SPATIAL ECOLOGY OF LONG-TAILED DUCKS AND WHITE-WINGED SCOTERS WINTERING ON NANTUCKET SHOALS, MASSACHUSETTS

By

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ABSTRACT

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A substantial proportion, perhaps 30%, of the North American breeding population of Long-tailed Ducks (*Clangula hyemalis*) winter in the vicinity of Nantucket Island, Massachusetts. These birds spend the night on Nantucket Sound and commute during daylight hours to the Nantucket Shoals, which extend about 65 km offshore from the southeastern corner of Nantucket. Strip transects done from a single-engine plane in 1997 and 1998 indicated that Long-tailed Ducks foraged over the shallower (≤ 20 m depth) portions of the Nantucket Shoals, up to 70 km offshore. Diet analyses of ten birds collected in February 1999 and five in December 2006 showed that they fed principally (106.6 +/- 42.0 individuals per crop) on *Gammarus annulatus*, a pelagic amphipod that often forms large aggregations, and is consumed by several species of fish and marine mammals.

I conducted high-intensity aerial surveys to map the distribution and abundance of foraging sea ducks on Nantucket Shoals, MA in February 2008 – Spring 2011.

For these surveys, west/east transect orientation ran perpendicular to bathymetric gradients, and covered a greater extent of Nantucket Shoals than did our preliminary surveys in 1997 and 1998. Core foraging areas of Long-tailed Ducks and White-winged Scoters (*Melanitta fusca*) overlapped along southwest Nantucket Shoals (mean foraging depth (m) ± SD: Long-tailed Ducks = 27.20 ± 8.25; White-winged Scoters = 29.8 ± 7.23), a zone where clams and pelagic amphipods are historically abundant. I mapped the spatial dispersion of Long-tailed Ducks and White-winged Scoters to determine if and where foraging aggregations persisted through space and time in relation to prey hotspots. Spatial dispersion of both species was strikingly concordant. Since previous studies have found very little dietary overlap between Long-tailed Ducks and White-winged Scoters, I sought to explain this high degree of spatial concordance. I also examined the potential physical and biological mechanisms (e.g., structural fronts, primary productivity) that may influence the spatial organization of Long-tailed Ducks, White-winged Scoters and their prey on Nantucket Shoals.

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DEDICATION

To Jessica Carol White

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CHAPTER 1

Introduction

In this thesis, I examine the wintering ecology of Long-tailed Ducks (*Clangula hyemalis*) and White-winged Scoters (*Mylanta fusca*) on Nantucket Shoals, Massachusetts in 2008 -2011. I specifically focus on Nantucket Shoals because of the substantial wintering population of diving ducks there (Veit and Petersen 1993, Davis 1997, White et al. 2009) and the dearth of information regarding their basic foraging ecology, spatial organization and habitat relationships. The waters surrounding Nantucket Island are a major wintering area for arctic and subarctic-breeding diving ducks: Long-tailed Ducks, White-winged Scoters, Surf Scoters (*Melanitta perspicillata)* Black Scoters (*Melanitta americana)* and Common Eiders (*Somateria mollissima)*. However the Long-tailed Duck population is notable as the highest wintering aggregation on the eastern seaboard (Veit and Petersen 1993). The Long-tailed Ducks in that area perform an unusual daily foraging commute, between nighttime roosting areas on Nantucket Sound and feeding locations on Nantucket Shoals (Mackay 1891, 1892, Veit and Petersen 1993, Davis 1997, White et al. 2009). Even less is known about White-winged Scoters on Nantucket Shoals in winter, as they do not commute, and most feed beyond the perimeter of what population counts from shore are able to detect with binoculars and spotting scopes. I use aerial and shipboard surveys to answer basic ecological questions that fall within the following categories concerning the Long-tailed Duck and White-winged Scoter wintering population on Nantucket Shoals: 1) spatial distribution and abundance 2) prey relations 3) habitat relations and 4) interspecific interactions among species.

