Movement and behavior of ocean sunfish, Mola mola, in the northwest Atlantic

Inga F. Potter
University of New Hampshire, Durham

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MOVEMENT AND BEHAVIOR OF OCEAN SUNFISH, *MOLA MOLA*, IN THE NORTHWEST ATLANTIC

BY

INGA F. POTTER
BS, Mary Washington College, 1997
MA, Boston University, 2000

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirement for the Degree of

Doctor of Philosophy
in
Zoology

May 2010
This dissertation has been examined and approved.

W. Hunting Howell, Ph.D., Dissertation Director,
Professor of Zoology, University of New Hampshire

Robert D. Kenney, Ph.D., Associate Marine Research Scientist and Professor, University of Rhode Island Graduate School of Oceanography

Molly Lutcavage, Ph.D., Associate Research Professor of Zoology and Director, Large Pelagics Research Center, University of New Hampshire

Tierney Thys, Ph.D., Ocean Sunfish Research and Tagging Program and Senior Research Advisor, Sea Steward Foundation

Winsor H. Watson, Ph.D., Professor of Zoology, University of New Hampshire

Date 1/26/06
DEDICATION

I am proud to dedicate this dissertation to my husband, Bancroft Potter, for his endless love, support, and sacrifice throughout this process. Without him, this certainly would not have been possible, and for that I am forever grateful. And to my children Penn, Fisher and Bancroft Potter, jr., who I hope will one day be proud of what their mother accomplished, and will grow up believing they can achieve whatever they dream of.
ACKNOWLEDGEMENTS

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ABSTRACT

MOVEMENT AND BEHAVIOR OF OCEAN SUNFISH, MOLA MOLA,

IN THE NORTHWEST ATLANTIC

By

Inga F. Potter

University of New Hampshire, May 2010

The ocean sunfish, Mola mola, has a worldwide distribution and is a common resident of the NW Atlantic Ocean. Notable for its unusual anatomy and large size, the biology of the species is largely unknown. I examined the movement and behavior of M. mola using pop-up satellite archival tags (PSAT’s). In addition, analysis of aerial survey data was conducted to determine the distribution of ocean sunfish (Family Molidae) in NW Atlantic shelf waters. Data was analyzed from twenty-five PSAT’s deployed on M. mola in the northwest Atlantic between 2005 and 2008. Tags were attached from 7-242 days. Results indicate that M. mola in the NW Atlantic leave New England waters in the late summer and early fall and move south along the continental shelf break. Fish traveled as far south as the Bahamas and the Gulf of Mexico, and were strongly influenced by their proximity to the Gulf Stream. Results suggest that M. mola in the northwest Atlantic exhibit a seasonal migration pattern south driven by decreasing temperatures and the search for patchily distributed gelatinous prey. Fish spent over 80% of time in the top 200 meters of the water column. Max depth recorded by any fish was 844 m.
Temperatures experienced by tagged fish ranged from 6 – 30°C. Vertical behavior of *M. mola* changed over temporal and seasonal scales. *M. mola* in northeast US waters in the summer months exhibited shallower swimming depths and more surface time than those that moved south in the winter and spring. This change in behavior is likely driven by temperature and thermocline depth, as fish adjusted their vertical behavior following a thermal gradient and/or searching for vertically migrating prey of the deep scattering layer (DSL). The shift in vertical behavior was especially apparent when fish entered the Gulf Stream. A diel pattern was observed in vertical behavior. Analysis of aerial survey data showed high numbers of animals in the northeast and mid-Atlantic in the summer and fall, and high numbers of animals in the southeast in the winter and spring, further demonstrating the seasonal migration of ocean sunfish along the eastern US shelf.
INTRODUCTION

The ocean sunfish, *Mola mola*, is a large, pelagic species distributed worldwide in both temperate and tropical ocean basins. A member of the family Molidae in the order Tetraodontiformes, *M. mola* is known for its unique body shape, large size (reaching 4.2 m and weighing up to 2300 kg), and atypical anatomy (Gregory and Raven 1934; Norman and Fraser 1949; Fraser-Brunner 1951; Roach 1983; Bass et al. 2005). In addition to *Mola mola*, which is the most common member of the family, there are three additional species of molid: the sharptail mola, *Masturus lanceolatus*, the rare slender mola, *Ranzania laevis*, and the southern sunfish, *Mola ramsayi*. *M. ramsayi*, first described by Giglioli (1883) is confined to the southern hemisphere and was recently resurrected based on a genetic study of the family (Bass et al. 2005). A recent study of the phylogenetic relationship of ocean sunfish (*Mola* sp.) in Japan found there to be two genetically isolated clades in Japanese waters, one group consisting of southern Pacific coast specimens, and the other containing specimens from various locations around Japan as well as individuals collected in the Atlantic Ocean (Yoshita et al. 2009).

Though not a commercially important species in most regions, ocean sunfish are a valued food fish in Asia, with the major markets in Taiwan and Japan. The value of *Mola* meat has risen in recent years as catch rates for the region are decreasing (Thys 2005). *M. mola* makes up a large portion of bycatch in Pacific, Mediterranean, and South African commercial fisheries. In the Spanish Mediterranean, it is the primary bycatch of the
bluefin tuna longline fishery (Macias and de la Serna 2002). It also makes up a significant portion of the bycatch in the Mediterranean swordfish driftnet fishery, comprising 71% of the total catch in 1992, 93% in 1993, and 90% in 1994 (Silvani et al. 1999). In the Pacific, ocean sunfish are the most common bycatch in swordfish driftnet fisheries, making up approximately 25%, the largest of any species recorded (Cartamil and Lowe 2004; Lovgren 2004). According to data from the National Marine Fisheries Service (NMFS) Southwest Region, between 1990 and 1998, *M. mola* comprised 26.1% of driftnet catch (26,503 individuals), and 42.1% of the discards (Thys 2005). In South Africa, *M. mola* is a common bycatch species in longline fisheries targeting tuna and swordfish, and was the most common bycatch species in the Cape horse mackerel mid-water trawl fishery where it comprised 51% of total bycatch between 2002 and 2005 (Peterson 2005; Peterson and McDonnell 2007). Though it is a common resident, there are no data on occurrences of ocean sunfish bycatch in the Atlantic Ocean. A recent study on sea turtle bycatch in a region of the western North Atlantic called the NED (North East Distant Area) found *Mola* species to be among the 34 taxa of fish caught by commercial longline vessels making research sets there from July to October 2002 (Watson et al. 2005).

Little is known about *Mola mola*’s basic ecology, distribution, or population dynamics, and the global status of the species is completely unknown. Sunfish were so named for the common behavior of lying on one side near the surface, appearing to “sunbathe,” often with the dorsal fin protruding from the water. Considered obligate feeders on gelationous zooplankton, they are commonly found singly and are often associated with surface swarms of salps or jellyfish on which they are believed to feed (Norman and Fraser 1949; Fraser-Brunner 1951; Klein-MacPhee 2002; Pope et al. 2010). There are very few published reports of gut contents of *Mola mola*, noting a wide range of prey items including gelatinous zooplankton, specifically scyphomedusae,
hydromedusae, salps, and ctenophores (Fraser-Bruner 1951; Desjardins 2005). Though there is a lack of information on the occurrence of these organisms in the world’s oceans, several gelatinous species have been reported to occur in large numbers in New England waters, including the salp Salpa aspera, the siphonophore Nanomia cara, ctenophores Pleurobrachia pileus, Euplokamis dunlapae, and Bolinopsis infundibulum, and the hydromedusa Aglantha digitale (Mills 1995; Madin et al. 2006). Two Submersible cruises conducted in waters of the Northwest Atlantic off Massachusetts in 1986 and 1987 revealed high numbers of gelatinous zooplankton, and a high amount of species diversity including 10 species of hydromedusae, 13 species of siphonophores, 6 species of scyphomedusae, and 9 species of ctenophores (Mills 1995). In addition to gelationous zooplankton, the same gut content studies show that inshore ocean sunfish feed on crustaceans, ophiuriods, mollusks, hydroids, corals, and algae (Fraser-Bruner 1951; Desjardins 2005).

No studies have been conducted on age, growth, or development of molids, though captive animals have been maintained for more than eight years (Nakatsubo et al. 2007). Members of the family Molidae are recognized as the most fecund vertebrates, with a single 137-cm female producing an estimated $3 \times 10^8$ eggs at one time (Schmidt 1921). A study of M. mola in Japan estimated the spawning period to last from August to October, and found asynchronous egg development among individuals, suggestive of multiple spawning episodes (Nakatsubo et al. 2007). Five spawning areas have been suggested for molids—in the central gyres of the North Atlantic, South Atlantic, North Pacific, South Pacific, and Indian Ocean basins (Bass et al. 2005). In the North Atlantic, the few M. mola larvae on record were found primarily in the northern Sargasso Sea, the western North Atlantic, and the waters near Grand Bahama Island (Schmidt 1921; Lyczkowski-Shultz 2003).
Previous Studies: Movement/Behavior

Few studies have been conducted on the distribution and movement patterns of *M. mola*. Members of the family Molidae are globally distributed, and *M. mola* is a common resident of the shelf and offshore waters of the Northwest Atlantic during the spring and summer months. The number of ocean sunfish in shelf waters from the Gulf of Maine south to Cape Hatteras, North Carolina, was estimated to reach 18,000 in the summer months (Kenney 1996). There is no evidence of its presence in Northeast US shelf waters in the winter and early spring.

There are conflicting reports about the swimming ability of ocean sunfish. The fact that molas breach, leaping out of the water by as much as two body lengths, which may be a mechanism of parasite removal (Thys 2005), suggests that they are capable of short bursts of speed. Most existing information on natural history suggests that *M. mola* moves primarily by passive transport via ocean currents (Norman and Fraser 1949; Martin and Drewry 1978; Lee 1986; Klein-MacPhee 2002) but a more recent study using acoustic telemetry reported a highly directional swimming ability not related to current direction (Cartamil and Lowe 2004). A 2008 study that examined the swimming performance, behavior, and functional morphology of three ocean sunfish (*M. mola*) found they swam at speeds of 0.4–0.7 m/s and were not “slow swimmers” as the historical literature suggested (Wantanabe and Sato 2008). The study demonstrated that *M. mola* differs from other tetraodontiform fishes in its use of symmetrical dorsal and anal fins in a lift-based mode of swimming, essentially using these fins as a pair of wings. The authors suggested that the evolution of this more efficient mechanism of locomotion combined with neutral buoyancy due to a subcutaneous layer of incompressible gelatinous tissue enables these oddly shaped fish to travel efficiently over significant horizontal and vertical distances (Wantanabe and Sato 2008). Furthermore, a study examining genetic divergence in the
ocean sunfish family found species in Molidae to be subdivided on a global scale, dismissing the
theory of passive drifting as the primary mode of transport (Bass et al. 2005). A study of *M. mola*
in the western English Channel suggested that their inshore migration coincided with the
invasion of medusae and salps (Sims and Southall 2002). Reiger (1983) proposed that ocean
sunfish moved north with the Gulf Stream in the spring to forage and tagged three individuals
but received no results. This is the first study conducted on the specific migration and
distribution of the species in the northwestern Atlantic. It has been theorized, based on
superficial evidence, that because ocean sunfish of the western North Atlantic appear so much
larger than those seen in the eastern Atlantic, they migrate around the entire North Atlantic basin
(Lord 2000, personal communication).

**Previous Studies: Tagging**

A study using acoustic tags on *M. mola* in waters off southern California (Cartamil and Lowe
2004) found they spent the majority of their time in near-surface waters (75%), making periodic
dives to between 40 and 150 meters (and as deep as 400 m), thought to be related to prey
acquisition. The study area was characterized by a shallow thermocline, which may also have
influenced vertical movement in the water column. The study found a positive relationship
between maximum dive depth and duration of post-dive period in the near-surface mixed layer,
suggesting a mechanism of behavioral thermoregulation, or re-warming of the body to aid in
digestion, increased mobility, and recovery from a variety of stresses experienced at depth
(Cartamil and Lowe 2004). This has been suggested in other studies of ocean sunfish (Thys
2003; Thys 2007) and swordfish (Carey and Robinson 1981). There is currently no physiological
evidence from ocean sunfish to support this theory. A strong diel vertical pattern was also noted,
with nocturnal vertical movements confined to the surface mixed layer and thermocline, while
Diurnal vertical movements included repeated dives below the thermocline. This diel pattern in diving behavior, observed in other large pelagic fishes (blue sharks, swordfish, tunas) (Carey 1990; Carey and Scharold 1990; Block et al. 2001; Sims et al. 2003) is likely induced by changes in light intensity, and is thought to be motivated by prey acquisition. Other factors that have been suggested as physiological influences on *Mola*'s diving behavior include the depth of the chlorophyll maximum, changes in temperature, and a decreased oxygen concentration at depth (Thys 2003; Cartamil and Lowe 2004; Fulling et al. 2007).

A 2001 study using pop-up satellite archival tags (PSATs) on *Mola mola* in southern California found that dive behavior was dependent on both location of the fish and time of year. In August when the fish were tagged, diving was characterized by shallow, surface-oriented behavior. Tagged ocean sunfish only traveled short distances, but as the fish moved south into the fall and winter months, their time at greater depths increased. As the fish returned north, they resumed a pattern of shallow-water diving. Based on this behavior, the study suggested that sunfish regularly made dives into the deep scattering layer (DSL) to forage, and returned to upper waters to thermally recharge (Thys 2003). The DSL is the most studied migrating layer of gelatinous zooplankton, containing physonectid siphonophores and myctophid fishes (Barham 1966; Graham et al. 2001). It is found at a variety of depths in different ocean basins, up to several hundred meters, and it typically undergoes a diel vertical migration. Molas tagged in southern California did not make trans-basin migrations and moved only short distances southward from the tagging location before returning.

A *Mola mola* tagged with a PSAT off Japan exhibited diving behavior similar to that of the *Mola* tagged in the eastern Pacific (Thys et al. 2007). It remained primarily between the surface and 50 m, and occupied a broad temperature range, diving repeatedly to depths as great as 600 m. A diel
pattern was also observed in its diving. Of the eight fish tagged off Japan, no basin-scale movements were observed, and horizontal movements remained within 900 km of the initial tagging location. Northward movement of *Mola* in the summer months coincided with increased sea surface temperatures and a decrease in chlorophyll levels.

A study of three small ocean sunfish (70 cm TL) tagged with PSAT’s in the northeastern Atlantic found that the fish exhibited a seasonal pattern of migration (Sims et al. 2009). The two fish tagged in February moved north and west, while the fish tagged in August moved south. One fish showed a diel pattern. Maximum depth of all fish was 472 m. Thermal tolerance of the species was suggested to be the driving factor in the movement of animals south at the end of the summer. The fish in the study remained within a temperature range of 10°-19°C (Sims et al. 2009).

In 2009, three small (60-100 cm) ocean sunfish were tagged with fast-acquisition global positioning (Fastloc GPS) tags in the eastern Atlantic Ocean off Portugal (Sims et al. 2009b). Two of the tags detached prematurely after 5 and 15 days, and one fish was tracked for 92 days. The latter moved an estimated distance of 1819 km at a mean speed of 19.8 km/day, and moved south from the tagging location into warmer waters of the Gulf of Cadiz as the winter progressed. The utilization of GPS tags revealed new insights into the fine-scale movement of *M. mola*. The tagged individual often headed into or across prevailing currents, moved through frontal areas, and transitioned between restricted, slower movements and faster, directed movements. These periods of slower movement or “stopovers” interspersed between faster movements were likened to similar behavior in basking sharks and leatherback turtles, and were suspected to represent the sunfish feeding on patchily distributed gelatinous prey (Sims et al. 2009b).
Previous Studies: Distribution

Due to the conspicuous nature of *Mola mola* when basking at the ocean’s surface, there have been several studies on distribution of *Mola* species based on aerial survey data and shipboard survey records. A recent study of this nature in the northern Gulf of Mexico (Fulling et al. 2007) found sunfish species (both *Mola mola* and *Masturus lanceolatus*) to be present in the region year round, in both shallow inshore shelf waters and deeper offshore waters. Molids were sighted with the greatest frequency in the Gulf of Mexico during the winter and spring. Sea surface temperatures where molids were sighted averaged 19.9°C (±0.45°). The study suggested that water temperature in combination with thermocline depth may be important drivers in the distribution of *Mola mola* (Fulling et al. 2007).

A study examining the distribution of *Mola mola* in the Irish and Celtic Seas (Houghton et al. 2006) found fewer than 100 molas sighted over a three-year period during the months of June–September, averaging 1 meter or smaller in size. The study simulated the likely association between sunfish and jellyfish, assuming distribution of both groups was random across the study area. They found that for all species associations of *Mola* and jellyfish, the observed co-occurrence was greater than the modeled co-occurrence, implying that neither jellyfish nor sunfish are randomly distributed, but co-occur more in the same areas than expected by chance. Molas were found in all areas where jellyfish were most abundant, and were found in greater densities than the other apex jellyfish predator, the leatherback turtle. The study suggested increased gelatinous zooplankton productivity in temperate waters makes the habitat a worthwhile part of *Mola*’s migration route (Houghton et al. 2006).

A study examining the occurrence of *Mola* in the western English Channel during the years 1995–2001 found juveniles in modest numbers in frontal waters during the months of June and
The molas were observed to be active swimmers, found at the surface near inshore fronts. They were observed in deeper waters (50-70m) during the years when the front occurred further offshore. The close association of *Mola* sightings with frontal features was presumed to be linked to foraging (Sims and Southall 2002).

**Species with Similar Biology**

The leatherback sea turtle, *Dermochelys coriacea*, is the largest of the sea turtles. Like *M. mola*, *D. coriacea* is a large pelagic species that feeds primarily on gelatinous zooplankton. Leatherbacks are endothermic, and are capable of maintaining their core body temperatures much warmer than the surrounding water mass (Frair et al. 1972; Greer 1973; Standora et al. 1984). Due to extensive research driven by the high fishery-induced mortality incurred by leatherbacks, there is information on the migration patterns and behavior of *D. coriacea* that may provide insight into possible migratory behavior of *M. mola*. Because of their specialized, low energy “jellyfish” diet, it has been suggested that leatherbacks must habitually select large and dependable supplies of prey (Lutcavage 1996). These large prey concentrations are typically found along oceanic frontal systems and within the water column along vertical gradients within fronts (Graham et al. 2001). Leatherbacks then may seek associations with oceanic fronts, filaments, and meanders found along the western wall of the Gulf Stream, or the Gulf of Mexico Loop Current, which enhance their chances of finding food (Lutcavage 1996). Both *M. mola* and leatherbacks are found frequently in the Gulf of Maine in summer months (Lazell 1980; Shoop and Kenney 1992; Kenney 1996). These waters are thought to be foraging habitats, and leatherbacks and ocean sunfish have been observed together in these areas, sometimes with concentrations of large *Cyanea* sp. (Shoop and Kenney 1992). There is a gradual decline in
leatherback sightings in the Gulf of Maine as water temperatures decrease that indicates migration to warmer waters (Shoop and Kenney 1992).

