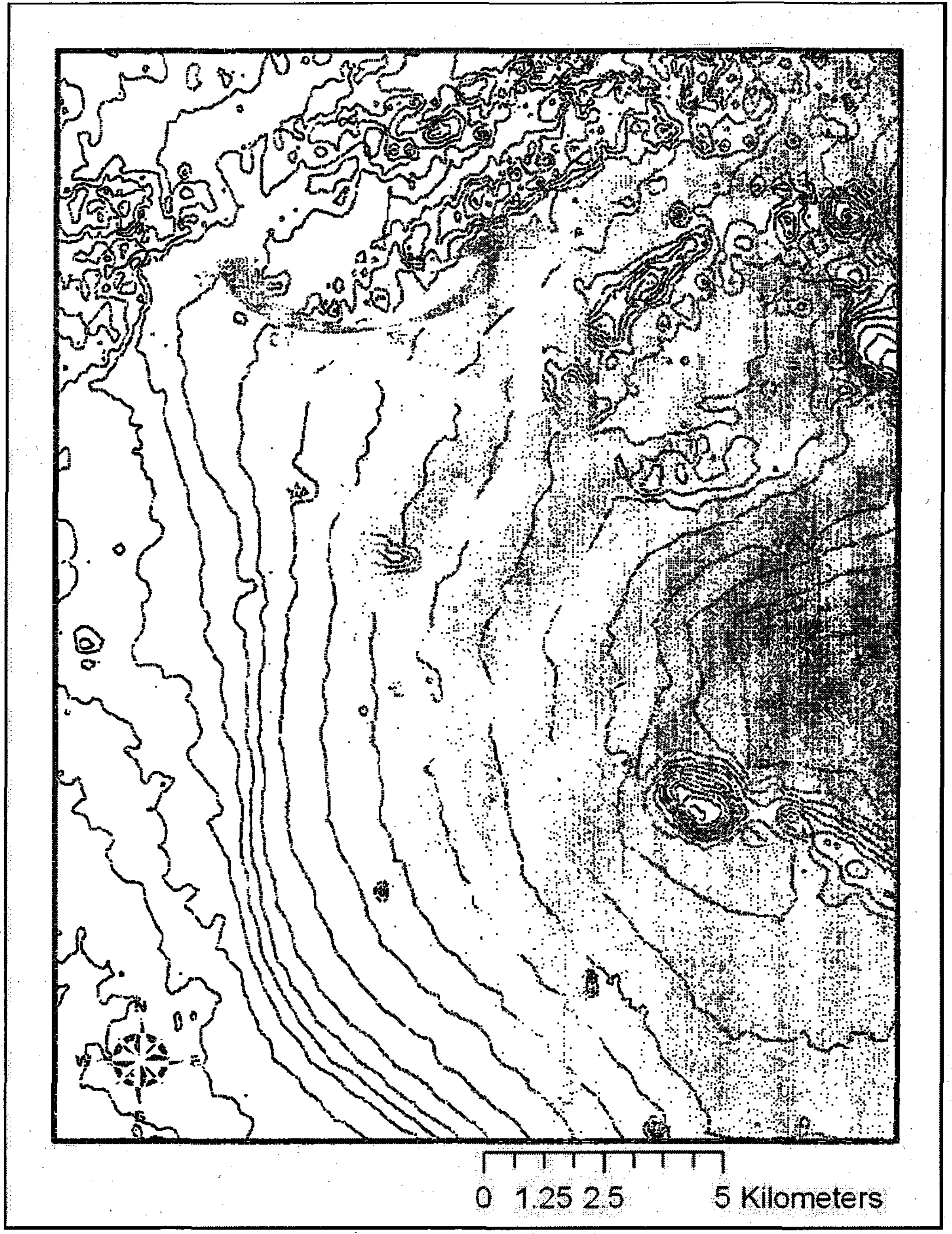

Fig. 23. Exit tracks for seven cod tracked moving past multiple VR2 receivers in < 24 h before disappearing from the spawning ground. Receiver locations are indicated by red stars. Southernmost location indicates VR2 that was dragged south and detected fish while it was missing.

4. 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 I 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. These combined data suggest 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.