In winter, the waters surrounding Nantucket Island, Cape Cod and Martha's Vineyard are host to the highest concentration of sea ducks (Family: Anatidae, Tribe: Mergini) on the eastern seaboard (Mackay 1891, 1892, Veit and Petersen 1993). The most abundant and persistent species throughout winter include: Long-tailed Duck, Surf Scoter (*Melanitta perspicillata*), White-winged Scoter, Common Eider (*Somateria mollissima*), and to a lesser extent, Black Scoter (*Melanitta nigra*) (Mackay 1891, Veit, R.R. and Petersen 1993, Davis 1997, White et al. 2009). These species breed on inland lakes and lagoons of Northern Canada and Alaska (Brown and Fredrickson 1997, Savard et al. 1998, Goudie et al. 2000, Robertson and Savard 2002, Bordage and Savard 2011). Breeding populations of Black and Surf Scoters, which winter on eastern coastal waters, are thought to originate from eastern localities, i.e. Quebec and Labrador (Brown and Fredrickson 1997, Savard et al. 1998). Common Eiders are residential year-round in the Canadian Maritime Provinces and have a widespread breeding distribution across Hudson Bay and the Canadian arctic (Goudie and Reed 2000). White-winged Scoters, breed along west/northwest Canada and Alaska. Long-tailed Ducks are high-artic breeders having an extensive breeding distribution in Newfoundland and around Hudson Bay, and then north to the fringes of tundra in the Northwest Territories (Brown and Fredrickson 1997). Winter migrants arrive to coastal waters of Cape Cod, Nantucket Island and Martha's Vineyard, at the beginning of October. Scoters and eiders migrate south and arrive in the vicinity of Nantucket before the arrival of Long-tailed Ducks, which are most abundant later in the season. In some years, blizzards of Long-tailed Ducks, flocks composed of 10s of thousands of individuals, show up early (around the end of November) and commute between Nantucket Sound and Nantucket Shoals. However, there is interannual variation in arrival times and number of commuters, and commuting flocks are sometimes not observed until late December (Veit and Petersen 1993, T. White pers. obs).

Long-tailed Ducks are considered opportunistic foragers as they feed upon a wide diversity of prey species, and are deep divers, reaching depths of up to 70m using their wings for propulsion (Schorger 1951, Johnsgaard 1975, Bustnes and Systad 2001) Their ecological plasticity likely facilitates access to a wide variety of prey types in the water column and along the benthos, of which a variety of benthic types are reported as habitat for Long-tailed Ducks (Cottam 1939, Nilsson 1972, Sanger and Jones 1984, Goudie and Ankney 1988, Guillemette et al. 1993, Roberston and Savard 2002, Schummer et al. 2008, White et al. 2009)**.** In the Western Palearctic, when foraging on bivalves (e.g., mussels and clams), Long-tailed Ducks select small individuals dick says to mention where: bivalve length ≤ 16mm**.** Barnes and Thomas (1987) classified the Long-tailed Duck as a carnivorous species based on analysis of gut morphology, and they are reported to target prey of high-energy density when available (e.g., fish, fish spawn, crustaceans).

Long-tailed Duck Feeding Strategies

For Long-tailed Ducks, selecting soft-bodied prey (prey without shells) may improve foraging efficiency - handling, digestion, and assimilation time - compared with bivalve prey. As compared to larger sea ducks (e.g. White-winged Scoters), Long-tailed Ducks feed more often (based on the proportion of the day diving) than larger ducks in winter as a function of small body size (~750g), smaller reserves, higher metabolic rate and thermal conductance, so the seeking out of energy-dense prey is likely a strategy to maintain thermoregulatory balance in harsh conditions when day length is limiting (Sanger and Jones 1984, Systad et al. 2000, Jameison et al. 2001, Robertson and Savard 2002, White et al. 2009). In the Baltic Sea, Long- tailed Ducks selected energy-rich crustacean prey in sandy habitats where infaunal clams (*Macoma balthica*) were relatively unavailable, likely due to burial depth; and epifaunal mussels (*Macoma balthica*) in habitats with hard-bottom (cobble and boulders). Body condition of Long-tailed Ducks did not differ between habitats, again result supportive of the ecological-plasticity hypothesis for this species (Zydelis and Ruskyte 2005**).**