Though the existence of a narrow migration corridor has been established for this species in the Pacific, leatherbacks in the North Atlantic actively disperse over the entire basin. Ocean currents do not appear to be the driving force in broad-scale movement patterns of leatherbacks in the North Atlantic (Ferraroli et al. 2004; Hays et al. 2004). Two main migration patterns of leatherbacks tracked from nesting beaches in the Caribbean have emerged: some turtles move north towards the Gulf Stream, and others disperse east and remain in tropical waters (Ferraroli et al. 2004; Hays et al. 2004). Leatherbacks moving north swim at constant headings, moving across the entire subtropical gyre, and after crossing the Gulf Stream, turn east into the plankton-rich transition zone between the subtropical and subpolar gyres. In these areas, the distribution of leatherbacks has been correlated with oceanographic conditions along ocean fronts, suggestive of foraging along these productive areas where gelatinous zooplankton is highly concentrated (Ferraroli et al. 2004; Hays et al. 2004).

A 1996 study on the distribution of leatherbacks and sunfishes in the Northwest Atlantic based on aerial survey data showed leatherbacks and molids to have overlapping spatial occurrence patterns in the region (Kenney 1996). Numbers of molids in continental shelf waters between Cape Hatteras and the Gulf of Maine were estimated to be 18,000 in the summer months, which is a population size twenty times larger than that of leatherback turtles in the region. The study also noted the same temporal occurrence patterns between the two species with a peak in waters off the northeastern United States during late summer months. Based on these data, there is potential for competition between molids and leatherback turtles due to dietary and habitat overlap.
Diet studies on leatherbacks show that they feed primarily on scyphomedusae, hydromedusae, siphonophores, and pelagic tunicates (James and Herman 2001; Desjardins 2005). Sunfish also consume gelatinous zooplankton including scyphomedusae, hydromedusae, salps, and ctenophores, but studies also indicate that inshore they also feed on crustaceans, ophiuroids, mollusks, hydroids, corals, and algae (Desjardins 2005). Since they are dependent on similar food resources, their distributions may be driven by the abundance of prey items. The distribution of gelatinous zooplankton is known to be largely dictated by currents, wind, and reproductive biology of the species. Jellyfish are likely to aggregate at areas of physical discontinuities within the ocean including currents, water mass boundaries, thermal fronts, and upwelling zones (Graham et al. 2001). Swarms of pelagic tunicates are a common though unpredictable feature, particularly in coastal waters. Due to their periodic abundance, rapid rate of reproduction, and high protein content they are suggested to be a patchy but significant source of prey for gelatinous zooplanktivores (Madin 1974; Alldredge and Madin 1982). Both leatherbacks and Molas may use temperature gradients and oceanographic features as cues to prey availability, and may migrate to these areas to forage (Desjardins 2005).

A 2005 study examined spatial and temporal overlap of leatherback sea turtles and Mola mola in western Atlantic shelf waters based on aerial survey records and pelagic longline data from 1978 to 2002 (Desjardins 2005). The study found that leatherbacks and molids showed a similar pattern of distribution associated with season in the shelf waters off New England, and roughly the same spatial and temporal patterns for both species in this region. As other studies have indicated, sunfish were much more abundant and evenly distributed throughout the area, and present in the region from the months of February to December, with a peak in June. Aerial survey sightings from southeastern United States shelf waters indicated that both species utilized
these waters during the colder months of the year (January–March). The two species differed in spatial and temporal patterns of distribution in the Gulf of Mexico: leatherbacks were sighted year-round with a more uniform temporal distribution, while molas were sighted during the late winter/spring and again in the late summer/fall, with peak abundance in March. Molas were also sighted much closer to each other in New England shelf waters than in the Gulf of Mexico. The study concluded that both species exhibit migrations associated with season, citing the dramatic increase/decrease in animals sighted in the waters off New England as evidence of a seasonal migration into/out of the region.

A recent study comparing vertical movement in *Mola mola* and *Dermochelys coriacea* in waters off South Africa found that the four molas tagged with PSATs in the study stayed in the same general area off the southern coast for several months while the leatherbacks migrated much greater distances (Hays et al. 2009). The fish spent the majority of time in waters less than 200 m with periods of deep-water use (dives deeper than 200 m) exhibited by all individuals over varied temporal patterns. The fish exhibited active vertical movement in the water column throughout the tagging period. The authors suggested that individual sunfish respond to patchily distributed planktonic prey with differing levels of diel vertical migration, similar to the behavioral plasticity of the leatherback turtles, where individuals shift from predation on seasonally abundant surface medusa in the summer months towards vertically migrating deep-water gelatinous species in the winter months (Hays et al. 2009; Pope et al. 2010). The two leatherbacks tagged in the study spent significantly less time than the sunfish at depths deeper than 200 meters. Based on the differences in vertical behavior between the two species, the study suggested that because molas are not constrained in their foraging behavior like the air-breathing leatherbacks, they are able to exploit deeply distributed prey beyond the leatherback’s diving range (Hays et al. 2009).
Another species that shares some biological traits with *M. mola* is the basking shark, *Cetorhinus maximus*. It is a large pelagic planktivore, and like sunfish, sightings indicate they are often associated with frontal habitats (Sims and Southall 2003). Basking sharks grow slowly, reach maturity at a late age, and have a low reproductive rate. Until recently, the movement of basking sharks in the Northwest Atlantic was a mystery. A recent study reported the movements of 18 basking sharks tagged off Cape Cod, Massachusetts during the summer and fall between 2004 and 2006 (Skomal et al. 2009). Results of this study showed that sharks migrated south during the winter months out of New England waters. While some remained in shelf waters off the southeastern United States, several individuals traveled as far as the Caribbean, Sargasso Sea, Guyana, and Brazil. Basking sharks in the study traveled greater distances than previously reported, and well beyond the previously known range of the species. Several sharks spent extended periods of time (up to 5 months) at mesopelagic depths (200–1000 m) without excursions to the surface. A shift in vertical behavior was described, from sharks occupying productive surface waters in temperate New England waters in the late spring through early fall, to sharks moving south into tropical waters and moving to mesopelagic depths (Skomal et al. 2009). While movement of basking sharks out of New England to the southeastern US shelf during the winter months was attributed to prey availability, the extensive migrations into tropical waters observed in the study were suggested to be linked to the reproductive biology of the species (Skomal et al. 2009).

A 2003 study examined the seasonal movements and habitat preferences of *C. maximus* in the northeastern Atlantic using PSATs, and related these movements to areas of primary and secondary productivity (Sims and Southall 2003). The study found that the sharks engaged in broad-scale seasonal movements in response to primary/secondary production associated with
large-scale geographic (tidal and shelf-break frontal) features. Seasonal movements of sharks were associated with the continental shelf and not the open ocean. Movement patterns of the tagged animals were associated with productivity in both inshore and offshore, shelf-edge areas. Basking sharks spent less time at the surface in the winter than the summer. The vertical movements of sharks up and down in the water column were suggested to represent prey-searching behavior following olfactory trails or discrete layers of vertically migrating prey that form the deep scattering layer (DSL). Deep diving was thought to facilitate the sampling of a large number of vertically layered water masses over short period of time. This behavior has been noted in other large pelagic fishes and sharks (Carey 1990; Boustany et al. 2002). Basking sharks showed a diel diving pattern suggested as a response to vertically migrating zooplankton. The vertical and horizontal behavior of C. maximus observed in the satellite-tagging (PSAT) study indicates that survival on patchily distributed zooplankton by large-bodied animals requires both extensive vertical and horizontal movements. In this manner, fish such as basking sharks and molids may have an advantage over their zooplanktivorous air-breathing competitors such as marine mammals and sea turtles by exploiting deep-water communities beyond the latter’s range (Sims and Southall 2003; Hays et al. 2004).

It has been suggested that studies of basking shark distribution may be indicative of nutrient-rich areas of primary productivity that can be associated with other commercially important or endangered marine organisms such as whales, sea turtles, and bluefin tuna (Sims et al. 2003). It is therefore possible that, like basking sharks, ocean sunfish may respond to zooplankton gradients, and serve as “plankton recorders.” If so, then they may be used as detectors of trends in abundance of gelatinous zooplankton species in the North Atlantic (Sims and Quayle 1998).
The swordfish, *Xiphias gladius*, shares several similar life-history characteristics with *Mola mola* including: a worldwide distribution inhabiting temperate and tropical waters; occurrence in warm-season aggregations along the edge of the continental shelf and offshore banks; long-distance movement by non-spawners between coastal and oceanic waters along the continental shelf and slope; and a "basking behavior" in warm surface waters believed to be a mechanism of recovery and a digestive aid after foraging at depth. Swordfish have large eyes and are efficient visual predators at low light levels, feeding on cephalopods and a variety of fishes. A great portion of their diet consists of vertically migrating and benthic organisms inhabiting depths up to 600 m (Sedberry and Loefer 2001). Results from an acoustic-tagging study of swordfish in the Pacific and Atlantic Oceans suggested that swordfish moved offshore to deeper waters at night to feed on vertically migrating organisms concentrated on the surface as a means of maximizing their foraging success. Similar patterns have been observed in skipjack tuna and several shark species (Carey and Robinson 1981). Bottom topography and the resulting changes in current patterns were suggested as potential cues used by the fish in their movements.

A clear diel pattern of vertical movements was observed in swordfish—going deep during daylight hours and coming to surface at night, suggesting that light level is a driving factor in vertical behavior of *X. gladius* (Carey and Robinson 1981). Greatest depths were reached at noon when light at the surface was at a maximum, and fish appeared to adjust their vertical position in the water column in order to maintain a constant level of illumination. Environmental factors such as the Gulf Stream, oxygen levels, and cold temperatures below the thermocline may also alter the vertical behavior of the fish.

A 2001 study using PSATs to examine the movement of swordfish off the Charleston Bump (31°30'N, 79°W) in the northwestern Atlantic found that fish moved north/northeast along the
western wall of the Gulf Stream (Sedberry and Loefer 2001). Temperature preferences averaged 10°C during the day and 28°C at night, suggestive of a diel vertical migration to warmer surface waters at night and deeper waters during the day. Swordfish were attracted to the Charleston Bump region and western wall of the Gulf Stream due to the high occurrence of thermal fronts and the complex, high-relief bottom structure that generates these oceanographic features (Sedberry and Loefer 2001).

**Study Objectives**

The present study is the first to examine the pattern of distribution, movement, and behavior of *Mola mola* in the Northwest Atlantic. Given that there is little existing information on ocean sunfish despite their world-wide distribution and presence in large numbers in the region, I chose to study aspects of the movement and behavior of *Mola mola* in hopes of providing some insight into its basic biology, migratory patterns, and habitat preferences. My primary objectives were to study the movement and migratory patterns of *M. mola* in the Northwest Atlantic, and to quantify its temperature and depth preferences. The study tested the following hypotheses:

Hypothesis 1: *M. mola* exhibits a seasonal north-south movement pattern along the northeastern coast of the United States.

Hypothesis 2: *M. mola* has directed movement.

Hypothesis 3: Ocean sunfish do not swim against the Gulf Stream due to the high energetic costs such a migration route would require, but their movement is influenced by the Gulf Stream and North Atlantic Gyre.

To achieve my objectives and test these hypotheses, I attached pop-up satellite archival tags to individuals during the summer and fall off the coast of New England (Nantucket Sound and the Gulf of Maine) in order to track their vertical and horizontal movements over time. Prior to the
tagging of individuals, I examined existing aerial survey data for *Mola mola* in northeastern shelf waters from the North Atlantic Right Whale Consortium Database (1974-present) and from the OBIS-SEAMAP Database (1989-present) to determine a general pattern of distribution of *Mola mola* off the northeastern coast of the United States.

The present study includes the following three topics: 1) the horizontal movement of (tagged) *M. mola* in the northwestern Atlantic; 2) the vertical movement and behavior of (tagged) *M. mola* in the Northwest Atlantic; and 3) the distribution of *Mola mola* in eastern US shelf waters based on existing aerial survey records.
CHAPTER 1

HORIZONTAL MOVEMENT OF OCEAN SUNFISH, *MOLA MOLA*, IN THE
NORTHWEST ATLANTIC

Abstract

The ocean sunfish, *Mola mola*, has a worldwide distribution and is a common resident of the northwestern Atlantic Ocean. Notable for its unusual anatomy and large size, the biology of the species is largely unknown. The present study examined the horizontal movement of *Mola mola* using pop-up satellite archival tags (PSATs). Data were analyzed from 25 PSATs deployed on ocean sunfish between 2005 and 2008. Tags remained attached from 7 to 242 days, with a mean attachment period of 107 days. Analysis of the geolocation data indicates that ocean sunfish in the northwestern Atlantic leave the Gulf of Maine and southern New England in the late summer and early fall and move south along the continental shelf break. The maximum straight-line distance traveled by a tagged *Mola mola* was 2520 km in 130 days. Fish traveled as far south as the Bahamas and the Gulf of Mexico. Proximity to the Gulf Stream and Gulf Stream meanders and eddies played a significant role in the movement patterns of tagged fish. Results suggest that *M. mola* in the northwestern Atlantic exhibits a seasonal southward migration pattern driven by decreasing temperatures and the search for patchily distributed gelatinous prey. Travel routes along the shelf edge and the frontal features of the Gulf Stream increase the likelihood of encountering prey. Two tagged fish entered the Gulf of Mexico, one in the winter and one in the summer. The movement of both was
closely associated with the Loop Current, warranting further examination of the species’ presence in the region.

KEYWORDS: ocean sunfish, *Mola mola*, pop-up satellite archival tag, Northwest Atlantic

**Introduction**

The ocean sunfish, *Mola mola*, is a large pelagic species distributed worldwide in both temperate and tropical ocean basins. A member of the family Molidae in the order Tetraodontiformes, *M. mola* is known for its unique body shape, its large size (reaching 4.2 m and weighing up to 2300 kg), and its atypical anatomy (Gregory and Raven 1934; Norman and Fraser 1949; Fraser-Brunner 1951; Bass et al. 2005). Sunfish are valued food fish in Asia and comprise a large portion of bycatch in Pacific, Mediterranean, and South African commercial fisheries (Silvani et al. 1999; Macias and de la Serna 2002; Cartamil and Lowe 2004; Lovgren 2004; Thys 2005; Peterson 2005; Peterson and McDonell 2007). *M. mola* is a common resident of the offshore waters of the northwestern Atlantic during the spring and summer months, with an estimated summer abundance of 18,000 (Kenney 1996). Little is known about *Mola mola*’s basic ecology, distribution, or population dynamics, and the status of the species in the northwestern Atlantic, or any part of the world, is unknown.

Few studies have been conducted on the distribution and movement patterns of *M. mola*, and there is limited information on the migration and distribution of the species in the northwestern Atlantic. A study using acoustic telemetry to track ocean sunfish in
California reported a highly directional swimming ability not related to current direction (Cartamil and Lowe 2004). A recent satellite tagging study of *Mola mola* in South Africa found that ocean sunfish stayed in the same general area off the southern coast for several months, while *Mola mola* tagged in the Northeast Atlantic exhibited a seasonal pattern of migration (Hays et al. 2009; Sims et al. 2009).

*M. mola* is often associated with surface swarms of salps or jellyfish on which it is believed to feed (Norman and Fraser 1949; Reiger 1983; Klein-MacPhee 2002; Sims and Southall 2002), and commonly occurs along frontal features where these prey are concentrated (Sims and Southall 2002; Desjardins 2005; Houghton et al. 2006). As has been suggested for the basking shark, *Cetorhinus maximus*, another large pelagic zooplanktivore, data on the distribution and seasonal movements of *Mola mola* may provide a useful indication of nutrient-rich areas with high productivity, where other important marine organisms are found (Sims et al. 2003).

The present study is the first to examine the horizontal movement of *Mola mola* in the Northwest Atlantic. The study’s objectives were to examine the seasonal movement and migratory patterns of *M. mola* in the Northwest Atlantic by attaching pop-up satellite archival tags (PSATs) to sunfish during the summer and fall off the coast of New England.

The use of PSATs for tracking the vertical and horizontal movements of large pelagic animals over time has been established for many species, including tuna, billfishes and
sharks (Sims et al. 2003; Weng and Block 2004; Block et al. 2005; Wilson et al. 2005; Domeier 2006; Skomal et al. 2009). Once attached to the study animal, pop-up satellite tags record and store the time of sunrise and sunset, for use in geo-locating the tag each day, together with hourly temperature and pressure readings. These data can be recorded for over a year within the tag and then transmitted to Argos, via the tag, after the tag detaches and “pops up.” The tag can be programmed to release either on a specific date or after a preset time on the fish (e.g., three months). After the preset release date/time has been reached, the PSAT releases from its tether, floats to the surface, and initiates data transmissions to Argos. Each PSAT is equipped with a fail-safe mechanism that initiates release and data transmission if the tag reaches its depth limit (1200 m) or remains at a constant depth (i.e., does not change its depth significantly enough to be discerned by the tag’s pressure sensor) for 4 consecutive days. This mechanism is intended to release the tag if the animal is dead or the tag is floating at the surface.

**Materials and Methods**

**Tagging**

Between 2005 and 2008, a total of 31 pop-up archival tags (PSATs: model PTT-100, Microwave Telemetry, Columbia, MD, USA) was deployed on ocean sunfish, *Mola mola* in the Northwest Atlantic. Twenty-nine were deployed during the summer or fall (August–October) of 2005, 2006, and 2007 (Figure 1). Fish were tagged in the Gulf of Maine (n=7) and in shelf waters to the south and east (within 80 km) of Nantucket Island (n=22). Five fish were tagged in 2005 as a pilot study, 14 fish were tagged in 2006, and 10 fish were tagged in 2007. Two additional fish were tagged in March 2008 in shelf
waters off the coast of Georgia, USA. The objective of tagging fish in southeastern US waters was to capture their movement patterns in this region, as we observed many of the fish we tagged off the northeastern US during 2006 and 2007 to travel to this area during the late winter and early spring. PSATs were preprogrammed to release at either five or eight months.