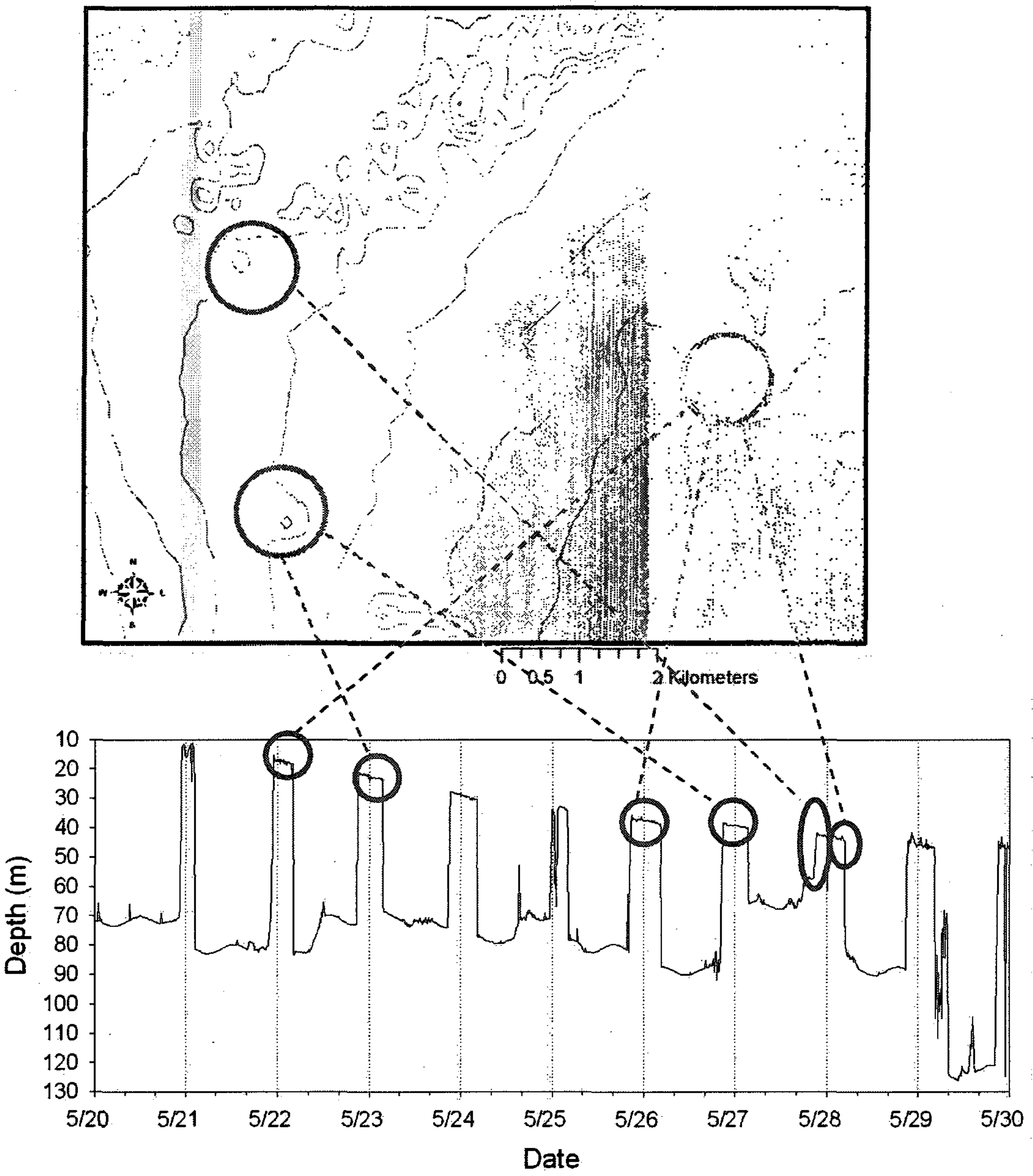

Fig. 24. Comparison of DST depth profile and tracking positions from the same fish (DST 241 & transmitter T76). During its recovery phase, this cod exhibited an equilibration pattern and made dramatic ascents each night. It was detected by VR2s stationed at various humps only during these nocturnal ascents.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