White-winged Scoter feeding strategies

White-winged Scoters are on average approximately twice as heavy as Long-tailed Ducks (~1750g vs. ~ 750g, respectively) and select predominately bivalve prey items in winter (e.g. clams and mussels), which tend to be substantially larger (ca. 40mm) than those selected by other scoter species and Long-tailed Ducks (Sanger and Jones 1984,Vermeer and Borne 1984, Brown and Fredrickson 1997); Gastropods are also an important prey item for White-winged Scoters (Locum and Keller 1961). The sand lance (Ammodytes spp.), a small sand-burrowing fish was selected by White-winged Scoters in New England (McGilvrey 1967), however, White-winged Scoters avoided this fish in Kachemak Bay, Alaska, where it foraged over cobbles and shell debris; although the sand lance represented 24% of prey for Long-tailed Ducks in Kachemak Bay, where they fed over mud and sand substrates (Sanger and Jones 1984). The White-winged Scoter tends to forage at depths between 5 – 20m and frequently over sandy substrate (Cottam 1939, Stott and Olson 1973, Sanger and Jones 1984, Fox 2003) however, they forage farther from shore than the other scoter species and at greater depths, similar to Long-tailed Ducks ≤ 65 m (Sanger and Jones 1984, Žydelis et a. 1999). Moreover, White-winged Scoters and Long-tailed Ducks are reported to feed upon similar prey other than bivalves, e.g., fish, gastropods, crustaceans. As a function of its larger body size, the White-winged Scoter may have greater flexibility in governing nutritional stress associated with harsh and deteriorating winter conditions (Goudie and Ankney 1986).

Productive waters

Tidally-driven nutrient-rich Gulf of Maine waters flow into and over the sandy bottom of Nantucket Sound (located between Cape Cod and Nantucket Island) and Nantucket Shoals (south of Nantucket Island), and advect abundant larvae of diverse crustacean and molluscan species, which flourish in sandy substrate and locally well-mixed productive waters (Meyer et al. 1979, Cargnelli et al. 1999, Townsend et al. 2006, Johnson et al. 2011) . The attractiveness of a predictable and energetically profitable food base is likely powerful motivation for diving ducks to revisit and exploit prey resources around the waters of the Cape and Islands when daylight is limiting in harsh winter months (Goudie and Ankney 1986).

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Nantucket Shoals

Nantucket Shoals, a shallow sandy bank south of Nantucket Island is approximately 5 - 50 meters, and extends roughly 80 km south of Nantucket Island into the Atlantic Ocean. The topography of Nantucket Shoals is similar to that of Georges Bank some 100km east-northeast, having a sloped perimeter and strong topographically rectified currents around its margins, as well as a tidal front (Perry et al. 1993, Lough and Manning 2001, Townsend et al. 2006, Wishner et al. 2006)**.** The tide on Nantucket Shoals floods east and ebbs west, thus producing upwelling during flood tides and convergence during ebb flow, common with structural fronts associated with gradually sloping topography. (Pingree et al. 1974, Ullman and Cornillon 1999, 2001b, Lough and Manning 2001, He and Wilkin 2006, Wilkin 2006, Belkin et al. 2009)**.** These areas are manifested as steep gradients of sea surface temperature and chlorophyll a (a proxy for phytoplankton density).

Nantucket Shoals is tidally well-mixed year-round as a function of its shallow depth, and is awash with nutrients from the Gulf of Maine (Ullman and Cornillon 2001, Thomas et al. 2003, Townsend et al. 2006, Belkin et al. 2009, Sherman et al. 2011). Currents connecting the Gulf of Maine to Nantucket Shoals are steered by topography, which flow from the north to the margins of Nantucket Shoals by following complex topography around to the western side of the Shoals (Loder 1980, Limeburner and Beardsley 1982, Lough and Manning 2001, He and Wilkin 2006). Tidal forces flood