Fish were tagged from commercial tuna vessels (F/V Peregrine, F/V Tenacious; n=10) and a charter fishing vessel (F/V Monomoy; n=19) in the waters off the northeastern United States, and from a research vessel in Georgia (R/V Margaurite, Georgia Department of Natural Resources). Fish basking at the surface were approached slowly by the vessel, and tags were attached via a modified wooden harpoon tagging pole 2.5 m in length. Monofilament tethers (25 cm long, 250-lb test) were used to attach the PSATs to black nylon umbrella darts (darts designed and produced by Michael Domeier, Marine Conservation Science Institute). Tags were placed into the musculature approximately 15 cm below the base of the dorsal fin, just anterior to the clavus. Because the fish were not brought onboard or retained during the tagging procedure, measurements of size and weight were not taken. Based on observation, the *Mola mola* individuals tagged in the region were estimated to weigh an average of approximately 130–230 kg with total lengths of 1.35 to 1.64 m (estimated using growth equation from Watanabe and Soto 2008).

The PSATs recorded ambient light levels, temperature (resolution 0.17°C), and depth (resolution 5.38 meters). Temperature and depth were sampled in most cases at 15-min
intervals and stored as summary data. Of 31 PSATs deployed in total, 25 successfully reported data back to Argos (Table 1). For purposes of data analyses, the horizontal tracks of fish with tags attached less than 30 days (n=6) were not included in the study. In analyses of vertical movement, tags with data retrieval of less than 30% were omitted (n=3).

**Horizontal Movement**

Daily geolocation position estimates of the fish were established from recorded high-resolution light data stored in the PSAT using a proprietary algorithm (Microwave Telemetry, Inc.). From the light-level data, estimates of sunrise and sunset were internally derived by the tag, and were used to calculate longitude based on the time of local noon, and latitude based on local day length. The resulting geolocation is subject to some inaccuracy due to several factors. Light-based estimations of latitude are problematic, particularly around the two equinox periods when day length is approximately equal at all latitudes (Sibert et al. 2003). Also, in the case of our study, the fish made frequent dives to depths where light was limited. Such light data, when left unfiltered, are considered “noisy” and severely limited in accuracy (Sibert et al. 2003; Teo et al. 2004; Neilsen et al. 2006, 2009).

I used the methods of Galuardi et al. (2009) to derive the most likely migration paths of tagged fish based on the raw geolocation data. The analysis involves a two-step process: the first applies a state-space Kalman filter (in some cases sea surface temperature (SST) inclusive), and the second step applies a bathymetric correction. Use of the state-space
Kalman filter as a statistical model for archival tag data is well established in PSAT studies (Sibert et al. 2003). Accuracy of position estimates established by this method is increased with the application of other information stored by the tag, including temperature and pressure data (Teo et al. 2004; Neilsen et al. 2006; Teo et al. 2007). The Kalman filter is a statistical model that assumes the movement of a fish from one time to the next is a biased random walk. The Kalman filter describes the transition of the system from one state to the next, the errors in the process of measuring the state of the system, and the variance at each step (Sibert et al. 2003). The accuracy of light-based geolocation estimates have been studied using fixed buoys, and the range of absolute longitude errors (0.15 ± 0.12 to 0.29 ± 0.83°) was less than the that of latitude errors (1.49 ± 2.72 to 4.36 ± 5.78°) (Musyl et al. 2001). A study applying an SST latitude estimation algorithm to the geolocation estimates from PSAT’s attached to large pelagic fishes and comparing the results to satellite telemetry tags saw an improvement in the accuracy of latitude estimates (range of absolute latitude errors 0.73±0.54 to 1.41±1.28°) (Teo et al. 2004).
surface that integrates land topography and ocean bathymetry built from numerous global and regional data sets) were used to constrain position estimates based on the maximum daily depth of the fish stored by the PSAT’s pressure sensor. Using the daily position estimates and surrounding confidence regions established by the first step of the process (the UKF), 300 bathymetric points were sampled for each position estimate and all points shallower than the maximum daily depth of the fish were discarded. Geolocation position estimates and confidence regions were then re-estimated from the mean and covariance of the valid bathymetric points. Locations were further constrained by minimized distance to the previous location and land constraints. The “start” (deployment location) and “endpoint” (pop-off location) of the track were incorporated into the estimated migration path, and the resulting track was plotted with confidence intervals indicating the 95% confidence area.

To examine temporal patterns in distribution of *Mola mola*, fixed kernel density utilization contours were created to represent 50% and 95% of the pooled daily geolocation estimates (kernel function based on Silverman 1986). The data were analyzed using ArcMap 9.3 (ArcGIS version 9, Environmental Systems Research Institute, Inc., Redlands, California, USA), the ArcMap Spatial Analyst extension, and the Hawth’s Analysis Tools extension (version 3.27, Beyer 2006). Daily geolocation estimates were plotted against maps of sea surface temperature using Maptool, (a product of SEATURTLE.ORG) to study the relationship between travel routes of *Mola mola* and SST and the Gulf Stream. Data from Maptool’s bathymetry grid are from the ETOPO2 two-minute bathymetric coverage data, and daily sea surface temperature data are derived
from NOAA's GOES daily SST satellite data (spatial resolution of 6 km and validated to ±0.5°C)

**Results**

Of 31 PSATs deployed in total, 25 successfully reported data back to Argos (Table 1, Figure 1). Tag attachment periods varied, as did the amount of data that were successfully stored and reported. Tag attachment periods ranged from 5 to 242 days. Mean attachment period of all the tags reporting data was 107.2 ± 80.6 (SD) days, and mean data reported was 69.7 ± 33.1% (n=25). Eighteen tags were attached for 50 days or more, 10 tags were attached for 150 days or more, and 4 tags were attached for at least 240 days. Eleven tags (35%) remained attached for the programmed time period (n=7 for 5 months and n=4 for 8 months).

In my 2005 pilot season, of the five tags that were deployed in the waters off New England, three never reported, one detached prematurely (<30 d), and one remained attached for 130 days. Though this last tag showed poor data return (22%), the information relayed by the tag was significant to the study in that it popped off in January 2006 while the fish was in the Gulf of Mexico, over 2500 km away from the deployment location. It was the longest track of any fish tagged.

In 2006, 14 tags were deployed in the waters off New England (2 tags deployed in the Gulf of Maine, 12 tags deployed in shelf waters to the south and east of Nantucket Island). Two tags never reported data to Argos satellites, and two detached prematurely (<30 d). Of the 12 tags that reported data to Argos satellites, mean retention was 137.5 ±
81.2 days, and mean data reported was 20.6 ± 18.1%. Ten tags remained attached and reported data for 30 days or longer. Two of those popped off prematurely after 70-72 days, and the remaining 8 tags remained attached for the programmed time period. Five remained attached for a 5-month period (approximately 153 days), and three remained attached for an 8-month period (approximately 242 days). Data reported by the tags decreased as retention time increased. In 2006, data reported from the 5-month tags ranged from 31 to 64% (mean 49.4 ± 12.2%) and data reported for the 8-month tags ranged from 4 to 40% (mean 20.7 ± 18.1%).

In 2007, ten tags were deployed in the waters off New England (3 in the Gulf of Maine, 7 in shelf waters to the south and east of Nantucket). One tag failed to report data to Argos satellites, and 3 tags released between 5 and 11 days. Of the tags that reported data to Argos satellites, mean retention duration was 64.1 ± 58.5 days, and 90.7 ± 11.6% of the data were reported (n=9). Six tags remained attached for 30 days or longer. One detached prematurely at 31 days, one at 50 days, and one at 68 days. One tag remained attached for 98 days, and two tags remained attached for the programmed time period (5 months or 153 days). As observed in 2006, data reported by the tags decreased as retention time increased. Data reported from the 2 tags attached for 5 months was 72.5 ± 0.7% (n=2), while data reported for the 3 tags attached for between 50 and 98 days ranged from 84% to 96% (mean 90.6 ± 6.1%).

In March 2008, two fish were tagged in shelf waters off the coast of Georgia (USA) by a research team from the University of New Hampshire studying leatherback turtles in the
region. These fish were reportedly smaller in size than the *Mola mola* tagged in northern Atlantic waters. One tag remained attached for 57 days, and reported 64% of data to Argos satellites. The remaining tag stayed attached for the programmed time period of 8 months (242 days), and returned 33% of data.

**Horizontal Movement**

Geolocation information was retrieved for 25 tags, and analyzed for 19 tags that remained attached for 30 days or more. The maximum straight-line distance traveled by a tagged *Mola mola* was 2520 km in 130 days, with an estimated average speed of 19.38 km/day. Maximum average speed was 31.92 km/day. Average daily movements were difficult to determine because of the inaccuracies in geolocation data. The horizontal tracks of seven fish with attachment periods >30 days are shown in Figures 2-9, while the tracks of the remaining 12 fish with PSAT attachments <30 days are found in the Appendix (Figures 1-12). Depth and temperature data retrieved by the tags will be discussed in Chapter 2.

One tag that was attached in September 2005 popped off, after 130 days, in the Gulf of Mexico (Fig. 2). Although the tag showed poor data return (22%), the information relayed by the tag is significant to the study in that it showed that *M. mola* was capable of traveling significant distances—in this case over 2500 km from the deployment location. Depth data recorded by the tag also showed the fish reaching depths of 800 m; deeper than previously recorded for the species. Using the methods of Royer et al. (2006), a horizontal track for this fish (without estimates of error) was calculated (Figure 2).
In 2006, 10 fish were tagged with PSATs that remained attached for 30 days or more (Figure 3a). All 10 fish tagged in the waters off New England in August and September moved south off the shelf initially, and continued on southerly courses while remaining within 100 km of the shelf edge. The trend in movement, observed in nine fish, was toward South Atlantic Bight waters (Figures 4, 5 and 6) while one fish, ID 67330 moved farther east off the shelf once it reached the Mid-Atlantic Bight, and remained there within 200-600 km of the shelf edge for the duration of the 5-month tagging period (September 2006-May 2007) (Figure 7). Five of the nine fish that continued moving south during the fall months stopped once they reached the Charleston Bump and remained there for the duration of the tagging period into the winter and spring months (from January to May 2007). Four of those five fish remained off the shelf in deeper water as illustrated by one track (ID 67323) in Figure 4, while one (ID 67565) moved both on and off the shelf during that time period (Figure 5). Four fish continued to move south on a more direct route, reaching the Bahamas between late November 2006 and January 2007, as illustrated by one track (ID 67321) in Figure 6.

In 2007, six fish were tagged with PSATs that remained attached for 30 days or more (Figure 3b). Due to an increased number of premature PSAT detachments in 2007, attachment periods were shorter than for most fish tagged in 2006. Even those with longer deployments (5 months) did not travel as far south as those in 2006 (n=2). Sunfish tagged in 2007 exhibited two distinct movement patterns over the tagging period (September 2007–March 2008). As observed with the majority of fish in 2006, three fish tagged in 2007 moved south over the continental shelf or just off the shelf edge. Two of
these fish were tagged off Nantucket in September, and one was tagged in the Gulf of Maine in early October. The fish that traveled the farthest south (ID 77070) reached North Carolina shelf waters by mid-November (68d) with a straight-line distance (SLD: shortest distance between the tag start and end points) of 1105 km (Figure 8). Three fish moved east off the shelf and then south, remaining 100–200 km off the shelf for the duration of the tracking period. Two of the three tags were on for a 5-month period (September 2007 to February 2008) and none of the fish moved farther south than the Mid-Atlantic Bight (Maryland/Virginia) (Figure 9).

In March 2008, two fish were opportunistically tagged in shelf waters off the coast of Georgia. The goal was to capture the movement of Mola mola from the spring (which was when the majority of our tags detached), through the following summer. One fish (ID 77074) was tagged for 57 days, and remained over the shelf in the Georgia Bight for the entire time. The tag detached when the fish was approximately 100 km north of the tagging location, after a total SLD traveled of 110 km. The second fish was tagged for 8 months, from March to November 2008. This fish also started moving over the shelf to the north of its tagging location, then proceeded to move south over Florida shelf waters and into the Gulf of Mexico in the summer months before visiting the Bahamas and then returning to the shelf edge 250 km to the northeast of its tagging location (Figure 10).

**Seasonal Distribution**

There were both seasonal and inter-annual differences in the distribution of tagged Mola mola (Figures 11 and 12). For 2006, in the late summer and early fall months (August–
October), there was a wide distribution indicating the fish moved rapidly south from the tagging location. The 50% volume contour extended from the southern Gulf of Maine, Cape Cod, and Nantucket south over the shelf to the off-shelf waters of the Mid-Atlantic Bight. The 95% volume contour extended as far as the shelf edge at the North Carolina coast (Figure 11a). Over the winter months (November 2006–February 2007), the 95% volume contour overlapped that of the fall, and continued as far south as Florida and the Bahamas, and the 50% volume contour was concentrated at the Charleston Bump, slope of the Blake Plateau, and surrounding bathymetric features (Figure 11b). In the spring months (March–May 2007), the 50% volume contour remained primarily in the same region of the Charleston Bump/Blake Plateau with a secondary, smaller contour located far to the north at the 4500-m isobath off New Jersey (Figure 11c).

In 2007, PSAT retention rates were shorter than in the previous year for most of the fish tagged. In the fall (September–October 2007), the distribution pattern was similar to that in 2006, with the 95% contour extending from the Gulf of Maine and southern New England south to the North Carolina shelf. Unlike 2006, the distribution also extended east to offshore waters in New England (Figure 12a). The distribution of *Mola mola* in the winter months (November 2007 – February 2008) was different than that in 2006, in that the fish remained, in large part, in offshore waters of the Mid-Atlantic, with a secondary smaller distribution contour located on the shelf edge off North Carolina (Figure 12b.) In the spring (March 2008), the 50% and 95% volume contours were located in the same area as that of the winter, in offshore waters off Virginia (Figure 12c).
Gulf Stream Interaction

In both years, tagged sunfish were found along frontal features where water masses of different temperatures meet, specifically frontal features created by the warm Gulf Stream waters meeting the cooler waters of the Gulf of Maine and continental shelf. In 2007, when more fish moved offshore in the mid-Atlantic region rather than continuing south along the shelf break as in 2006, the Gulf Stream and eddies were deflected well off the shelf edge (between 100 and 200 km) and the resulting front was located in offshore waters. In 2006, the front occurred closer to shore, resulting in warmer temperatures on the shelf (Figure 13a-b). In 2006, *Mola mola* also entered the Gulf Stream itself and associated fronts on the Gulf Stream’s western edge (Figure 13a).

Discussion

Aside from a preliminary tagging study in 1983 (Reiger) that first speculated on the distribution and movement of ocean sunfish in western North Atlantic, the present study is the first to describe movement and behavior of *Mola mola* in the region. Results indicate that *Mola mola* is a strong swimmer capable of extensive, highly directed movement, with a mean straight line rate of movement (= SLD/number of days tagged) reaching 31.9 km/day. *M. mola* maintains this rate of movement potentially even against swiftly moving currents such as the Gulf Stream. A previous study using GPS technology to track the movement of an ocean sunfish in the eastern Atlantic Ocean found it to be an active swimmer (average rate of 10-20 km/day) that often headed into or across prevailing currents associated with mesoscale eddies (Sims et al. 2009b). Ocean sunfish leave the Gulf of Maine and southern New England in the late summer and early fall and
move south. This pattern of movement in the Northwest Atlantic has been observed in other large pelagic species including bluefin tuna, swordfish, basking sharks, and leatherback sea turtles (Richards 1976; Rivas 1978; Shoop and Kenney 1992; Stokesbury et al. 2004; Block et al. 2005; Hays et al. 2005; Wilson et al. 2005; Skomal et al. 2009). A study of the movement of three *Mola mola* in the eastern North Atlantic found that they exhibited a similar pattern of traveling north at the end of the winter and south at the end of the summer (Sims et al. 2009a), and a study of *M. mola* in western Pacific waters off Japan found they also exhibited a seasonal north–south migration pattern (Thys et al. 2007). Studies on movement of *Mola mola* on both the California coast and off South Africa, where ocean temperatures are more consistent year-round, found that they did not travel extensively from the tagging locations (Thys et al. 2007; Hays et al. 2009).

None of the *Mola mola* tagged remained in New England shelf waters beyond the month of October when water temperatures drop to 10-11°C. Previous studies examining aerial survey data for *M. mola* along the east coast of the United States found that the animals move seasonally out of the northeastern US in the late fall and appear again in the early summer (Kenney 1996; Desjardins 2005). The presence of *Mola mola* in this region on a seasonal basis is likely due to environmental conditions in New England shelf waters in the late spring, which include warm water temperatures and increased primary productivity (Lalli and Parsons 2006)(Appendix Figure 12). Increased primary productivity can cause seasonal increases in gelatinous zooplankton during the late spring and summer months, making this region an attractive foraging ground for gelatinous zooplanktivores like *M. mola* and leatherback sea turtles, *Dermochelys coriacea*.
A study of the seasonal occurrence of *Cyanea* medusae in a Connecticut estuary found they occurred from spring through early summer in a highly predictable annual pattern of growth and abundance, and suggested this may also be the case with neritic and oceanic populations (Brewer 1989). Evidence suggests that leatherbacks use northern slope and shelf waters in the summer months primarily for foraging on gelatinous prey (Hays et al. 2006). In the late fall, decreasing temperatures and a decline in productivity in Northeast waters may serve as a cue for ocean sunfish to move south in search of prey. A study of the seasonal distribution of leatherbacks in northeastern U.S. waters found few animals in the region during the fall, and no turtles were detected in the winter months (Shoop and Kenney 1992). Similarly, the seasonal decline of copepod abundance in northeastern U.S. waters has been suggested as the motivating factor for the southward migration of basking sharks to winter residence in southeastern U.S. shelf waters (Skomal et al. 2004; Skomal et al. 2009). A study of the movement patterns of *Mola mola* in the Northeast Atlantic suggested that thermal tolerance of the species was the driving factor in the movement of animals south at the end of the summer (Sims et al. 2009a).

Of the 18 tags deployed on *M. mola* in New England that remained attached into the late fall and winter (attachment periods >30 days), most moved south in close proximity to the shelf break to the southeastern United States. Several fish moved as far as the Charleston Bump region and resided there for several months, and fewer still reached the Bahamas and Gulf of Mexico. A smaller fraction moved to offshore waters in the mid-Atlantic. In the spring, fish remained concentrated in two areas: the southeastern US
(Charleston Bump and surrounding bathymetric features) or the offshore waters of the Mid-Atlantic. Similar travel routes and aggregation “hot spots” have been documented in several large pelagic fishes in the Northwest Atlantic (Cramer 1996; Sedberry and Loefer 2001; Stokesbury et al. 2004; Wilson et al. 2005).