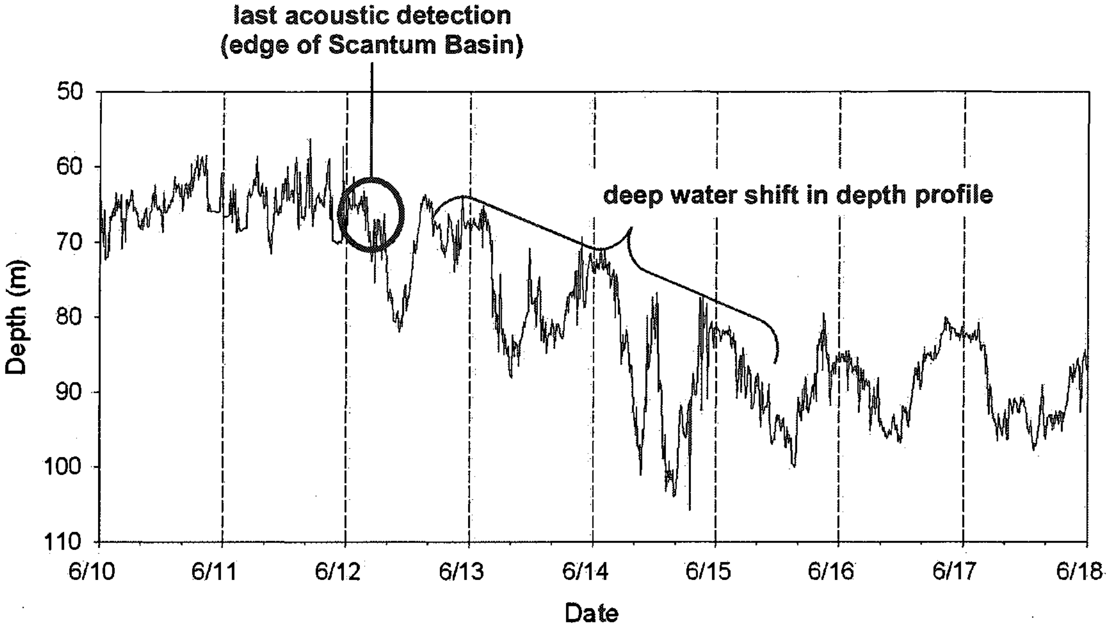

Fig. 25. Depth profile of DST 207 (transmitter T61) indicating the timing of it last acoustic detection and its shift to deep water outside of Ipswich Bay.

CHAPTER VI

ACOUSTIC TRACKING DISCUSSION

1. Limitations of telemetry equipment and project design

Tracking proved to be successful despite the size of the study area. Most fish were located on about half of the days of their estimated "residence" – the days between their release and final detection (Table 8). The VR100's directional hydrophone was useful for determining the direction of a fish's location relative to the boat, but using the tag's signal strength to follow a signal to its source, and identify a fish's precise position, was time-consuming in the large search area. The estimated ~700 m range of the VR100 (and potentially double that in ideal conditions) made it useful for determining the presence of a fish in a general area, but not for determining exact position. VR2 receivers posed similar limitations but with a narrower (~ 550 m) range.

This positional uncertainty left two questions unanswered about fine-scale behavior. First, when fish spent several days in a given area, such as the east end of Whaleback, it was often unclear whether they were stationary or active within a ~1 km^2 range. Second, I was unable to know precisely how close cod were to bathymetric features. The directional hydrophone effectively indicated cod were largely adjacent to the body of Whaleback rather than above it, but in the case of smaller, isolated humps, telemetry did not reveal whether cod were above these features, flush against them, or simply within a few hundred meters. Echosounders on the fishing vessels used in this study clearly indicated fish were aggregated both above and around small humps like Stacy's (VR2 #2). DST data indicated that cod occupied a relatively uniform depth on the spawning ground, but many elevated features were small enough that fish could have moved on and off of them and remained within their typical 10 – 20 m vertical range.

Manual tracking and stationary receivers indicated slightly different locations of cod activity concentration (Fig. 20). Nevertheless, both data sources complemented one another, and VR2 receiver data often filled in gaps between manual tracking days. Together, both tracking methods provided a more complete picture of cod distribution. VR2 receivers were effective in tracking cod movement to the south, out of Ipswich Bay, because several receivers were deployed south of aggregation focal points. Many cod were tracked moving east on Whaleback before disappearing, however, and given the breadth of DST recapture locations (Fig. 5), I believe VR2s deployed east of Whaleback would have detected post-spawning departures through Scantum Basin, Jeffreys Ledge and Jeffreys Basin as well.