Nantucket Shoals on its western slope, this western flux promotes localized upwelling as the ocean is forced up sloped topography and over the shallows of Nantucket Shoals; a well-mixed convergence zone, also known as a tidal front forms around its margins in close proximity to its slopes (Limeburner and Beardsley 1982, Campbell and Esaias 1985, Lough and Manning 2001, Ullman and Cornillon 2001a, He and Wilkin 2006, Wilkin 2006, Belkin et al. 2009, Manning et al. 2009)**.** The signature of the tidal front is manifested by a sharp drop in the thermal gradient of the water and also a sharp increase in phytoplankton density. This inverse relationship of ocean temperature and phytoplankton density is a function of turbulent mixing in the water column due to vertical current and tidal flux**.**

Oceanographic drivers

Structural fronts in the northern hemisphere are well-documented and many are considered as biological hotspots due to enhanced biomass and complex trophic levels associated with these narrow bands of high production (Perry et al. 1993, Hunt Jr. et al. 1999, Hyrenbach et al. 2000, Doniol-Valcroze et al. 2007, Belkin et al. 2009, Bost et al. 2009). At the upwelling/convergent fronts, enhanced phytoplankton density is a function of elevated nutrient availability and mixing; secondary production (i.e., zooplankton grazers) respond to elevated standing stocks of primary production (Lalli and Parsons 1997). Along convergent zones, secondary production zones may accumulate passively (i.e. weak zooplankton swimmers); stronger zooplankton swim against the upward and downward flow of upwelling and convergence, respectively, to maintain depth and position in vertical/horizontal flow, possibly to avoid advection out of the area and to remain in where food density is high (Franks 1992, Genin et al. 2005) . Where these vertical currents upwell and down well can lead to retention zones of zooplankton forming persistent prey patches that become predictable to predators (Pingree et al. 1974, 1975, Loder 1980, Wolanski and Hamner 1988, Cairns and Schneider 1990, Schneider 1990a, Franks 1992, Sournia 1994, Olson et al. 1994, Decker and Hunt Jr. 1996, Russell, R., N.M. Harrison, and Hunt Jr. 1999, Lough and Manning 2001, Genin et al. 2005) Schneider et al. (1987) found that seabird aggregations were more likely to occur at strong flow gradients, and that persistent fronts were more important to large flocks of foraging seabirds than ephemeral fronts. Seabirds can learn where persistent prey patches or hotspots are located across the seascape, and use a combination of memory and local enhancement (i.e., finding groups of other feeding birds or prey-finding facilitation) to relocate prey; persistent and productive tidal fronts can provide the mechanism that supports complex trophic interactions (Schumacher et al. 1979, Loder 1980, Cairns and Schneider 1990, Coylel and Hunt 1990, Schneider 1990, Perry et al. 1993, Guillemette et al. 1993, Decker and Hunt Jr. 1996, Hyrenbach et al. 2000, Davoren et al. 2003a, Grünbaum and Veit 2003, Bump and Lovvorn 2004, Wishner et al. 2006, Seppänen and Forsman 2007)

Potential prey available to wintering Long-tailed Ducks and White-winged Scoters on Nantucket Shoals are the highly abundant pelagic Gammaridean amphipods; bivalve clams – ocean quahogs (*Arctica islandica*) and Atlantic surf clams (*Spisula solida*); and winter spawning sand lance (Ammodytes spp.) – an abundant sand-burrowing fish (Auster and Stewart 1986, Potter and Lough 1987, Avery et al. 1996, Cargnelli et al. 1999, NOAA/NMFS 2009).

Hypothesis

I postulate that Long-tailed Ducks and White-winged Scoters select gammarid amphipods and clams on Nantucket Shoals, as there is strong evidence to suggest that both target these abundantly available prey types. Past studies suggest that Long-tailed Ducks select soft-bodied crustacean prey and fish (e.g., amphipods and sand lance) over sandy habitat and for White-winged Scoters, shelled bivalve molluscs (e.g., clams), however, as both sea ducks species are not specialists, some dietary overlap on Nantucket Shoals likely exists (Cottam 1939, Meyer et al. 1979, Sanger and Jones 1984, Lewis et al. 2007, 2008) I analyze the distribution and abundance of Long-tailed Ducks and White-winged Scoters in relation to stomach content analysis, and in respect to prey sampling of the water column and substrate on Nantucket Shoals.