In addition to seasonal changes in water temperature, the seasonal movement of ocean sunfish south from New England waters is likely driven by their search for high concentrations of patchily distributed jellyfish prey. The seasonal movement of leatherbacks into the Gulf of Maine and Georges Bank in the late summer, then south into the bays and sounds of New England in the fall, followed by winter in the Gulf of Mexico and Florida, has been suggested as a route to maximize foraging opportunities on *Cyanea* species (Lazell 1980). Travel along the shelf break and the frontal features created there increases the likelihood of encountering these prey patches. Previous studies suggest that large pelagic fishes, such as bluefin tuna, aggregate at frontal features based a variety of cues including changes in phytoplankton distribution, changes in prey abundance or distribution, and enhanced foraging opportunities (Fiedler and Bernard 1987; Humston et al. 2000; Brill et al. 2002). A study of *M. mola* in the western English Channel found they occurred near surface fronts at about the same time each year (Sims and Southall 2002).

Though patterns of jellyfish distribution are often unpredictable and therefore difficult to establish, gelatinous zooplankton aggregations are known to concentrate around sharp density discontinuities such as those found at shelf/slope fronts (Graham et al. 2001). There is evidence suggesting that the slope-water region south of New England is an area
where large salp swarms recur on a regular basis (Madin et al. 2006), and the presence of a migratory DSL has been established in these waters (Cole et al. 1971). A study of the co-occurrence of *Mola mola* and jellyfish in the Irish and Celtic seas found ocean sunfish in all areas where jellyfish were most abundant (Houghton et al. 2006). That study suggests increased gelatinous zooplankton productivity in temperate waters makes the habitat a worthwhile part of the *Mola*’s migration route. Basking sharks are known to inhabit the shelf areas off the southeastern U.S. during the winter months (Skomal et al. 2004; Skomal et. al 2009), and many large pelagic fishes such as swordfish and marlins are known to aggregate, feed, and spawn at the Charleston Bump (Sedberry and Loefer 2001; Stokesbury et al. 2004). The Charleston Bump is an attractive habitat due to the bottom topography and oceanographic features (including currents and thermal fronts) that result from its interaction with the Gulf Stream. Ocean sunfish moving south from New England may inhabit this region to take advantage of the high concentration of prey found there. Schools of bluefin tuna are known to inhabit the Straits of Florida and waters adjacent to the Bahamas in May and June prior to their migration north to New England. Tuna observed in the region did not engage in typical feeding behaviors, and sightings of tuna were associated with strong winds and associated oceanographic conditions (Lutcavage et al. 1997b). Like tuna, ocean sunfish may inhabit this region to take advantage of the oceanographic features associated with the strong currents and Gulf Stream interaction.

Proximity to the Gulf Stream and Gulf Stream meanders and eddies plays a significant role in the movement pattern of *Mola mola*. In 2007, more sunfish moved to offshore
waters in the Mid-Atlantic, while in 2006 most sunfish remained in close proximity to the shelf break as they continued moving south. These patterns are in part associated with the position of the Gulf Stream during those years. In 2007, the Gulf Stream was deflected off the shelf up to several hundred kilometers, and the oceanographic features associated with the Gulf Stream were also farther offshore. By associating with these offshore frontal features, molas leaving New England in the early fall of 2007 were then more likely to encounter patches of jellyfish prey. In 2006, the Gulf Stream and Gulf Stream eddies remained in close proximity to the shelf break, and as a result ocean sunfish were more likely to remain along these frontal features associated inshore at the shelf break. A similar movement pattern has been observed in leatherback turtles (Dermochelys coriacea) in the Northwest Atlantic, which feed exclusively on jellyfish prey (Lutcavage 1996; Hays et al. 2006). Aerial survey data on bluefin tuna in the Northwest Atlantic also indicates an association between bluefin tuna aggregations and thermal front zones along the Gulf Stream edge (Lutcavage et al. 1997a). Ocean sunfish in the present study were associated with thermal fronts along the western edge of the Gulf Stream, as well as in the Gulf Stream itself and fronts on the eastern edge in the southeast United States.

The two fish that were tagged in the southeastern United States in the spring did not move north towards New England as expected, but instead remained on the Southeast US shelf or moved south into the Gulf of Mexico in the summer months before returning to the Southeast US shelf in the fall. This result suggests that there may be a second sub-population of Mola mola that inhabits Southeast US shelf waters and the Gulf of Mexico, and does not move north to New England waters in the summer months. Alternatively,
*M. mola* may exhibit a degree of behavioral plasticity that extends beyond single seasons. Additional PSAT tagging in the region and genetic testing of ocean sunfish in the Northwest Atlantic would provide information to help address this hypothesis.

Two ocean sunfish tagged in the study moved into the Gulf of Mexico. One was tagged in New England in September, entered the Gulf of Mexico in December, and remained there through January when the tag detached. The second fish was tagged on the Georgia shelf in March, entered the Gulf of Mexico in June, and remained there through August before leaving and returning to the Georgia shelf. Previous aerial survey data have established *Mola mola* as a year-round resident in the Gulf of Mexico (Desjardins 2005; Fulling et al. 2007). Aerial surveys indicate ocean sunfish are most abundant in the Gulf of Mexico in the winter months, followed by the spring (Desjardins 2005; Fulling et al. 2007). Horizontal tracks of both sunfish in the present study show their movements in the Gulf of Mexico to be closely associated with the Loop Current. Like in the Gulf Stream, *Mola mola* may associate with this current and the resulting frontal features at its boundaries as a region of increased productivity. Leatherback sea turtles, bluefin tuna, and several billfish species are known to associate with the Gulf of Mexico Loop Current (Maul et al. 1984; Block et al. 2005; Desjardins 2005; Wells et al. 2009). In addition to an area of increased productivity, the Gulf of Mexico’s Loop Current is an established spawning ground for several large pelagic fish species, including swordfish and bluefin tuna (McGowan and Richards 1989; Block et al. 2005; Stokesbury et al. 2004; Wells et al. 2009). With no data on sex and size of animals collected in the present study, nor any existing information on the reproductive biology of *Mola mola*, it is impossible to
determine whether they are utilizing this area for spawning. However, the presence of the species in both the summer and winter months, and the reasons why it travels there warrant further examination.

Of the 31 PSATs deployed on *Mola mola* between 2005 and 2008, only 11 remained attached until the programmed pop-up date. Six never reported data, and 14 detached prematurely. One reason for premature detachment was the activation of the tag’s fail-safe mechanism, which caused its release due to what was perceived by the tag as constant pressure (i.e., the change in the fish’s depth was less than the resolution of the tag (5.38 m) over a four-day period). This was known to occur for six tags, and in all of these cases the fish showed steady horizontal movement in shelf waters. This often occurred when fish were located in very shallow waters (<10 meters) around Nantucket Island where they presumably were feeding on large patches of gelatinous prey (salps and jellyfish) observed in the area. One fish apparently died and sank to the bottom shortly after tagging. Other possible causes of premature detachment include tag shedding/tissue rejection due to improper placement of the tag, corrosion or fouling of the tag, and mechanical failure. In species like *Mola mola* that are known to bask at the surface or spend extended periods of time in shallow water, the fail-safe mechanism on the tag should be modified to prevent premature detachment. Applying a tag with GPS (Global Positioning System) capabilities would provide valuable data on fine-scale movement patterns of the species when at the surface. The tagging method in the present study did not involve containment of the fish due to their large size and the resulting difficulty in handling them. In the future, developing a method that contained or captured the fish
prior to tagging would ensure proper tag placement and enable the collection of other valuable information such as length, weight, sex, and reproductive state via tissue collection and blood samples.

The present study is the most extensive to date on the movement and behavior of *Mola mola*. My results establish a baseline of information for the horizontal movement of ocean sunfish in the Northwest Atlantic, and provide early insight into the understanding of its habitat, migration routes, behavior, and environmental associations. Data on distribution and seasonal movements of *Mola mola* may prove useful indicators of nutrient-rich areas with high productivity, where other important marine organisms are found.

Future studies are needed to gain a more complete understanding of the seasonal movement patterns of the species in the Northwest Atlantic and other parts of the world. In addition to studies on movement and behavior, studies on such basic biological information as age, growth, and reproduction are necessary to thoroughly examine the biology of the species and its role in the North Atlantic ecosystem.
Table 1.1. Date of deployment, location of deployment and pop-off, number of days attached, straight line distance (SLD) traveled, and percentage of data reported for 31 PSAT's attached to Mola mola between 2005-2008.

<table>
<thead>
<tr>
<th>PSAT ID</th>
<th>Dep. Date</th>
<th>Deployment Location (°N) (°W)</th>
<th>Pop-off Location (°N) (°W)</th>
<th>Days attached</th>
<th>SLD (km)</th>
<th>Data reported</th>
</tr>
</thead>
<tbody>
<tr>
<td>14538</td>
<td>9/3/2005</td>
<td>41.37 69.31</td>
<td>23.21 85.73</td>
<td>130</td>
<td>2520</td>
<td>22%</td>
</tr>
<tr>
<td>8776</td>
<td>10/2/2005</td>
<td>42.04 70.02</td>
<td>40.19 68.93</td>
<td>24</td>
<td>222</td>
<td>100%</td>
</tr>
<tr>
<td>67322</td>
<td>8/17/2006</td>
<td>43.15 69.98</td>
<td>31.35 79.29</td>
<td>153</td>
<td>1565</td>
<td>55%</td>
</tr>
<tr>
<td>67325</td>
<td>8/18/2006</td>
<td>40.96 70.51</td>
<td>32.23 78.98</td>
<td>153</td>
<td>1206</td>
<td>46%</td>
</tr>
<tr>
<td>67321</td>
<td>8/23/2006</td>
<td>40.82 70.66</td>
<td>26.94 79.94</td>
<td>143</td>
<td>1685</td>
<td>64%</td>
</tr>
<tr>
<td>67331</td>
<td>9/1/2006</td>
<td>41.29 69.96</td>
<td>39.42 74.21</td>
<td>13</td>
<td>415</td>
<td>82%</td>
</tr>
<tr>
<td>67332</td>
<td>9/8/2006</td>
<td>42.24 70.03</td>
<td>27.18 78.33</td>
<td>74</td>
<td>1830</td>
<td>96%</td>
</tr>
<tr>
<td>67330</td>
<td>9/17/2006</td>
<td>41.26 69.28</td>
<td>38.86 71.19</td>
<td>242</td>
<td>312</td>
<td>40%</td>
</tr>
<tr>
<td>67565</td>
<td>9/17/2006</td>
<td>41.29 69.24</td>
<td>33.89 76.30</td>
<td>242</td>
<td>1022</td>
<td>18%</td>
</tr>
<tr>
<td>67327</td>
<td>9/19/2006</td>
<td>41.20 69.59</td>
<td>32.38 78.71</td>
<td>153</td>
<td>1250</td>
<td>31%</td>
</tr>
<tr>
<td>67333</td>
<td>9/19/2006</td>
<td>41.19 69.59</td>
<td>30.46 81.41</td>
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<td>1590</td>
<td>4%</td>
</tr>
<tr>
<td>67323</td>
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<td>41.17 69.58</td>
<td>32.56 78.37</td>
<td>153</td>
<td>1235</td>
<td>51%</td>
</tr>
<tr>
<td>67564</td>
<td>9/25/2006</td>
<td>41.31 69.99</td>
<td>39.92 70.17</td>
<td>14</td>
<td>148</td>
<td>100%</td>
</tr>
<tr>
<td>67328</td>
<td>9/25/2006</td>
<td>41.30 69.97</td>
<td>28.28 79.44</td>
<td>70</td>
<td>1690</td>
<td>78%</td>
</tr>
<tr>
<td>77073</td>
<td>9/7/2007</td>
<td>41.39 70.05</td>
<td>41.49 70.12</td>
<td>5</td>
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<td>100%</td>
</tr>
<tr>
<td>77079</td>
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<td>37.30 73.17</td>
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<td>84%</td>
</tr>
<tr>
<td>77070</td>
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<td>33.52 77.75</td>
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<td>92%</td>
</tr>
<tr>
<td>77075</td>
<td>9/20/2007</td>
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<td>39.63 74.10</td>
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<td>419</td>
<td>100%</td>
</tr>
<tr>
<td>77077</td>
<td>9/24/2007</td>
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<td>41.23 70.62</td>
<td>11</td>
<td>50</td>
<td>100%</td>
</tr>
<tr>
<td>77069</td>
<td>9/24/2007</td>
<td>41.21 70.14</td>
<td>38.64 67.76</td>
<td>153</td>
<td>338</td>
<td>73%</td>
</tr>
<tr>
<td>77071</td>
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<td>41.26 70.22</td>
<td>40.37 73.33</td>
<td>9</td>
<td>283</td>
<td>100%</td>
</tr>
<tr>
<td>77072</td>
<td>10/6/2007</td>
<td>42.63 70.37</td>
<td>36.55 75.64</td>
<td>50</td>
<td>793</td>
<td>96%</td>
</tr>
<tr>
<td>67326</td>
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<td>42.38 70.27</td>
<td>36.74 71.64</td>
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</tr>
<tr>
<td>77074</td>
<td>3/11/2008</td>
<td>30.79 80.76</td>
<td>31.74 80.17</td>
<td>57</td>
<td>110</td>
<td>64%</td>
</tr>
<tr>
<td>77078</td>
<td>3/11/2008</td>
<td>30.90 80.66</td>
<td>32.51 78.38</td>
<td>242</td>
<td>280</td>
<td>33%</td>
</tr>
</tbody>
</table>
Figure 1.1. Map of deployment locations (green circles) and endpoints (red triangles) of 31 PSATs attached to *Mola mola* between 2005 and 2008. Tags were attached in New England waters between the months of August and October in 2005-2007 (n=29) and in Georgia shelf waters in March 2008 (n=2). Tags were attached from 7 to 242 days. Blue line indicates 200m isobath.
Figure 1.2. The most probable track of a tagged *Mola mola* (PSAT 14538). The tag was deployed on 9/3/2005 off Nantucket and popped off after 130 days on 1/15/2006 in the Gulf of Mexico. Track was estimated from raw geolocation data using methods of Royer et al. (2006) and does not include uncertainty.
Figure 1.3a. Estimated positions of all *Mola mola* tagged with PSATs in 2006 (n=10) Most probable tracks were estimated from raw geolocation data using methods of Galuardi (2009). Green circles indicate deployment locations and red triangles indicate end points. Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color.
Figure 1.3b. Estimated positions of all *Mola mola* tagged with PSATs in 2007-08 (n=8). Most probable tracks were estimated from raw geolocation data using methods of Galuardi (2009). Green circles indicate deployment locations and red triangles indicate end points. Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color.
Figure 1.4. Most probable track of *Mola mola* PSAT 67323. The tag was deployed on 9/23/2006 (green circle) and popped off after 153 days on 2/23/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Dark blue line marks the 200m isobaths.
Figure 1.5. Most probable track of *Mola mola* PSAT 67565. The tag was deployed on 9/17/2006 (green circle) and popped off after 242 days on 5/17/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.6. Most probable track of *Mola mola* PSAT 67321. The tag was deployed on 8/23/2006 (green circle) and popped off after 143 days on 1/23/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.7. Most probable track of *Mola mola* PSAT 67330. The tag was deployed on 9/17/2006 (green circle) and popped off after 242 days on 5/17/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.8. Most probable track of *Mola mola* PSAT 77070. The tag was deployed on 9/14/2007 (green circle) and popped off after 68 days on 11/21/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.9. Most probable track of *Mola mola* PSAT 77069. The tag was deployed on 9/24/2007 (green circle) and popped off after 153 days on 2/24/2007 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.10. Most probable track of *Mola mola* PSAT 77078. The tag was deployed on 3/11/2008 (green circle) and popped off after 242 days on 11/11/2009 (red triangle). Track was estimated from raw geolocation data using methods of Galuardi (2009). Gray shading indicates 95% confidence interval. Monthly geolocation positions are labeled by color. Blue line marks the 200m isobath.
Figure 1.11. Kernel density percent volume contours for 50% (gray) and 95% (white) of pooled geolocation data for: a) August – October 2006 (n=10); b) November 2006 – February 2007 (n=10); and c) March – May 2007 (n=3). Geolocation estimates produced using methods of Galuardi (2009).
Figure 1.12. Kernel density percent volume contours for 50% and 95% of pooled geolocation data for: a) September – October 2007 (n=6); b) November 2007 – February 2008 (n=5); and c) March 2008 (n=1). Geolocation estimates produced using methods of Galuardi (2009).
Figure 1.13. Sea surface temperature, Gulf Stream position, and pooled daily geolocation data for tagged *Mola mola* during: a) November 2006 (n=10); and b) November 2007 (n=5). The black line indicates the 200m shelf break. Geolocation estimates produced using methods of Galuardi (2009). Maps produced using Maptool (a product of SEATURTLE.ORG).
CHAPTER 2

VERTICAL MOVEMENT AND BEHAVIOR OF OCEAN SUNFISH, *MOLA MOLA*, IN THE NORTHWEST ATLANTIC

Abstract

The ocean sunfish, *Mola mola*, has a worldwide distribution and is a common resident of the Northwest Atlantic Ocean. Notable for its unusual anatomy and large size, the biology of the species is largely unknown. The present study examined the vertical movement and behavior of *Mola mola* using pop-up satellite archival tags (PSATs). Data were analyzed from 25 PSATs deployed on ocean sunfish in the Northwest Atlantic between 2005 and 2008. Tags were attached from 7 to 242 days, with a mean attachment period of 107 days. Fish spent greater than 30% of their time in the top 10 m of the water column, and over 80% of time in the top 200 m. The maximum depth recorded by any fish was 844 m. Temperatures experienced by tagged fish ranged from 6 to 30°C. Vertical behavior of *Mola mola* changed over short-term and seasonal scales. Ocean sunfish in northeastern US waters in the summer months inhabited shallower swimming depths and spent more time at the surface than those that moved south in the winter and spring. The change in vertical behavior is likely driven by temperature and thermocline depth, as fish adjusted their vertical behavior following thermal gradients and/or searching for vertically migrating prey of the deep scattering layer (DSL). The shift in vertical behavior from shallow to deeper depths was especially apparent when fish
entered the Gulf Stream, where they spent little time at the surface and dove to depths of 400-800 meters. A diel pattern was observed in vertical behavior. There was no observed relationship between the amount of time per day that fish spent in cold water (<10°C) and the amount of time fish spent near the surface (0-6 m). This indicates a lack of evidence for *M. mola* basking at the surface as a mechanism for behavioral thermoregulation, or recovery from deep dives in cold water in the northwestern Atlantic. However, as sunfish moved south and encountered warmer, mixed water masses (particularly the Gulf Stream) they dove deeper and, if seeking a recovery period after time at depth, may have gained thermal benefit from the warm temperatures found at mid-water depths.