2. Timing of movements

It is interesting to note that the two convergences of fish around the aggregation 'hot-spot', Stacy's hump, occurred around the full moon (May 13) and for a longer period beginning around the new moon (May 27) (Fig. 22). However, since spawning events were not visually observed in Ipswich Bay (and vertical activity was relatively uniform), I could not determine when spawning events occurred or peaked during the cod's residence. There is no evidence from cod held in captivity to suggest a lunar periodicity to their spawning. However, numerous reef species' spawning aggregations are timed with the lunar cycle, and spawning usually occurs around the full moon and/or new moon in such aggregations (Domeier et al. 1997; Claydon 2005; Heyman et al. 2008). These lunar phases are hypothesized to act as cues to synchronize spawning activity (Domeier et al. 1997; Claydon 2005), and the same may be true of cod.

The departure window estimated from tracked fish (May 14 – June 15; average June 4) corresponded to that of DST-tagged fish (May 22 – June 18; average June 8). For each of the three cod that yielded data from both tags, the difference between last acoustic detection and a shift to deep water (from DST data) was 24 to 48 hours. These similarities suggest both estimation methods were relatively accurate indicators of a cod's departure from Ipswich Bay.

The three cod remaining at the end of the study (and presumed alive) settled around different humps in early June and remained there, and their activity level was difficult to discern. Cod have been found to remain inside bays through fall and winter while other members of the same aggregation seasonally move offshore (Wroblewski et al. 1994), and previous telemetry work found cod to become seasonally sedentary and remain within 1 km² areas for months (Green et al. 2000; Righton et al. 2001). DST records from this study also demonstrated that several cod became sedentary at fixed locations for weeks or months in the post-spawning phase. Cod such as these three may adopt post-spawning, sedentary behavior without leaving Ipswich Bay, and become available to the commercial fleet in July. An alternative explanation is that the fish carrying the tags had died. If true, then all cod left the spawning ground before July.

Catch data from this study and Howell et al. (2008) both suggest spawning cod begin to assemble in abundance within Ipswich Bay in late April, and both DST and acoustic tracking data show that the majority of cod departed by late June. Although there is undoubtedly some measure of interannual variability in arrival and departure times, these findings indicate the current timing of rolling closures in this area from April 1 – July 1 is appropriate for protecting spring spawning aggregations from commercial fishing.

3. Lekking and individual spawning behavior

It has been suggested, based on spawning behavior in captivity and skewed sex ratios on spawning grounds, that male cod establish spawning territories (Brawn 1961b; Hutchings et al. 1999; Windle et al. 2007). However, like previous acoustic telemetry efforts (Robichaud et al. 2003; Windle et al. 2007), this study's tracking data failed to provide evidence of male-dominated areas or sexual segregation. There was no inshore concentration of males, and both sexes assembled at the same bathymetric features. Males and females also followed the same circuits, although males remained longer on the spawning grounds. A study in Newfoundland also found that males remained longer on that spawning ground (Lawson et al. 2000a), and longer residence may be due to reportedly longer spawning periods than females (Hutchings et al. 1993).

Robichaud & Rose (2003) reported that males were easier to track than females, and suggested it might be due to their affiliation with spawning territories, compared to females that moved freely among them. In Ipswich Bay, males were relocated slightly more frequently, and were found on 2/3 of their estimated "residence" days, compared to females that were found on half of those days (Table 8). Despite occupying home ranges only a few square kilometers in size, I found that all males were quite mobile. They did not reside at a site and wait for females, but rather shifted with them to different locations. Because cod have a spawning period lasting from a few weeks to two months (Hutchings et al. 1993), it is likely that Ipswich Bay males spawned at multiple sites, and it therefore seems doubtful males defended spawning territories in Ipswich Bay unless they re-established them as they relocated.

Many core characteristics of a lekking behavior have been documented in cod, including male territoriality, male-male competition, sexual dimorphism and selection, and female mate choice (Nordeide et al. 2000). Although male territorial defense is common in lekking behavior, it is not essential, so my observed movement trends are not counter to the fundamental assertions about the cod mating system. Moreover, telemetry cannot elucidate individual cod mating interactions such as courtship and competition, and further understanding of cod spawning behavior in the wild may necessitate the use of video to observe spawning behaviors. The fine-scale spawning locations identified in this study would be ideal for such research.

4. Spawning habitat

Tracking data demonstrated that spawning cod aggregate around specific raised bathymetric features including 'humps' and broad slopes in Ipswich Bay. While there may be variability in the fine-scale sites that cod select, fishermen participating in this study predicted the precise locations of aggregations, indicating cod frequently spawn around the same specific humps and slopes each year while other nearby features are ignored. Anecdotal information from commercial fishermen in New Hampshire, and fishery scientists in Massachusetts (Michael Armstrong, pers. comm.) suggest spawning site fidelity to specific features is widespread in the western Gulf of Maine, but has not been well-documented. Federal fishery management's description of cod's Essential Fish Habitat has been broad and often ambiguous thus far (Lough 2004), but fine-scale bathymetric features that attract annual spawning aggregations represent a clear and detailed example of critical habitat for cod. Further identification, conservation and monitoring of such sites are warranted, and their protection may be important to rebuilding cod stocks in US waters.