In Chapter 2, I examine the at sea foraging distribution and abundance and stomach content analysis of Long-tailed Ducks on Nantucket Shoals in winter. These results provide a rare glimpse in to the spatial organization of foraging Long-tailed Ducks south offshore within the 50m isobath on Nantucket Shoals in winter; and the prey upon which they fed.

In Chapter 3, I examine the at sea distribution of Long-tailed Ducks and White-winged Scoters in the Nantucket Shoals area approximately 10 years later from 2008-2011, seasonally, in winter and spring. Here I examine the spatial overlap of Long-tailed Duck and White-winged Scoter distribution in relation to each other, and also in relation to persistent patches of potential prey – gammarid amphipods and bivalve molluscs: ocean quahogs and Atlantic surf clams.

In Chapter 4, I examine the potential physical and biological mechanisms (e.g., structural fronts, primary productivity, local enhancement, prey patchiness) that strongly influence the spatial organization of Long-tailed Ducks, White-winged Scoters and their prey on Nantucket Shoals.

CHAPTER 2

Feeding Ecology of Long-tailed Ducks Clangula hyemalis Wintering on the Nantucket Shoals

Abstract

A substantial proportion, perhaps 30%, of the North American breeding population of Long-tailed Ducks (*Clangula hyemalis*) winter in the vicinity of Nantucket Island, Massachusetts. These birds spend the night on Nantucket Sound and commute during daylight hours to the Nantucket Shoals, which extend about 65 km offshore from the southeastern corner of Nantucket. Strip transects done from a single-engine plane in 1997 and 1998 indicated that Long-tailed Ducks foraged over the shallower (≤ 20 m depth) portions of the Nantucket Shoals, up to 70 km offshore. Diet analyses of ten birds collected in February 1999 and five in December 2006 showed that they fed principally (106.6 +/- 42.0 individuals per crop) on *Gammarus annulatus*, a pelagic amphipod that often forms large aggregations, and is consumed by several species of fish and marine mammals. Our findings emphasize the importance of conservation of the Nantucket Shoals and the prevention of oil spills or other potentially harmful accidents.

2.1 INTRODUCTION

Long-tailed Ducks (*Clangula hyemalis*) breed in Arctic Canada south to Hudson Bay, and winter along both coasts of the United States and on the Great Lakes. On the Atlantic Coast, the largest concentrations have been found near Nantucket and off Chesapeake Bay (Forsell 1999, National Audubon Society 2002, Robertson and Savard 2002). Between 300,000 and 500,000 Long-tailed Ducks (*Clangula hyemalis*) have been counted during daily dawn and dusk flights between Nantucket Sound and the open ocean south of Nantucket each year from the late 1970s to the present (Davis 1997, National Audubon Society 2002). The Long-tailed Ducks are present in the Nantucket area from mid November to mid April, with largest numbers recorded in December and January. Christmas Bird Count (CBC) data indicate a substantial increase of ducks wintering near Nantucket during the 1970's (Fig. 2.1), but they have always been present in some numbers (Mackay 1892). Prior to our offshore surveys in 1997 and 1998, no information was available on where these Long-tailed Ducks went to forage, or upon what they fed.

At Nantucket, Long-tailed Ducks commute between Nantucket Sound and the open ocean twice a day for most of the winter. Flights of tens to hundreds of thousands of ducks have been seen at dawn and dusk flying either directly over Nantucket, or between Nantucket and the adjacent islands of Tuckernuck and Muskeget (Davis 1997). During the flights, the ducks continue beyond the limits of visibility, so it has not been clear where they stop to roost for the night or where they feed during the day.

We have assumed that the birds roost at night and feed during the day, as previous studies have revealed no evidence of nocturnal foraging (Goudie and Ankney 1986, Systad et al, 2000).