**KEYWORDS:** ocean sunfish, *Mola mola*, pop-up satellite archival tag, Northwest Atlantic

**Introduction**

The ocean sunfish, *Mola mola*, is a large pelagic species distributed worldwide in both temperate and tropical oceans. A member of the family Molidae in the order Tetraodontiformes, *M. mola* is known for its unique body shape, large size (reaching 4.2 m and weighing up to 2300 kg), and atypical anatomy (Gregory and Raven 1934; Norman and Fraser 1949; Fraser-Brunner 1951; Bass et al. 2005). Sunfish are valued food fish in Asia and comprise a large portion of bycatch in Pacific and Mediterranean commercial fisheries (Silvani et al. 1999; Macias and de la Serna 2002; Cartamil and Lowe 2004; Lovgren 2004; Thys 2005). *M. mola* is a common resident of the offshore waters of the Northwest Atlantic during the spring and summer months, with an estimated summer population of 18,000 (Kenney 1996). Little is known about *Mola*
mola's basic ecology, distribution, or population dynamics, and the global status of the species is unknown.

Few studies have been conducted on the movement or behavior of M. mola, and there is no such information on the species in the northwestern Atlantic. Results from previous tagging studies on M. mola in other parts of the world indicate they spend the majority of their time in the top 50 m of the water column, with occasional dives to deeper depths (400-600 m) (Thys 2003; Cartamil and Lowe 2004; Thys et al. 2007; Sims et al. 2009a). A diel pattern has been observed in the vertical movements of ocean sunfish (Cartamil and Lowe 2004; Thys et al. 2007; Sims et al. 2009). Nocturnal vertical movements were limited to near-surface waters, while diurnal vertical movements included repeated dives below the thermocline. This diel pattern in diving behavior has been observed in other large pelagic fishes (blue sharks, swordfish, tunas) (Carey and Scharold 1990; Block et al. 2001; Sims et al. 2003) and is thought to be motivated by prey acquisition. In addition to prey acquisition and thermocline depth, other factors have been suggested as physiological influences on M. mola's diving behavior, including the depth of the DSL or chlorophyll maximum, changes in temperature, and a decreased oxygen concentration at depth (Thys 2003; Cartamil and Lowe 2004; Fulling et al. 2007). Ocean sunfish were so named for the common behavior of lying on their sides near the surface, appearing to "sunbathe," often with the dorsal fin protruding from the water. This has been suggested to be a mechanism of "thermal recharging" after deep dives in cold water (Thys 2003; Cartamil and Lowe 2004), or to solicit cleaning/parasite removal from below the surface (Thys, pers. communication 2009).
A tagging study on *Mola mola* in the North Pacific found dive behavior was dependent on both location of the fish and time of year. As fish moved south into the fall and winter months, their time at greater depths in deep water increased. As the fish returned north, they resumed a pattern of shallow diving (Thys 2003). Recent studies of ocean sunfish in both the North Pacific and eastern North Atlantic Oceans found a seasonal pattern of migration related to sea surface temperatures/thermal tolerance and decreasing chlorophyll levels (Thys et al. 2007; Sims et al. 2009).

The use of PSATs for tracking the vertical and horizontal movements of large pelagic animals over time has been established for many species including tuna, billfishes and sharks (Sims et al. 2003; Weng and Block 2004; Block et al. 2005; Wilson et al. 2005; Domeier 2006). Once attached to the study animal, PSATs record and store the time of sunrise and sunset, for use in geo-locating the tag each day, together with hourly temperature and pressure readings. These data can be recorded for over a year within the tag and then transmitted to Argos, via the tag, after the tag detaches and “pops up.” The tag can be programmed to release either on a specific date or after a preset time on the fish. After the preset release date/time has been reached, the PSAT releases from its tether, floats to the surface and initiates data transmissions to Argos. Each PSAT is equipped with a fail-safe mechanism that initiates release and data transmission if the tag reaches its depth limit (1200 m) or remains at a constant depth (i.e., does not change its depth significantly enough to be discerned by the tag’s pressure sensor) for 4 consecutive days. This mechanism is intended to release the tag if the animal is dead or the tag is floating at the surface.
The present study is the first to examine the movement and behavior of *Mola mola* in the northwestern Atlantic. The study's objectives were to examine the behavior and movement patterns of *M. mola* by attaching pop-up satellite archival tags (PSATs) to ocean sunfish during the summer and fall off the coast of New England.

**Materials and Methods**

Between 2005 and 2008, a total of 31 pop-up satellite archival tags (PSATs: model PTT-100, Microwave Telemetry, Columbia, MD, USA) was deployed on ocean sunfish, *Mola mola*, in the Northwest Atlantic. Twenty-nine were deployed during the summer and fall (August - October) of 2005, 2006, or 2007 (Figure 1). Fish were tagged in the Gulf of Maine (n=7) and in shelf waters to the south and east (within 80 km) of Nantucket Island (n=22). Five fish were tagged in 2005 as a pilot study. Fourteen fish were tagged in 2006, and 10 fish were tagged in 2007. Two additional fish were tagged in March 2008 in shelf waters off the coast of Georgia, USA. The objective of tagging fish in southeastern US waters was to capture their movement patterns in this region, as we observed many of the fish we tagged off the northeastern US during 2006 and 2007 to travel to this area during the late winter and early spring. PSATs were preprogrammed to release either five or eight months after deployment.

Fish were tagged from commercial tuna vessels (F/V *Peregrine*, F/V *Tenacious*; n=10) and a charter fishing vessel (F/V *Monomoy*; n=19) in the waters off the northeastern United States, and from a research vessel in Georgia (R/V *Margaurite*, Georgia DNR).
Fish basking at the surface were approached slowly by the vessel, and tags were attached via a modified wooden harpoon tagging pole, 2.5 m in length. Monofilament tethers (25 cm long, 250-lb test) were used to attach the PSATs to black nylon umbrella darts (darts designed and produced by Michael Domeier, Marine Conservation Science Institute). Tags were placed into the musculature approximately 15 cm below the base of the dorsal fin, just anterior to the clavus. Because the fish were not brought onboard or retained during the tagging procedure, measurements of size and weight were not taken. Based on observation, individual *Mola mola* tagged in the region were estimated to weigh approximately 130 to 230 kg with a total length of 1.35 to 1.64 m (estimated using growth equation from Watanabe and Soto 2008).

The PSATs recorded ambient light levels, temperature (resolution 0.17°C), and depth (resolution 5.38 m). Temperature and depth were sampled in most cases at 15-min intervals and stored as summary data.

**Horizontal Movement**

Daily geolocation position estimates of the fish were established from recorded high-resolution light data stored in the PSAT using a proprietary algorithm (Microwave Telemetry, Inc.), sea surface temperature, and bathymetry using the methods of Galuardi et al. (2009). The horizontal movement of tagged *M. mola* in the northwestern Atlantic is discussed in Chapter 1.
Vertical Movement

Depths and temperatures were recorded by the PSAT at 15-min intervals. To identify the presence of a diel pattern in vertical behavior, I used day-night differencing (mean daily depth – mean nightly depth), and applied a t-test to test for significant differences. The periods of “day” and “night” were defined for each individual and day depending on the location of the fish on each particular day and the resulting day length. Depth and temperature data retrieved by the tags were used to construct depth/temperature profiles that provided information on the surrounding water mass characteristics. The depth and temperature profiles based on PSAT data were compared to data from stationary buoys in the Gulf of Maine (part of the GOMOOS system) to confirm accuracy, and in combination with the corrected geolocation data, were used to identify the location of tagged fish. Depth-temperature plots were created from the raw PSAT data in R using methods of Galuardi (2009). For some analyses, the fish were divided into two groups—north and south of 35°N latitude. This was done to separate “northern/mid-Atlantic fish” and “southern fish,” because when they moved south of about 35°N latitude, their vertical behavior changed. Those fish defined as “northern/mid-Atlantic fish” or “northern” fish never moved below 35°N (n=14). Those defined as “southern fish” were tagged in New England and moved south of 35°N at some point during the course of their tagging period (n=9). Vertical behavior of fish was examined relative to water temperature by comparing depth data from individuals when in warm water (>24°C) to that of the same individuals in offshore, cooler water (<24°C). The basking behavior of *Mola mola* was examined by analyzing, for each fish, the amount of time per day fish spent in cold water (<10°C) and the amount of time during that same day that fish spent at the surface (0-6 m). If, as has
been suggested, ocean sunfish bask at the surface to recover from prolonged dives in cold water, then on days when the fish entered deep water, I expected they would spend a disproportionate amount of time afterwards (on the same day) thermally recharging at the surface.

**Results**

Twenty-five PSATs reported data back to Argos (Table 1). Tag attachment periods varied, as did the amount of data that was successfully stored and reported. Tag attachment periods ranged from 5 to 242 days. Eighteen tags were attached for 50 days or more, 10 of those were attached for 150 days or more, and 4 of them were attached for at least 240 days. Mean attachment period of all the tags reporting data was 107.2 ± 80.6 days, and mean data reported was 69.7 ± 33.1% (n=25). Two tags that were attached for 240 and 242 days, but with data retrieval of less than 20%, were removed from the analysis. Histograms of proportion of time spent at depth and temperature for individual fish with attachment periods >30 d (n=19) can be found in the Appendix (Figures 14-33). Fish spent 31.7% of their time in the top 10 m of the water column, and 59.8% of their time in the top 50 m (Fig. 2a). A very large proportion of total time—84.1%—was spent in the top 200 m, and the maximum depth recorded by any fish was 844 m.

Tagged *M. mola* spent 24.0% of their time between 18 and 20°C and 68.0% of their time between 14 and 22°C (Fig. 2b). Temperatures experienced by tagged fish ranged from 6 to 30°C. Examination of the behavior of southern fish (n=9) compared to the behavior of northern fish (n=14) showed southern fish exhibited more time at depth and less surface
time than northern fish (Figure 3a). Southern fish spent 24.1% of time at depths greater than 200 m, whereas fish that stayed north spent 10.6% of time at these depths, and twice as much time as southern fish in the top 10 m of the water column. Southern fish experienced warmer water temperatures than those that remained north (Figure 3b), with 17.4% of time spent at temperatures >22°C compared to 3.3% of time spent in these temperatures by northern fish. Southern fish encountered warm sea surface temperatures for a longer period of time in shelf waters (14° to 19°C during the months of November through May) and were in closer proximity to the warm waters of the Gulf Stream (>26°C) than fish that remained in northern shelf and offshore waters (8 to 20°C during the months of August through May).

There was a diel pattern in vertical behavior. Tagged *M. mola* spent more time at depth during the day and inhabited shallower waters at night. Mean daytime depth of all fish pooled in the dataset was 107.8 (±21.2) m and mean nightly depth was 72.0 (±12.4) m (n=23). Mean day-night difference of all fish was 51.8 (±12.0) m (t-test, p=0.004). Though those fish that traveled south experienced a greater range of depth, the day-night difference was the same as for fish that remained north. Mean daytime depth of all southern fish was 150.0 (±32.2) m and mean nightly depth was 101.8 (±15.4) m (n=9). Mean day-night difference for southern fish was 45.2 (±18.8) m (t-test, p=0.047). Mean daytime depth for northern fish was 67.4 (±23.6) m and mean nightly depth was 26.9 (±7.01) m (n=9). The mean day-night difference was not significant for northern fish (45.3±18.2 m; t-test, p=0.055). A table listing the day-night differences of all individual fish can be found in Appendix Table 2. Ocean sunfish changed their dive behavior over
the course of the tagging period, from shallow dives with a high proportion of surface
time to deeper dives and less time at the surface. Mean daily depth of each individual
(mean depth of fish during daylight hours) increased as did the mean day-night difference
(Figure 4a-e). Mean daily depth and mean day-night difference of remaining tagged fish
with attachment periods of >30 days and data return >30% (n=14) can be found in the
Appendix.

Vertical behavior of *Mola mola* changed as the fish traveled south. When in New
England shelf waters, tagged fish exhibited shallow, frequent diving to depths of 50-100 m with a high frequency of surface time. During the first several days of the tagging
period for those fish tagged inshore, the maximum dive depth exhibited by an individual
may have reached the bottom. However, within a one-week period fish moved to deeper
water and maximum dive depths did not approach the depth of the bottom. Analysis of
the mean and maximum daily depths compared to the bottom depth was examined for
several individuals, and apart from the initial few days after tagging, bottom depths were
much deeper than maximum daily depth. In contrast, as fish moved off the shelf to the
south and east they changed both the depth and frequency of diving (Figure 5a-c). Plots
of the depth data of individual fish with concurrent temperature data show *M. mola*
making regular descents below the thermocline into cooler waters. As fish moved into a
water mass with a deeper mixed layer they adjusted their vertical behavior to dive below
it (Figure 6a-b). This was especially apparent when fish entered the Gulf Stream as they
spent little time at the surface and dove to depths of 400-600 m. In some cases, fish spent
a period of days at depth with no surface interval. The mean hourly depth of four fish in
warm, Gulf Stream water (SST >24°C) was significantly deeper (150-400 m) than the mean hourly depth of the same fish when in cooler, offshelf water (15-35 m) (repeated measures ANOVA, p<0.001; Figure 7 (a-b)).

There was no observed relationship between the amount of time per day fish spent in cold water (<10°C) and the amount of time fish spent at the surface (0-6 m) (Figure 8). At the beginning of the tagging period, tagged ocean sunfish spent little to no time in cold water, and exhibited a high daily proportion of surface time. As the tagging period progressed, fish spent more time per day in cold water, and little to no time at the surface (Appendix Figure 58). Examination of the raw depth/temperature data of an individual fish (Appendix Figure 59) is used as an example. Even when this individual remained in very cold water (<5°C) for about 5 hours (1700-2200 h) it did not spend a disproportionately long time in the warmer surface waters after it ascended. Though the fish did not surface, it returned to warmer water at mid-water depths after prolonged exposure to very cold temperatures. Examining this phenomenon on a broader scale however, showed there to be no observed relationship between the amount of time per day fish spent in cold water (<10°C) and the amount of time fish spent in warm water (>20°C) (Appendix Figure 60). Because depth data were limited to 15-minute intervals, I was not able to calculate the individual rates of descent and ascent for tagged animals, however a previous study of juvenile (small) ocean sunfish using acoustic tags found the typical rate of descent to be 8.4 ± 5.6 m/min (Cartamil and Lowe 2004). Based on this information, it is not likely that tagged ocean sunfish were surfacing from depths > 200 meters in between the 15-minute intervals when depth of the fish was recorded by the tag.
Two of the 25 sunfish tagged entered the Gulf of Mexico. One fish tagged in September 2005 in New England reached the Gulf of Mexico in December before the tag detached. The second fish was tagged in Georgia shelf waters in March of 2008, traveled south to the Gulf of Mexico in June, and remained there until early July. Data return from these tags was limited (22% and 33%). Analysis of data from the second fish shows that, like other individuals tagged in the study, the fish showed a diel pattern in its diving behavior, with a mean day-night difference of 23.2 m. Once in the Gulf of Mexico, the fish altered its diving behavior to greater depths and shorter surface times when compared to its behavior in Southeast US shelf waters (Figure 9). Prior to entering the Gulf of Mexico, over the shelf and shelf edge off the southeastern United States during the spring and early summer, the fish spent 69% of its time in the top 25 m of the water column, 90% of its time in the top 200 m, and occasionally dove to between 200 and 250 m. Once in the Gulf of Mexico in June and July, the fish spent less than 3% of time in the top 10 m of the water column, 90% of its time between 25 and 200 m, and had occasional dives to 400 m (Figure 10). While in the Gulf of Mexico, the fish experienced temperatures ranging from 8.3°C to 28°C, with 22.8% of time spent between 20 and 22°C and an average water temperature of 18.23 (± 4.96)°C.

Discussion

PSAT-tagged sunfish exhibited a wide range of vertical behavior, which varied over both geographic and temporal scales. Ocean sunfish in northeastern US waters in the summer months exhibited shallower swimming depths than those that moved south in the winter
and spring. The change in vertical behavior was likely driven by temperature and thermocline depth. In some cases, particularly in shallow shelf waters, diving depth was constrained. During the tagging period from late August to October, sea surface temperatures off New England ranged from 17° to 20°C. In the summer and fall, the water column in the region is highly stratified with a strong thermocline in the top 10-20 m and a shallow mixed layer (Lalli and Parsons 2006; Mann and Lazier 2006). Tagged ocean sunfish in the region at this time spent a high proportion of time near the surface with frequent dives to depths of less than 200 m. These waters comprise a well-established foraging ground for many large pelagic species during the summer months (Carey and Robinson 1981; Block et al. 2001; Stokesbury et al. 2004; Wilson et al. 2005). The leatherback sea turtle, another gelatinous zooplanktivore, exhibits a similar behavior pattern in the shelf and slope waters of the northeastern United States during the summer months. Leatherback dive depths are shallow, and durations are short, which has been identified as feeding behavior (James et al. 2005; Eckert 2006). Like leatherbacks, ocean sunfish are believed to feed primarily on gelatinous zooplankton, and the distribution of M. mola has been associated with areas where jellyfish are abundant (Desjardin 2005; Houghton et al. 2006). The similarities in vertical behavior between the species suggests that like leatherbacks, M. mola is foraging in northeastern US shelf and slope waters, taking advantage of the high concentrations of gelatinous prey found in the region (Shoop and Kenney 1992; Madin et al. 2006).

Ocean sunfish that moved south into the waters of the mid-Atlantic and southeastern United States in the winter and early spring spent less time at the surface and more time
at depths deeper than 200 m. This shift in vertical behavior was associated with a move to weakly stratified water masses with a deep mixed layer. The shelf waters off the Mid-Atlantic are weakly stratified in the winter due to mixing and cooling (Werner 1999). As ocean sunfish moved into these waters, they adjusted their vertical behavior to deeper depths, perhaps following a thermal gradient and/or searching for vertically migrating prey of the deep scattering layer (DSL). The DSL is the most studied migrating layer of gelatinous zooplankton, containing physconectid siphonophores and myctophid fishes (Barham 1966; Graham et al. 2001). Diel vertical migration (DVM) is widespread among hydromedusae and ranges from a few to hundreds of meters (Graham et al. 2001; Madin et al. 2006; Hosia and Bamstedt 2008). Studies of other large pelagic species such as bluefin tuna and basking sharks in both the Pacific and North Atlantic have noted similar differences in vertical distribution associated with water column structure on a seasonal scale (Lutcavage et al. 1997b; Kitagawa et al. 2000; Sims et al. 2003; Wilson et al. 2005).

A study on ocean sunfish in the Pacific also found the fish exhibited differing dive behaviors dependent on location and season. In August, vertical movement was shallow and surface oriented (to 40 m), and shifted to deeper depths (100-300 m) as the fish moved south in the winter months. It was suggested that *Mola mola* decreased time spent at the surface in the fall and winter months as a result of a seasonal increase in surface wave action in the region (Thys 2003). In waters of the southeastern United States, leatherback sea turtles, *D. coriacea*, dive deeply for long periods of time which is a reflection of their foraging in the DSL (Eckert 2006). A study comparing the vertical niche overlap of leatherbacks and ocean sunfishes in waters off South Africa suggested
that like leatherbacks, ocean sunfish exhibit plasticity in their vertical behavior.