To my knowledge, an association between coastal spawning and specific bottom features has only been described in Icelandic cod that aggregate at large seamounts (Thorsteinsson 1995). However, spawning fidelity to specific bottom features has been described in detail for dozens of reef fish species that also undertake seasonal spawning migrations and form dense aggregations (Domeier et al. 1997; Sala et al. 2003; Burton et al. 2005; Heyman et al. 2008). Serranids, lutjanids, and carangids make spawning migrations to features ranging from shelf breaks and walls to reef edges and coral ridges, but all incorporate vertical relief to varying degrees (Domeier et al. 1997; Claydon 2005). Many spawning sites are alongside gentle slopes from shallow plateaus down to open areas of finer sediment (Domeier et al. 1997) comparable to Whaleback, while some aggregations show annual fidelity to small coral spurs the height of Stacy's hump (< 5m) (Heyman et al. 2008). These similarities imply fish in diverse ecosystems may share similar selection criteria for spawning locations. While reef species often have brief spawning periods lasting only a few days (Domeier et al. 1997), cod have a protracted spawning period lasting weeks or more, and their shuttling movements between specific humps and the ends of Whaleback suggest they may utilize (or at least investigate) several spawning locations during that time.

As many as 17 different reef fish species have been documented to form transient spawning aggregations at the same site < 1 km² in size (Heyman et al. 2008). Many believe sites predictably attract spawning aggregations because they possess beneficial qualities absent from other locations, yet the myriad hypotheses attempting to identify these advantages have been difficult to prove (Claydon 2005). Overall, three major rationales have been used to explain selection and fidelity to spawning grounds: 1) specific locations may enhance egg and larval survival via predation avoidance, food availability, local retention, wide dispersal, or directed transport to specific nursery areas; 2) specific locations may facilitate aggregation and the synchronization of spawning activity; and 3) spawning history, established by several generations of fish, may be the overriding factor that determines spawning location, and this may be far more significant than any qualities the site currently possesses (Claydon 2005).

Any and all of these hypotheses may explain why cod predictably spawn in Ipswich Bay, and on a smaller spatial scale, why they aggregate around specific features. Small features may be structural refuge or visual landmarks that attract the start of an aggregation, which in turn grows into its own conspicuous feature to attract fish on the spawning ground. Ipswich Bay may have additional environmental properties that distinguish it from other areas. At least one multi-species reef spawning ground was found to have significantly higher current speed and current variability than neighboring areas (Heyman et al. 2008). Ipswich Bay may have thermal gradients, currents or eddies shaped by local bathymetry that facilitate migration and synchronized spawning or optimize the survival of eggs and larvae.

Huret et al. (2007), working with a larval transport model, found that most successful cod recruits from Ipswich Bay were locally retained or transported south to Massachusetts Bay, and that transport success (i.e., larval survival) from spawning areas in the western Gulf of Maine was linked to the degree of local retention. Huret et al. (2007) also hypothesized that micro-site selection within spawning grounds could potentially enhance transport and recruitment, and concluded that fine-scale descriptions of spawning locations, spawning dates, and local bathymetry were needed to accurately calculate the retention and overall successful recruitment from each spawning ground. Much of that information for Ipswich Bay has been collected in this study, and can be applied to future modeling to identify the adaptive qualities this area possesses.

CHAPTER VII

CONCLUSION AND FUTURE DIRECTIONS

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 racking 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) which 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 interannual 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.

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.

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.

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. 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.

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APPENDIX A – ANIMAL CARE AND USE APPROVAL DOCUMENTATION

UNIVERSITY of NEW HAMPSHIRE

November 8, 2005

Howell, William
Zoology
Spaulding Life Sciences Center
Durham, NH 03824

IACUC #: 050904
Approval Date: 09/23/2005
Review Level: C
Project: Activity and Distribution of Cod in the Ipswich Bay Spawning Area

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this study. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Roger Wells at 862-2726 or Julie Simpson at 862-2003.

For the IACUC,

Jessica Bolker

Jessica Bolker, Ph.D.
Chair

cc: File

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building,
51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564