Individual ocean sunfish respond to patchily distributed gelatinous prey with differing levels of diel vertical migration, which is reflected in a shift from predation on seasonally abundant surface medusa during the summer to vertically migrating gelatinous species found at deeper depths during the winter months (Hays et. al 2009; Pope et al. 2010).

The shift in vertical behavior from shallow to deeper depths was especially apparent when tagged sunfish entered the Gulf Stream. Once in the Gulf Stream, fish spent little time at the surface and dove to depths of 400-800 m. In some cases, fish spent a period of days at depth with no surface interval. The Gulf Stream flow field extends deep into the water column where nutrient concentrations are maximized (Palter and Lozier 2008), and a migratory DSL has been detected in the Gulf Stream with diurnal migration to depths of 450 meters (Cole et al. 1971). The deep diving exhibited by ocean sunfish in the Gulf Stream is likely a reflection of prey searching behavior, and exploiting the high concentration of prey at depth. In addition to the warm sea surface temperatures and a deeply mixed water column, swift northward moving surface currents may have motivated southward moving fish to remain at depth and avoid the surface currents. The increase in deep diving and time at depth observed in _M. mola_ in the Gulf Stream differs from the behavior of bluefin tuna, which upon entering the Gulf Stream decreased their depths and ceased diving. The strong thermal gradients associated with the Gulf Stream and the cooler underlying water were suggested to influence the dive behavior of bluefin tuna in the Gulf Stream, causing them to stop any extensive vertical movement. Once out of the Gulf Stream and in cooler, relatively homogenous waters along its edge, deep
diving resumed (Wilson et al. 2005). Unlike fast-swimming, endothermic bluefin tuna for which adaption to such intense vertical thermogradients would be energetically costly, *M. mola* moves at slower swimming rates, and may benefit from the decreased metabolic demands of cooler temperatures found at depth in the Gulf Stream.

In addition to a shift to increased depth, ocean sunfish also altered the frequency of vertical behavior, shifting from high-frequency diving and surfacing to consecutive days of time at depth with no surface intervals. The high-frequency diving with extensive movement in the water column likely reflects prey searching behavior, and has been observed in another study of *Mola mola* in the eastern Atlantic (Sims et al. 2009), as well as in other large pelagic fishes such as the basking shark, *Cetorhinus maximus*, and bluefin tuna, *Thunnus thynnus* (Sims et al. 2003; Wilson et al. 2005). A recent study on the retinal topography of immature *M. mola* suggested that the location of their main visual axis allowed for prey detection when migrating vertically through the water column as well as when foraging near the sea bottom (Kino et al. 2009). In the study, the region of highest density of retinal ganglion cells of all individuals examined was located at the dorsatemporal margin, and the main visual axis was directed toward the lower frontal portion of the visual field (10-20° below the horizon). These results, combined with the established vertical migratory behavior of *M. mola*, led the investigators to suggest that ocean sunfish detect their prey during their descent through the water column, as well as on the ocean floor (Kino et al. 2009). Findings from the present study show ocean sunfish making frequent descents through the water column, deeper during the day and shallower at night, presumably searching for its diel vertically migrating
gelatinous prey.

It has been suggested that *M. mola* basks at the surface as a mechanism of “thermal recharging” after deep dives in cold water (Thys 2003; Cartamil and Lowe 2004). In the present study of ocean sunfish in the northwestern Atlantic, there was no observed relationship between the amount of time per day fish spent in cold water (<10°C) and the amount of time fish spent at the surface (0-6 m). Tagged ocean sunfish spent a large proportion of time at the surface in Northeast US waters in the late summer and early fall where the water was highly stratified with a shallow mixed layer and the warmest temperatures at the surface. Basking at the surface in the shelf waters off the northeastern United States has also been observed in swordfish, *Xiphias gladius*, and is believed to be part of a recovery process to warm muscles and aid in digestion after deep dives in cold water (Carey and Robinson 1981). Leatherback sea turtles exhibit a high proportion of surface time in northern waters and also bask at the surface, which has been suggested to facilitate digestion and maintenance of body temperatures after consuming large amounts of cold prey in cooler waters (Eckert et al. 1989). If *Mola mola* is also feeding on the large quantities of gelatinous zooplankton in the region, it may equally benefit from recovery time at the surface. As sunfish moved south and encountered warmer, mixed water masses (particularly the Gulf Stream) they dove deeper and, if seeking a recovery period after time at depth, may have gained thermal benefits from the warm temperatures found at mid-water depths. A study of swordfish in the Southeast Pacific found that during the day some fish combined deep dives with short stays above the thermocline and were thought to be feeding on organisms in the DSL (Abascal et al. 2009).
Basking behavior in ocean sunfish has also been suggested to facilitate recovery after diving into the oxygen minimum layer, as has been observed in other large pelagic fishes (Carey and Robinson 1981; Cartamil and Lowe 2004; Thys 2007). Given that the northwestern Atlantic is well oxygenated at depth, basking behavior may be observed with more frequency in populations inhabiting oceans where oxygen minimum zones occur. The large size of *M. mola* in the present study may also play a role in basking behavior if related to thermal tolerance, as larger fish may be buffered against temperature differences more so than smaller fish. Cartamil and Lowe (2004) found that dive ‘recovery times’ (i.e. the post-dive period) of ocean sunfish spent in the near-surface mixed layer increased significantly as a function of maximum dive depth in their study of eight fish with an average TL of 1.08 m. In the present study, fish ranged in size from approximately 1.35 to 1.64 m TL, and their large size may afford them the advantage of a higher thermal tolerance and the ability to remain in cool waters longer than smaller fish. The importance of large body mass in maintaining elevated body temperatures relative to the environment has been suggested for sea turtles and bluefin tuna (Sato et al. 1994; Kubo et al. 2008).

Basking behavior may also benefit *M. mola* as a mechanism of parasite removal. *M. mola* is known to harbor up to 40 different genera of parasites, and seagulls have been observed picking parasites from the bodies of basking individuals, though this relationship has not been examined (Thys 2000; Pope et al. 2010). Basking at the surface is also likely to attract cleaning species from below, as a floating ocean sunfish serves as “flotsam”, and acts as a natural attractant for marine animals. *M. mola* have been
associated with cleaner fish in both California and Indonesia (Cartamil and Lowe 2004; Pope et al. 2010).

There was a clear diel pattern in vertical behavior of *Mola mola*. *Mola* visited deeper depths during the daylight hours and remained in shallower waters at night. The diel pattern has been observed in other studies of the species (Cartamil and Lowe 2004; Thys et al. 2007; Sims et al. 2009), in other large pelagic fishes (basking sharks, blue sharks, swordfish, tunas) (Carey 1990; Carey and Scharold 1990; Block et al. 2001; Sims et al. 2003), and in leatherback sea turtles (Eckert et al. 1989). In the present study, ocean sunfish maintained these distinct differences in vertical behavior even as their overall depth profiles shifted to deeper waters over time which reflects the prey searching and foraging behavior of the species in different water masses. Once in open water, ocean sunfish were likely foraging on organisms in the DSL, a vertically migrating layer of fishes and siphonophores, which is typically found at depths up to 750 meters during the day and migrates to the surface, or near-surface, waters at night (Barham 1966; Graham et al. 2001; Lalli and Parsons 2006). Leatherback sea turtles and swordfish exhibit similar diel patterns, reaching great depths during the daylight hours, and are believed to feed on organisms in the DSL (Eckert et al. 1989; Abascal et al. 2009).

Two fish in the study entered the Gulf of Mexico during different times of year: winter (December – January) and summer (June – July). *Mola mola* is a year-round resident of the northern Gulf of Mexico with the greatest densities reported in the winter and spring (Desjardin 2005; Fulling et al. 2007). The fish that entered the Gulf of Mexico during
summer encountered sea surface temperatures approaching 30°C, warmer than
temperatures that other tagged fish encountered, and warmer than previous studies
suggest is the thermal preference of the species (Thys 2007; Fulling 2007; Sims et al.
2009). While in the Gulf of Mexico, fish spent little time at the surface, more time at
depth, and remained in close proximity to the shelf and Loop Current. Similar behavior
was noted in a sharptail mola, *Masturus lanceolatus*, tagged with a PSAT in the northern
Gulf of Mexico (Seitz et al. 2002). The fish rarely surfaced and spent most of its time in
the top 200 m of the water column, with occasional dives to deeper than 700 m. It was
suggested that sea surface temperatures in the Gulf of Mexico may have been above the
fish’s thermal tolerance. A study of blue marlin, *Makaira nigricans*, in the Gulf of
Mexico Loop Current found that they spent a large proportion of time at depths around
200 m, where the thermocline is found (Wells et al. 2009). Likewise, the shift in vertical
behavior of *Mola mola* when it entered the Gulf of Mexico is likely a result of the deep
thermocline found there. Leatherback sea turtles, bluefin tuna, and several billfish species
are known to associate with the Gulf of Mexico Loop Current (Maul et al. 1984; Block et
al. 2005; Desjardins 2005; Wells et al. 2009). The motivation for these animals to enter
the region is not known, however the Gulf of Mexico and specifically the Loop Current is
an established spawning ground for several large pelagic fish species, including
swordfish and bluefin tuna (McGowan and Richards 1989; Block et al. 2005; Stokesbury
et al. 2004; Wells et al. 2009). More investigation is needed into the reproductive biology
of the species as well as the presence of *Mola mola* in the Gulf of Mexico.
Of the 31 PSATs deployed on *Mola mola* between 2005 and 2008, 11 remained attached until the programmed pop-up date. Six never reported data, and 14 detached prematurely. One reason for premature detachment was the activation of the tag’s fail-safe mechanism that caused its release due to what was perceived by the tag as constant pressure (i.e., the change in the fish’s depth was less than the resolution of the tag (5.38 m) over a four-day period). This was known to occur for six tags, and in all of these cases the fish showed steady horizontal movement in shelf waters. This often occurred when fish were located in very shallow waters (<10 meters) around Nantucket Island where they presumably were feeding on large patches of gelatinous prey (salps and jellyfish) observed in the area. One fish, however, ceased horizontal movement, and apparently died and sank to the bottom shortly after tagging. Other possible causes of premature detachment include tag shedding/tissue rejection due to improper placement of the tag, corrosion or fouling of the tag, and mechanical failure. In species like *Mola mola* that are known to bask at the surface or spend extended periods of time in shallow water, the fail-safe mechanism on the tag should be modified to prevent premature detachment. The tagging method in the present study did not involve containment of the fish due to their large size and the resulting difficulty in handling them. In the future, developing a method that contained or captured the fish prior to tagging would ensure proper tag placement and enable the collection of other valuable information such as length, weight, sex, and reproductive state.

The present study is the most extensive to date on the movement and behavior of *Mola mola*. My results establish a baseline of movement and behavior data from ocean sunfish
in the Northwest Atlantic, and provide early insight into the understanding of its habitat preferences, migration routes, behavior, and environmental associations. Data on distribution and seasonal movements of *Mola mola* may prove useful indicators of nutrient-rich areas with high productivity, where other marine organisms of important commercial value or endangered status are found.

Future studies are needed to gain a more complete understanding of the movement and behavior patterns of the species in the Northwest Atlantic and other parts of the world. In addition to studies on movement and behavior, studies on such basic biological information as age, growth, and reproduction are necessary to thoroughly examine the biology of the species and its role in the North Atlantic ecosystem.
Table 2.1. Date of deployment, location of deployment and pop-off, number of days attached, straight line distance (SLD) traveled, and percentage of data reported for 31 PSAT’s attached to *Mola mola* between 2005-2008.

<table>
<thead>
<tr>
<th>PSAT ID</th>
<th>Dep. Date</th>
<th>Deployment Location (°N)</th>
<th>Deployment Location (°W)</th>
<th>Pop-off Location (°N)</th>
<th>Pop-off Location (°W)</th>
<th>Days attached</th>
<th>SLD (km)</th>
<th>Data return</th>
</tr>
</thead>
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<tr>
<td>14538</td>
<td>9/3/2005</td>
<td>41.37</td>
<td>69.31</td>
<td>23.21</td>
<td>85.73</td>
<td>130</td>
<td>2520</td>
<td>22%</td>
</tr>
<tr>
<td>8776</td>
<td>10/2/2005</td>
<td>42.04</td>
<td>70.02</td>
<td>40.19</td>
<td>68.93</td>
<td>24</td>
<td>222</td>
<td>100%</td>
</tr>
<tr>
<td>67322</td>
<td>8/17/2006</td>
<td>43.15</td>
<td>69.98</td>
<td>31.35</td>
<td>79.298</td>
<td>153</td>
<td>1565</td>
<td>55%</td>
</tr>
<tr>
<td>67325</td>
<td>8/18/2006</td>
<td>40.96</td>
<td>70.51</td>
<td>32.23</td>
<td>78.98</td>
<td>153</td>
<td>1206</td>
<td>46%</td>
</tr>
<tr>
<td>67321</td>
<td>8/23/2006</td>
<td>40.82</td>
<td>70.66</td>
<td>26.94</td>
<td>79.94</td>
<td>143</td>
<td>1685</td>
<td>64%</td>
</tr>
<tr>
<td>67331</td>
<td>9/1/2006</td>
<td>41.29</td>
<td>69.96</td>
<td>39.42</td>
<td>74.21</td>
<td>74</td>
<td>1830</td>
<td>96%</td>
</tr>
<tr>
<td>67332</td>
<td>9/8/2006</td>
<td>42.24</td>
<td>70.03</td>
<td>27.18</td>
<td>78.33</td>
<td>13</td>
<td>415</td>
<td>82%</td>
</tr>
<tr>
<td>67330</td>
<td>9/17/2006</td>
<td>41.26</td>
<td>69.28</td>
<td>38.86</td>
<td>71.19</td>
<td>242</td>
<td>312</td>
<td>40%</td>
</tr>
<tr>
<td>67565</td>
<td>9/17/2006</td>
<td>41.29</td>
<td>69.24</td>
<td>33.89</td>
<td>76.30</td>
<td>242</td>
<td>1022</td>
<td>18%</td>
</tr>
<tr>
<td>67327</td>
<td>9/19/2006</td>
<td>41.20</td>
<td>69.59</td>
<td>32.38</td>
<td>78.71</td>
<td>153</td>
<td>1250</td>
<td>31%</td>
</tr>
<tr>
<td>67333</td>
<td>9/19/2006</td>
<td>41.19</td>
<td>69.59</td>
<td>30.46</td>
<td>81.41</td>
<td>240</td>
<td>1590</td>
<td>4%</td>
</tr>
<tr>
<td>67323</td>
<td>9/23/2006</td>
<td>41.17</td>
<td>69.58</td>
<td>32.56</td>
<td>78.37</td>
<td>153</td>
<td>1235</td>
<td>51%</td>
</tr>
<tr>
<td>67564</td>
<td>9/25/2006</td>
<td>41.31</td>
<td>69.99</td>
<td>39.92</td>
<td>70.17</td>
<td>14</td>
<td>148</td>
<td>100%</td>
</tr>
<tr>
<td>67328</td>
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<td>41.30</td>
<td>69.97</td>
<td>28.28</td>
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<td>1690</td>
<td>78%</td>
</tr>
<tr>
<td>77073</td>
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<td>41.39</td>
<td>70.05</td>
<td>41.49</td>
<td>70.12</td>
<td>5</td>
<td>30</td>
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<tr>
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<td>41.29</td>
<td>69.95</td>
<td>37.30</td>
<td>73.17</td>
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<td>84%</td>
</tr>
<tr>
<td>77070</td>
<td>9/14/2007</td>
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<td>69.95</td>
<td>33.52</td>
<td>77.75</td>
<td>68</td>
<td>1105</td>
<td>92%</td>
</tr>
<tr>
<td>77057</td>
<td>9/20/2007</td>
<td>41.27</td>
<td>69.98</td>
<td>39.63</td>
<td>74.10</td>
<td>31</td>
<td>419</td>
<td>100%</td>
</tr>
<tr>
<td>77077</td>
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<td>41.13</td>
<td>70.03</td>
<td>41.23</td>
<td>70.62</td>
<td>11</td>
<td>50</td>
<td>100%</td>
</tr>
<tr>
<td>77069</td>
<td>9/24/2007</td>
<td>41.21</td>
<td>70.14</td>
<td>38.64</td>
<td>67.76</td>
<td>153</td>
<td>338</td>
<td>73%</td>
</tr>
<tr>
<td>77071</td>
<td>10/3/2007</td>
<td>41.26</td>
<td>70.22</td>
<td>40.37</td>
<td>73.33</td>
<td>9</td>
<td>283</td>
<td>100%</td>
</tr>
<tr>
<td>77072</td>
<td>10/6/2007</td>
<td>42.63</td>
<td>70.37</td>
<td>36.55</td>
<td>75.64</td>
<td>50</td>
<td>793</td>
<td>96%</td>
</tr>
<tr>
<td>67326</td>
<td>10/6/2007</td>
<td>42.38</td>
<td>70.27</td>
<td>36.74</td>
<td>71.64</td>
<td>152</td>
<td>645</td>
<td>72%</td>
</tr>
<tr>
<td>77074</td>
<td>3/11/2008</td>
<td>30.79</td>
<td>80.76</td>
<td>31.74</td>
<td>80.17</td>
<td>57</td>
<td>110</td>
<td>64%</td>
</tr>
<tr>
<td>77078</td>
<td>3/11/2008</td>
<td>30.90</td>
<td>80.66</td>
<td>32.51</td>
<td>78.38</td>
<td>242</td>
<td>280</td>
<td>33%</td>
</tr>
</tbody>
</table>
**Figure 2.1.** Map of deployment locations (green circles) and endpoints (red triangles) of 31 PSATs attached to *Mola mola* between 2005 and 2008. Tags were attached in New England waters between the months of August and October in 2005–2007 (n=29) and in Georgia shelf waters in March 2008 (n=2). Tags were attached from 5 to 242 days.
**Figure 2.2.** Histograms showing proportion of time at depth (a) and proportion of time at temperature (b) for all fish (n=23). Fish were tagged in New England waters between the months of August and October in 2005–2007 and in Georgia shelf waters in March 2008. Tags were attached from 7 to 242 days.
Figure 2.3. Histograms showing proportion of time at depth (a) and time at temperature (b) for ocean sunfish that remained above 35°N and fish that traveled below 35°N. Fish were tagged in New England waters between the months of August and October in 2005–2007. Fish that remained above 35°N had attachment periods from 7 to 242 days (mean=86 d; n=9). Fish that traveled below 35°N had attachment periods from 68 to 153 days (mean=122 d; n=14).
Figure 2.4. Mean daily depth (a, d), mean nightly depth (b, e), and mean day-night difference (c, f) of two tagged *Mola mola*. ID 67328 (a, b, c) was tagged on 9/25/06 off Nantucket Island. The tag was attached for 70 days and popped off when the fish was in offshore waters off Florida on 12/7/06. ID 77069 (d, e, f) was tagged off Nantucket Island on 9/24/07 and was attached for 153 days before detaching when the fish was in mid-Atlantic offshore waters on 2/24/08.
Figure 2.4. Mean daily depth (a, d), mean nightly depth (b, e), and mean day-night difference (c, f) of two tagged *Mola mola*. ID 67328 (a, b, c) was tagged on 9/25/06 off Nantucket Island. The tag was attached for 70 days and popped off when the fish was in offshore waters off Florida on 12/7/06. ID 77069 (d, e, f) was tagged off Nantucket Island on 9/24/07 and was attached for 153 days before detaching when the fish was in mid-Atlantic offshore waters on 2/24/08.
Figure 2.4. Mean daily depth (a, d), mean nightly depth (b, e), and mean day-night difference (c, f) of two tagged *Mola mola*. ID 67328 (a, b, c) was tagged on 9/25/06 off Nantucket Island. The tag was attached for 70 days and popped off Florida on 12/7/06. ID 77069 (d, e, f) was tagged off Nantucket Island on 9/24/07 and was attached for 153 days before detaching in mid-Atlantic offshore waters on 2/24/08. The Y-axis label “Day” in figures c and f refer to a 24 hour period.
Figure 2.5. Depth data (m) for fish 67321 for three 7-day periods when located in: a) coastal/shelf waters off New England; b) offshore waters off Virginia and North Carolina; and c) offshore waters off Florida. The fish was tagged on 8/23/06 in waters off New England. The tag was attached for 143 days and popped off when the fish was around the Bahamas on 1/23/07. Gray bars indicate night.
Figure 2.6. Depth and corresponding temperature data from: a) fish 67321; and b) fish 67332. 67321 was tagged on 8/23/06 in waters off New England. The tag was attached for 143 days and popped off when the fish was around the Bahamas on 1/23/07. 67332 was tagged on 9/8/2006 in the Gulf of Maine. The tag was attached for 74 days and came off when the fish was around the Bahamas on 11/25/06.
Figure 2.7. Mean hourly depths (± SD) of four tagged ocean sunfish during a one-week period when they were in warm offshore water (>24°C) (a) and a one-week period in cooler offshore water (<24°C) (b). Time is in GMT.
Figure 2.8. Daily surface time (proportion of time at 0-6m per 24h) vs. time in cold water (proportion of time in temperatures <10°C per 24h) for four ocean sunfish (ID’s: 67321, 67332, 67328, 67322).
Figure 2.9. Depth and corresponding temperature data from fish 77078. The fish was tagged over the Georgia shelf on 3/11/2008. The tag was attached for 242 days and popped off when the fish was on the shelf edge off South Carolina. Arrow indicates when the fish entered the Gulf of Mexico.
Figure 2.10. Histogram showing proportion of time-at-depth for ocean sunfish ID 77078 when it was in the Gulf of Mexico (n=28 d) and in southeast US waters (n=92 d). The fish was tagged from 3/11/2008 to 11/11/2008.
CHAPTER 3

DISTRIBUTION OF OCEAN SUNFISH (FAMILY MOLIDAE) IN US EASTERN SHELF WATERS BASED ON EXISTING AERIAL SURVEY RECORDS

Abstract

The ocean sunfish, *Mola mola*, has a worldwide distribution and is a common resident of the Northwest Atlantic Ocean. Notable for its unusual anatomy and large size, the biology and distribution of the species is largely unknown. Aerial survey data from the OBIS-SEAMAP database were used to analyze the distribution of the ocean sunfish (Family Molidae), in US East Coast shelf waters. Three areas along the eastern shelf were defined for analysis using latitude (40-45°N, 35-40°N, and 28-35°N). For each designated area, a mean SPUE (*Mola* per survey hour) was determined for each month. Ocean sunfish were not the targeted species for the surveys, therefore there was a lack of data in certain regions and times of year. Analysis of sightings data showed high numbers of animals in the Northeast and Mid-Atlantic in the summer and fall, and high numbers of animals in the Southeast in the winter and spring. Results demonstrate the annual shift in distribution of ocean sunfish along the eastern US shelf, suggesting a seasonal migration from Northeast to Mid-Atlantic and Southeast shelf waters. Cooling sea surface temperatures and decreasing productivity in the Northeast during the fall are likely driving factors in the migration of ocean sunfish south. Though helpful in determining spatial and temporal patterns of distribution, reliance on aerial survey data for abundance
estimates of ocean sunfish is problematic. When combined with tagging studies, such data provide a more complete picture of the movement pattern of the species.

KEYWORDS: ocean sunfish, *Mola mola*, aerial survey data, Northwest Atlantic

**Introduction**

The ocean sunfish, *Mola mola*, is a large, pelagic fish that is distributed worldwide in both temperate and tropical oceans. A member of the family Molidae in the order Tetraodontiformes, *M. mola* is known for its unique body shape, large size (reaching 4.2 m and weighing up to 2300 kg), and atypical anatomy (Gregory and Raven 1934; Norman and Fraser 1949; Fraser-Brunner 1951; Bass et al. 2005). In addition to *Mola mola*, which is the most common member of the family, there are three additional species of molid: the sharptail mola, *Masturus lanceolatus*, the rare slender mola, *Ranzania laevis*, and the southern sunfish, *Mola ramsayi*. *M. ramsayi*, first described by Giglioli (1883) is confined to the southern hemisphere and was recently resurrected based on a genetic study of the family (Bass et al. 2005).

Little is known about *Mola mola*’s basic ecology, distribution, or population dynamics, and the global status of the species is completely unknown. Sunfish were so named for the common behavior of lying on their sides near the surface, appearing to “sunbathe,” often with the dorsal fin protruding from the water. They are commonly found singly, are often associated with surface swarms of salps or jellyfish on which they are believed to feed (Norman and Fraser 1949; Klein-MacPhee 2002.), and commonly occur along frontal features where these prey are concentrated (Sims and Southall 2002; Desjardin 2005; Houghton et al. 2006). As has been suggested for the basking shark, *Cetorhinus*...
maximus, another large pelagic zooplanktivore, data on the distribution and seasonal movements of Mola mola may provide a useful indication of nutrient-rich areas with high productivity, where other marine organisms of commercial important or endangered status are found (Sims et al. 2003).

Few studies have been conducted on the distribution of M. mola. Members of the family Molidae are globally distributed, and M. mola is a common resident of the offshore waters of the Northwest Atlantic during the spring and summer months, with an estimated summer population of 18,000 (Kenney 1996). It is virtually absent in these areas in the winter and fall. There are conflicting reports about the swimming ability of ocean sunfish. Existing information on natural history suggests M. mola moves primarily by passive transport via ocean currents (Norman and Fraser 1949; Lee 1986; Klein-MacPhee 2002) but recent studies using acoustic telemetry and satellite tagging show that ocean sunfish are active swimmers, capable of highly directional vertical and horizontal movement (Thys 2003; Cartamil and Lowe 2004; Sims et al. 2009). Furthermore, a study examining genetic divergence in the ocean sunfish family found species in the family Molidae to be subdivided on a global scale, dismissing the theory of passive drifting as the primary mode of transport (Bass et al. 2005).

The conspicuous nature of ocean sunfish when basking at the ocean’s surface is conducive to studies on its distribution based on aerial survey data and shipboard survey records. The earliest study of this nature by Kenney (1996) examined aerial survey records (source: Cetacean and Turtle Assessment Program (CETAP)) of ocean sunfish.
(family *Molidae*) and the leatherback turtle, *Demochelys coriacea*, in waters off the northeastern United States. Peak monthly sighting frequency of ocean sunfishes was in August (27% of all sightings), with peak abundances during the spring on Georges Bank and during the summer in the Gulf of Maine. There were no sightings reported during the winter in the Gulf of Maine, Georges Bank, and southern New England. The number of ocean sunfish in shelf waters from the Gulf of Maine south to Cape Hatteras, NC, was estimated to reach 18,000 in the summer months. Leatherbacks and ocean sunfishes shared the same temporal pattern of occurrence, with a peak off the northeastern United States during the late summer months.

Desjardin (2005) examined aerial surveys (sources: National Marine Fisheries Service (NMFS) and CETAP) of ocean sunfish (family *Molidae*) and the leatherback turtle, *Demochelys coriacea*, from the years 1978 to 2002, to estimate the seasonal distribution and co-occurrence of the two groups in western Atlantic shelf waters. Leatherbacks and ocean sunfishes were studied together because, like the leatherback, ocean sunfishes are suspected to feed primarily on gelatinous zooplankton, potentially making the two groups competitors (Kenney 1996; Desjardin 2005). Results of the study showed leatherbacks and ocean sunfishes to have similar patterns of distribution associated with season in the northeastern United States, though ocean sunfish were more abundant and evenly distributed throughout the region. Members of the family *Molidae* (*Mola mola* or *Masturus lanceolatus*) were present in New England waters from February to December with a peak in June. Southeast surveys (from Cape Hatteras, North Carolina to central Florida within the 200-m isobath) conducted between January and March reported
sightings, indicating these waters were inhabited by both species during colder months of year. In the Gulf of Mexico, leatherbacks and ocean sunfish showed different spatial and temporal patterns, with leatherbacks observed year-round and molids only sighted during some months of the year (February, March, May, July – November). The study suggested that molids and leatherbacks leave New England waters in the autumn and winter and return to the region in large numbers during the spring and summer in correspondence with warming water temperatures and an increase in zooplankton. Observations of leatherbacks and ocean sunfishes also showed a great amount of overlap in northern shelf waters of the Mid-Atlantic south to Cape Hatteras, which is known to be a highly productive region due to the interactions between shelf waters and the Gulf Stream and Gulf Stream rings (Werner et al. 1999).

A recent study of ocean sunfish in the northern Gulf of Mexico (Fulling et al. 2007) examined aerial survey and shipboard data, opportunistic sightings, incidental fisheries bycatch, stranding records, and published tagging data for Molid species to document the family’s distribution in the region. The study found Molid species (both *Mola mola* and *Masturus lanceolatus*) to be present in the northern Gulf of Mexico year round, in both shallow inshore shelf waters and deeper offshore waters. Ocean sunfish were sighted with the greatest frequency in the region during the winter and spring. Sea surface temperatures where sightings occurred averaged 19.9°C. The study suggested that water temperature, in combination with thermocline depth, may be important drivers in the distribution of ocean sunfish (Fulling et al. 2007).
A study examining the distribution of *Mola mola* in the Irish and Celtic Seas based on aerial survey records (Houghton et al. 2006) found fewer than 100 fish, averaging 1 m or smaller in size, sighted over a three-year period during the months of June – September. The study simulated the likely association between sunfish and jellyfish, assuming distribution of both groups was random across the study area. Results indicated that for all species associations of *M. mola* and jellyfish, the observed co-occurrence was greater than the modeled co-occurrence, implying that neither jellyfish nor sunfish are randomly distributed, but co-occur more in the same areas than expected by chance. *M. mola* was found in all areas where jellyfish were most abundant, and was found in greater densities than the other apex jellyfish predator, the leatherback turtle. The authors suggested that increased gelatinous zooplankton productivity in temperate waters makes the habitat a worthwhile part of the migration route of ocean sunfish (Houghton et al. 2006).

A study examining the occurrence of *M. mola* in the western English Channel during the years 1995-2001 found juvenile ocean sunfish in modest numbers in frontal waters during the months of June and July (Sims and Southall 2002). Ocean sunfish in the study were observed to be active swimmers, and were found at the surface near inshore fronts. They were observed in deeper waters (50-70 m) during the years when the front occurred further offshore. The close association of sightings with frontal features was presumed to be linked to foraging (Sims and Southall 2002).

The present study is the first to examine both the distribution and movement of *Mola mola* in the Northwest Atlantic. The study’s objectives were to examine the seasonal
movement and migratory patterns of *M. mola* in the Northwest Atlantic by attaching pop-up satellite archival tags (PSATs) to ocean sunfish in the region. As part of the approach to achieving these objectives, I first examined existing aerial survey data for ocean sunfish in Northeast Shelf waters from the North Atlantic Right Whale Consortium Database (1978–2006) and from the OBIS-SEAMAP Database (1989–2006) to determine a general pattern of distribution of *Mola mola* off the northeastern coast of the United States.

**Materials and Methods**

Maps of the seasonal distribution of ocean sunfish (Family Molidae) in US Atlantic shelf waters were created using pooled aerial survey data (source: North Atlantic Right Whale Consortium (NARWC) (1978-2006); Ocean Biogeographic Information System - Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) (1979-2006); Cetacean and Turtle Assessment Program (CETAP) (1979-1982) (Publisher: OBIS-SEAMAP); NOAA Southeast Cetacean Aerial Surveys (SECAS) (1992,1995) (Publisher: OBIS-SEAMAP) in ArcMap 9.3. The NARWC database contains thousands of sightings of marine species in the North Atlantic Ocean, from southeastern U.S. continental shelf waters to Nova Scotia, Canada. The purpose of most of the surveys in the database is to provide the documentation of right whale sightings in the North Atlantic Ocean, as well as sightings of many other marine species. Data from aerial surveys are available from the 1978 to present. The OBIS-SEAMAP database is an online archive for mammal, seaturtle, and seabird data and is comprised of data from contributors world-wide. Within the OBIS-SEAMAP archive, I obtained both the CETAP and the SECAS datasets. The
CETAP program was conducted between October 1978 and January 1982 by the University of Rhode Island in outer continental shelf waters of the northeastern U.S. from Cape Hatteras, North Carolina, to the Gulf of Maine. Population surveys were conducted by CETAP to characterize the abundance, distribution, and seasonality of marine mammals and turtles in the region for use in policy-making decisions regarding oil and gas development. The SECAS surveys were conducted from January to March in 1992 and 1995 by NOAA Southeast Fisheries Science Center (SEFSC) to estimate cetacean abundance. This data set contains sightings of cetaceans and sea turtles as well as other species from Cape Hatteras to the central Florida coast (inside the 1000-m isobath).

Aerial survey data from the CETAP and SECAS datasets within the OBIS-SEAMAP database were used to analyze the distribution of the ocean sunfish, *Molid spp.*, in East Coast shelf waters. Since the aerial survey data used in the analysis are from different sources over different periods of time, data were normalized and analyzed using an SPUE (sightings per unit effort) of sighted number of *Molid spp.* per survey hour. Sightability of ocean sunfishes was not considered in these analyses, and no attempt was made to estimate the population density of the species. Three areas along the eastern shelf were defined for analysis using latitude: Northeast = 40-45°N, Mid-Atlantic = 35-40°N, and Southeast = 28-35°N (Figure 1). For the Northeast and the Mid-Atlantic, data from the Cetacean and Turtle Assessment Program (CETAP) aerial surveys (1979-1982) were used. For the Southeast, data from NOAA Southeast Cetacean Aerial Surveys (SECAS) were used (1992, 1995). For each designated area, a mean SPUE (*Molid spp.* per survey hour) was determined for each month. For the Southeast, data were only available for the months of January – March, as this is when the NOAA SECAS surveys were conducted.
For each survey area, data were logarithmically transformed (N+1) to allow parametric testing, and geometric mean SPUE, SD, and SE were determined for each month. Significant differences in monthly means were determined using analysis of variance (one-way ANOVA) and if significant variability was found (P<0.05), Tukey’s tests were used for pairwise comparisons.

**Results**

Maps of pooled sightings of ocean sunfish in eastern US shelf waters show high numbers of animals in the Northeast and Mid-Atlantic in the summer (June – August) and fall (September – November) and high numbers of animals in the Southeast in the winter (December – February) and spring (March – May) (Figure 2 a-d). Temporal coverage of the surveys is biased, in that surveys in the southeast (Georgia and Florida) are limited to a few hundred surveys per year (from December to March). However for the purpose of mapping the general patterns of distribution, these surveys establish the presence of ocean sunfish in the region during the winter.

In the analyses of distribution, the greatest number of Molid spp. in both the Northeast and Mid-Atlantic were present in the summer months. There were differences in SPUE between some months in the Northeast (one-way ANOVA, p < 0.001). In the Northeast the highest SPUE occurred in August (2.30 Molid spp./survey hour) followed by June, July, September, and October (Table 2, Figure 3). The SPUE for August was not significantly different than the SPUE for June, July, September, and October (Tukey’s pairwise comparison test, p > 0.05). The remaining months were significantly lower.
There were differences in SPUE between some months in the Mid-Atlantic (one-way ANOVA, p = 0.010). In the Mid-Atlantic, the highest SPUE occurred in June (0.82 survey hour) (Table 3, Figure 4). The SPUE for June was not significantly different than the SPUE for February, May, July, August, September, and October (Tukey’s pairwise comparison test, p > 0.05). In the Southeast, there was no difference in SPUE for January, February, or March (one way ANOVA, p=0.72). Though differences were not significant, February was the month with the highest SPUE (1.11/survey hour) (Table 4, Figure 5). When comparing SPUE across all areas during all months, the Northeast had the greatest number of ocean sunfish present in August and the remaining summer months, followed by Area C in February and March (Table 5).

Discussion

These analyses demonstrate the annual shift in distribution of *Mola mola* out of northeastern US shelf waters, suggesting a seasonal migration from northeast to mid-Atlantic and southeast shelf. Ocean sunfish are in high numbers in shelf waters off the northeastern United States during the summer months, dropping off significantly during the late fall and winter. The decrease in numbers of in the region during this time is not a reflection of reduced survey effort, as there were 17 surveys and nearly 90 hours flown in January resulting in no sightings. A similar pattern of distribution was found in a previous study of aerial survey data on ocean sunfish in the region, with a drastic increase and decrease in numbers of animals spotted in consecutive months, indicating a large-scale movement of animals entering and exiting northeast US waters (Desjardin 2005).
The presence of *M. mola* in this region on a seasonal basis is likely due to environmental conditions in New England shelf waters in the late spring and summer months, which include warm water temperatures and increased primary productivity (Lalli and Parsons 2006). As a result of the peak in primary productivity in the spring, gelatinous zooplankton that feed directly on phytoplankton, such as salps, respond with a rapid population increase, and carnivorous medusae such as scyphozoans, appear in the region following the increase in secondary productivity (Alldredge and Madin 1982; Brewer 1989; Madin et al. 2006). These waters then become favorable foraging grounds for gelatinous zooplanktivores like *M. mola* and leatherback sea turtles, *Dermocheyles coriacea* (Desjardins 2005). In the late fall, decreasing temperatures and a decline in productivity in northeastern waters may serve as a cue for ocean sunfish to move south in search of prey. A study of the movement patterns of *M. mola* in the Northeast Atlantic suggested that thermal tolerance of the species was the driving factor in the movement of animals south at the end of the summer (Sims et al. 2009a).

Ocean sunfish appeared in lower numbers in the Mid-Atlantic, but were present more consistently throughout the year, with a peak in early summer. There is evidence suggesting that the slope water region south of New England is an area where large salp swarms recur on a regular basis (Madin et al. 2006). A study of the co-occurrence of *M. mola* and jellyfish in the Irish and Celtic seas found ocean sunfish in all areas where jellyfish were most abundant. The study suggested that increased gelatinous productivity in temperate waters makes the habitat a worthwhile part of the molas’ migration route (Houghton et al. 2006). In the Southeast, though the data are limited to the winter
months, ocean sunfish were present in high numbers. Though the surveys in the region were mainly targeting the coast, the Charleston Bump is found in the region and is an attractive habitat due to the bottom topography and oceanographic features (including currents and thermal fronts) that result from its interaction with the Gulf Stream. Many large pelagic fishes such as swordfish and marlins are known to aggregate, feed, and spawn at the Charleston Bump (Sedberry and Loefer 2001; Stokesbury et al. 2004). This deepwater bottom feature lies beyond the shelf edge off South Carolina and Georgia. It is a deepwater bank with a rocky bottom, reaching depths of over 700 m. The Charleston Bump also deflects the flow of the Gulf Stream, causing eddies, gyres and upwelling zones. The combination of rocky bottom and thermal fronts created by the disrupted flow of the Gulf Stream make the region attractive to large pelagic fishes. (Sedberry and Loefer 2001). Ocean sunfish moving south from New England may inhabit this region to take advantage of the high concentration of prey found there.

Though helpful in determining spatial and temporal patterns of distribution, reliance on aerial survey data for population estimates of ocean sunfish is problematic. Estimates of abundance from aerial surveys are based solely on when the animal is at or near the surface, and unlike leatherback turtles or marine mammals, ocean sunfish have no air-breathing requirement. Aerial survey data, when combined with tagging studies provide a more complete picture of the movement pattern of a species. By providing data on the vertical movements and distribution patterns of a species, tagging studies give indication of the likelihood of the animal’s visibility at the ocean’s surface on seasonal and temporal scales, and abundance estimates based on aerial surveys can be adjusted accordingly.
(Brill et. al. 2002). Additional data are needed to further examine distribution of ocean sunfish in these areas, along with studies of the movement, behavior, and biology of *Mola mola* in the Northwest Atlantic Ocean and in other parts of the world to gain a more complete understanding of the species.
Figure 3.1 Map showing 3 defined areas for analysis of distribution of *M. mola* in East Coast shelf waters. Area A (Northeast) = 40-45°N latitude, Area B (Mid-Atlantic) = 35-40°N latitude, and Area C (Southeast) = 28-35°N latitude. Aerial survey data for areas A and B from CETAP surveys (1978-1981). Survey data for area C from NOAA SECAS surveys (1992,
Figure 3.2. Ocean sunfish sightings (Family Molidae) in eastern US shelf waters from aerial survey data during the summer (a. June - August) and fall (b. September - November).
Figure 3.2. Ocean sunfish sightings (Family Molidae) in eastern US shelf waters from aerial survey data during the winter (c. December – February) and spring (d. March – May).
**Figure 3.3.** Monthly relative abundance (SPUE = \# Mola/hour) of *Mola* from the Northeast, Area A (40-45°N). Data were normalized before analysis. There were differences in SPUE between some months (one way ANOVA, \( p < 0.001 \)). Bars with the same letters have no significant difference in SPUE (Tukey's pairwise comparison test, \( p > 0.05 \)). Survey data from CETAP surveys (1978-1981).
Figure 3.4. Monthly relative abundance (SPUE = #Mola/hour) of Mola from the Mid-Atlantic, Area B (35-40°N). Data were normalized before analysis. There were differences in SPUE between some months (one way ANOVA, p = 0.010). Bars with the same letters have no significant difference in density (Tukey’s pairwise comparison test, p > 0.05). Survey data from CETAP surveys (1978-1981).
Figure 3.5. Monthly relative abundance (SPUE = # Mola/survey hour) of Mola from the Southeast, Area C (28-35°N). Data were normalized before analysis. There were no significant differences in SPUE between months (one way ANOVA, p =0.72). Survey data from NOAA SECAS surveys (1992,1995).
Table 3.1. Mean monthly distribution of *Mola* (SPUE = *Mola*/hour) for Area A, the Northeast (40-45 N latitude). Differences in abundance were present in some months (one way ANOVA, *p* < 0.001). Survey data from CETAP surveys (1978-1982).

<table>
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<th>Month</th>
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<th>hours</th>
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<th>SD SPUE</th>
<th>SE SPUE</th>
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<tr>
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Table 3.2. Mean monthly distribution of *Mola* (SPUE = *Mola*/hour) for Area B, the mid-Atlantic (35-40 N latitude). Differences in abundance were present in some months (one way ANOVA, *p* = 0.010). Survey data from CETAP surveys (1978-1981).

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<tr>
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Table 3.3. Mean monthly distribution of *Mola* (SPUE= *Mola*/hour) for Area C, the Southeast (28-35 N latitude). There were no significant differences in SPUE between months (one way ANOVA, \( p = 0.72 \)). Survey data from NOAA SECAS surveys (1992, 1995).

<table>
<thead>
<tr>
<th>Month</th>
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<th>SD SPUE</th>
<th>SE SPUE</th>
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Table 3.4. Monthly SPUE of *Mola* (*Mola*/survey hour) from highest to lowest for three designated survey areas (A=Northeast, B=Mid-Atlantic, C=Southeast).

<table>
<thead>
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<th>Area</th>
<th>Mean SPUE</th>
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</tr>
<tr>
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<td>C</td>
<td>1.11</td>
</tr>
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<td>78-81</td>
<td>A</td>
<td>1.05</td>
</tr>
<tr>
<td>March</td>
<td>92,95</td>
<td>C</td>
<td>1.04</td>
</tr>
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<td>July</td>
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<td>January</td>
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<tr>
<td>November</td>
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DISCUSSION AND FUTURE DIRECTIONS

The present study is the first to describe the movement, behavior, and habitat preferences of *Mola mola* in the Northwest Atlantic. *Mola mola* is a strong swimmer capable of extensive, highly directed movement. Ocean sunfish in the Northwest Atlantic migrate seasonally from Northeast to Mid-Atlantic and Southeast shelf waters, traveling as far as the Bahamas and the Gulf of Mexico before returning north. In addition to traveling great distances (up to several thousand kilometers) along their migratory route, ocean sunfish exhibit a wide range of vertical behavior over geographical and temporal scales (reaching depths of up to 844 m). These changes in diving behavior are likely driven by temperature and depth of the thermocline. Ocean sunfish in the Northwest Atlantic leave the Gulf of Maine and southern New England in the late summer and early fall and move south, a pattern of movement observed in several other large pelagic species (Stokesbury et al. 2004; Block et al. 2005; Hays et al. 2005; Wilson et al. 2005). While in Northeast US waters in the summer, they remain in shallow water and spend a high proportion of time at the surface (with SST’s between 11 and 14°C). These waters, which are highly stratified with a strong thermocline and a shallow mixed layer (Lalli and Parsons 1997; Mann and Lazier 2006) are a well established foraging ground for many large pelagic species during the summer months (Carey and Robinson 1981; Block et al. 2001; Stokesbury et al. 2004; Wilson et al. 2004). Ocean sunfish are likely foraging in Northeast US shelf and slope waters, taking advantage of the high concentrations of gelatinous prey found in the region (Madin et al. 2006).
In the late fall, ocean sunfish move south from New England along Mid-Atlantic and southeast US shelf waters, traveling as far as the Bahamas or Gulf of Mexico. Seasonal changes in water temperature and the search for high concentrations of jellyfish prey are likely driving factors in this southward movement, and thermal tolerance of the species has been suggested to play a significant role in its migration (Sims et al. 2009). By traveling along the shelf break and its associated frontal features, as well as aggregating around bathymetric features such as the Charleston Bump, ocean sunfish increase the likelihood of encountering their patchily distributed jellyfish prey. Similar travel routes and aggregation “hot spots” have been documented in several large pelagic fishes in the Northwest Atlantic (Sedberry and Loefer 2001; Stokesbury et al. 2004; Wilson et al. 2005). Once in mid-Atlantic and southeastern US waters in the winter and spring, ocean sunfish enter weakly stratified water masses with cooler temperatures and a deep mixed layer (Werner 1999). As a result, they shift their vertical behavior to spend less time at the surface and more time at depth, facilitating the search for vertically migrating prey of the deep scattering layer (DSL) such as physonectid siphonophores (Barham 1966; Hosia and Bamstedt 2008). Studies of *M. mola* and other large pelagic species in both the Pacific and North Atlantic have noted similar differences in vertical distribution associated with water column structure on a seasonal scale (Kitagawa et al 2000; Sims et al. 2003; Wilson et al. 2005). A study comparing the vertical behavior of leatherbacks and ocean sunfishes in waters off South Africa suggested that like leatherbacks, ocean sunfish exhibit plasticity in their vertical behavior and individuals may respond to patchily distributed gelatinous prey with differing levels of vertical migration on a seasonal scale. Individual ocean sunfish may shift from predation on seasonally abundant
surface medusa during the summer to vertically migrating gelatinous species found at
deeper depths during the winter months (Hays et. al 2009; Pope et al. 2010).

The migration route and diving behavior of ocean sunfish is also influenced by the
proximity to the Gulf Stream and Gulf Stream meanders and eddies. Ocean sunfish
associate with thermal fronts along the edges of the Gulf Stream as well as in the Gulf
Stream itself, and when doing so, spend little time at the surface and dive to depths of
800 m or deeper. By diving deeply in the Gulf Stream, ocean sunfish may be exploiting
high concentrations of prey deep in the water column and DSL (Cole 1971; Palter and
Lozier 2008).

Not all ocean sunfish along the eastern US shelf exhibit a north-south migratory pattern
along the coast. Rather, results from the present study suggest there may be a second sub-
population of *M. mola* in the southeastern United States that travels back and forth
between southeastern US shelf waters and the Gulf of Mexico. Previous studies establish
*M. mola* as a year-round resident in the Gulf of Mexico, most abundant in winter and
spring (Desjardins 2005; Fulling et al. 2007). Movement and behavior of ocean sunfish in
the Gulf of Mexico are closely associated with the Loop Current and its frontal features
due to the increased productivity found there and as a potential spawning ground for the
species. Leatherback sea turtles, bluefin tuna, and several billfish species are known to
associate with the Loop Current, and it is a known spawning ground for several large
pelagic fish species (Maul et al. 1984; McGowan and Richards 1989; Block et al. 2005;
Desjardins 2005; Stokesbury et al. 2005; Wells et al. 2007). The presence of *Mola mola* in both the summer and winter months, and the reasons why it travels there warrants further examination.

The present study found no evidence that *M. mola* in the Northwest Atlantic basks at the surface as a way of thermal recharging after deep dives in cold water, as has been previously suggested for the species in other regions (Thys 2003; Cartamil and Lowe 2004). In the Northwest Atlantic, ocean sunfish exhibit a high degree of surface time in northeastern US waters in the late summer and early fall, where warmest temperatures are found at surface. As they travel south and encounter warmer, mixed water masses (particularly the Gulf Stream) they dive deeper and, if seeking a recovery period after time at depth, may gain thermal benefit from the warm temperatures found at mid-water depths. Given that the northwestern Atlantic is well oxygenated at depth, basking behavior may be observed with more frequency in populations where oxygen minimum zones occur. Ocean sunfish exhibit a diel pattern in their vertical behavior, and maintain this pattern even when their overall depth profiles shift to deeper water, which reflects the prey searching and foraging behavior of the species in different water masses, and the targeting of organisms in the Deep Scattering Layer (DSL).

Of the 31 PSATs deployed on *Mola mola* between 2005 and 2008, 11 remained attached until the programmed pop-up date. Six never reported data, and 14 detached prematurely. One reason for premature detachment was the activation of the tag’s fail-safe mechanism that caused its release due to what was perceived by the tag as constant pressure (i.e., the
change in the fish's depth was less than the resolution of the tag (5.38 m) over a four-day period). This was known to occur for six tags, and in all of these cases the fish showed steady horizontal movement in shelf waters. This often occurred when fish were located in very shallow waters (<10 meters) around Nantucket Island where they presumably were feeding on large patches of gelatinous prey (salps and jellyfish) observed in the area. One fish, however, ceased horizontal movement, and apparently died and sank to the bottom shortly after tagging. Other possible causes of premature detachment include tag shedding/tissue rejection due to improper placement of the tag, corrosion or fouling of the tag, and mechanical failure. In species like *Mola mola* that are known to bask at the surface or spend extended periods of time in shallow water, the fail-safe mechanism on the tag should be modified to prevent premature detachment. The tagging method in the present study did not involve containment of the fish due to their large size and the resulting difficulty in handling them. In the future, developing a method that contained or captured the fish prior to tagging would ensure proper tag placement and enable the collection of other valuable information such as length, weight, sex, and reproductive state.

While the use of PSAT technology enables the tracking of pelagic species such as *Mola mola* whose behavior and movement patterns would otherwise remain a mystery, the error associated with light-based position estimates is reportedly up to hundreds of kilometers (Teo et al. 2004). Interpretation of these data may therefore lead to some misinterpretation of the behavior of the species. Though the estimates of the most probable track of tagged ocean sunfish in the present study provide a much needed
general picture of the movement and seasonal migratory pattern of the species in the
Northwest Atlantic, fine-scale movement and behavior, as they may be related to
oceanographic features, cannot be accurately determined. Based on the movement and
behavioral patterns observed/identified in this study, we can only speculate on what
factors may have influenced them. Further study of fine-scale movement of the species in
relation to oceanographic features, SST, and prey availability, facilitated by the use of
other tagging methods such as acoustic and GPS technology will provide a better
understanding of the biology and environmental associates of *Mola mola* (in the NW
Atlantic)

Though helpful in determining spatial and temporal patterns of distribution, reliance on
aerial survey data for population estimates of ocean sunfish, without additional data to
refine these estimates, is problematic. The biology and behavior of the species makes it a
poor candidate for such analysis for several reasons. Estimates of abundance from aerial
surveys are based solely on when the animal is at or near the surface, and unlike
leatherback turtles or marine mammals, ocean sunfish have no air-breathing requirement.
*M. mola* in the present study spent approximately 30\% of their time in the top 10 meters
of the water column, and fish spent less time at the surface as they moved south and
encountered warmer water masses. Therefore, data from aerial surveys reporting densities
of ocean sunfish (family Molidae) may underestimate the population size, particularly in
regions where fish spend less time at the surface. In addition, *M. mola* exhibit a diel
pattern in their behavior, typically diving to great depths during the day and inhabiting
shallow, near surface waters at night. Since aerial surveys are conducted during daylight
hours, it is likely that many individuals exhibiting this diel pattern are overlooked. Given these biases, results of aerial survey data are best used in combination with tagging studies. Aerial survey data establish the larger, seasonal, temporal or geographic patterns of distribution that cannot be adequately addressed by small scale, costly tagging studies. The information on distribution patterns provided by aerial surveys may then influence the design and scope of tagging studies. In the present study, the existing aerial survey records established the general pattern of distribution of *M. mola* along the east coast of the U.S. Based on that information, I formed hypotheses about the movement patterns of the species and determined when and where to tag animals. By providing data on the vertical movements and distribution patterns of a species, tagging studies give indication of the likelihood of the animal's visibility at the ocean’s surface on seasonal and temporal scales, and abundance estimates based on aerial surveys can be adjusted accordingly (Brill et. al. 2002). Tagged ocean sunfish decreased the proportion of time spent in surface waters as they moved south from the Northeast in the summer and early fall, to the mid-Atlantic and Southeast in the late fall and winter. Estimates of abundance based on aerial survey data in these regions would therefore need to be corrected to account for the significant number of fish that may be present in the mid-Atlantic and Southeast, but not detected. Together, aerial surveys and tagging studies provide a more complete picture of the movement of *M. mola* in the Northwest Atlantic than either would independently.

The present study is the most extensive to date on the movement and behavior of *Mola mola*. My results establish a baseline of information for the horizontal movement,
migratory routes, and habitat preferences of ocean sunfish in the Northwest Atlantic, and provide insight into the understanding of its habitat, behavior, and environmental associations. Results may contribute to the development of predictive models and strategies that will aid in the management of a poorly understood marine species, whose populations are believed to be declining in other parts of the world due to bycatch and commercial use in Asia. Data on the distribution and seasonal movements of *M. mola* may provide a useful indication of nutrient-rich areas with high productivity, where other marine organisms of commercial importance or endangered status may be found. Assumed to be a major jellyfish predator, *M. mola* provides natural ecological control of jellyfish populations. With recent reports of overabundance of jellyfish populations in various parts of the world, molids may play a significant role in helping to reduce jellyfish populations and the resulting negative impacts on fish and fisheries (Purcell et al. 2007).

Future studies are needed to gain a more complete understanding of the seasonal movement and behavior patterns of the species in the Northwest Atlantic and other parts of the world. In addition to continued use of PSAT’s and GPS-equipped satellite tags to further investigate both fine scale movement patterns and broader migration routes as well as temperature and depth preferences, there are several additional areas of analysis that would greatly improve the understanding of *M. mola*. Specifically, the application of molecular and chemical techniques to gut content and population studies would be beneficial to studies of ocean sunfish. The use of stable isotopes and natural tags to help to identify the relationship between populations of ocean sunfish, as has been done in
studies of other large pelagic fishes (Rooker et al. 2008) would reveal new, broad scale information on movement patterns and natal origin. A combination of stable isotope and stomach content analysis would provide a much needed baseline of information on diet and trophic position, and may reveal how much of the mola diet is comprised of gelationous zooplankton. Similar studies on bluefin tuna and sharks in the Northwest Atlantic have revealed information on prey preferences, seasonal shifts in prey types, and trophic levels (Estrada et al. 2003; Estrada et al. 2005). These analyses combined with studies on such basic biological information as age, growth, and reproduction are necessary to thoroughly examine the biology of the species and its role in the North Atlantic ecosystem and world ocean.
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June 15, 2005

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

IACUC #: 050503
Approval Date: 05/20/2005
Review Level: B
Project: Migration, distribution, and spawning of the ocean sunfish, Mola mola, in the North Atlantic

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 Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Roger E. Wells, D.V.M.
Vice Chair

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building, 51 College Road, Durham, NH 03824-3565 * Fax: 603-862-3564

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