Long-tailed Ducks have a less specialized diet than other sea ducks (Nilsson 1972, Stott and Olson 1973, Sanger and Jones 1984, Stempniewicz 1995, Zydelis and Ruskyte 2005). On saltwater wintering grounds, they capture epibenthic crustaceans, especially amphipods, mysids, and isopods (Cottam 1939, Johnson 1984, Sanger and Jones 1984, Goudie and Ankney 1986). They also take bivalves, gastropods, fish, and fish eggs at some sites (Lagler and Wienert 1948, Nilsson 1972, Vermeer and Levings 1977, Sanger and Jones 1984, Goudie and Ankney 1986). Recent winter studies in

Chesapeake Bay show that molluscs are the main food there (Perry et al. 2007). Unlike larger seaducks, Long-tailed Ducks sometimes eat schooling fishes; indeed, sand lance (*Ammodytes spp*.) can dominate the diet of Long-tailed Ducks in Kachemak Bay, Alaska and Nunuvut, Canada (Sanger and Jones 1984, Jamieson et al. 2001). Long-tailed Ducks have also been shown to select prey with higher caloric value than bivalve molluscs, such as amphipods (Goudie and Ankney 1986, Jameison et al. 2001), when foraging over less productive sandy habitats where bivalves are relatively unavailable, and during winter months to maintain thermoregulatory balance (Zydelis and Ruskyte 2005)

Sand lance dramatically increased in abundance between Cape Hatteras and the Gulf of Maine during 1974-1981 (Sherman et al. 1981, Fogarty et al. 1991), so we hypothesized that the increases of sand lance and Long-tailed Ducks were related. Intense fishing pressure on Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus*), principal predators of sand lance, has been cited as one causal factor of increased sand lance biomass (Fogarty and Murawski 1998). Stricter regulations on fisheries have resulted in a return of mackerel and herring stocks to historical densities; sand lance biomass has since plummeted (Read and Brownstein 2003, Fogarty et al. 1991). The links among these population changes has not been firmly established, Long-tailed Ducks have smaller bodies and higher metabolisms than larger sea ducks such as eiders and scoters (Jenssen and Ekker 1989), and have been shown to forage for > 80% of daylight during winter (Goudie and Ankney 1986, Nilsson 1972 , Systad et al. 2000).

2.2 METHODS

Study Area

Nantucket Shoals are located south and east of Nantucket Island, Massachusetts (40° N, 70° W; Fig. 2.2). The area is characterized by sandy bottom and depths ranging from 4m - 50 m. The Nantucket Shoals cover 2000 km^2 and lie within 20 km of some of the busiest shipping lanes in the world. The area represented by our transects in Figure 2.2 covers about 25% of the Nantucket Shoals. However, during informal searching prior to the surveys, we found no concentrations of Long-tailed Ducks on the shoal areas east of the transects.

Data Collection and Analysis

We conducted aircraft surveys using a single - engine, three-seated Cessna with flat windows during January 1997 and February 1998. A single observer (Veit) used standardized strip transects with a strip width of 200 m flying at an altitude of 300 m.

Strip width was determined by triangulation, using a hand-made sighting board. All birds at the boundaries of the strip were included in the total. This elevation is higher than that often chosen for waterfowl surveys (Camphuysen and Garthe 2004) but was dictated by the inherent danger of piloting a single engine plane over the ocean in winter. Using 10 power binoculars, we had no trouble either locating or identifying ducks from this distance. We surveyed 8 transects spaced approximately 4 km apart. Since we used Loran A to navigate, the spacing and exact position of transects shown on Figure 2.2 are approximate. However, we recorded Loran A coordinates at every aggregation of ducks, so the plotted locations of duck aggregations are accurate given the scale of the map. The 200 m strip was scanned using binoculars; flocks of Long-tailed Ducks were distinctive due to the coloration of the ducks and the spacing between individuals (more dispersed than either eiders or scoters). The surveys were conducted during calm weather (again, dictated by the potential hazards) and most or all birds present, including single birds like loons and alcids, were readily detected. Each survey covered 476 linear km and sampled approximately equal amounts of shoal (15-50 m) and deeper-water habitat.

We collected 9 Long-tailed Ducks from a boat on 12 February 1999 and 5 others on 17 December 2006. The 1999 birds were collected about five miles south of Nantucket near Miacomet Rip (41°13’ N, 70° 07’ W), where we had seen aggregations of Long-tailed Ducks from the plane. The 2006 birds were collected near Tuckernuck Shoal (41° 20’N, 70° 13’ W). All ducks were collected using 12-gauge shotgun; immediately after shooting, gullets (esophagus and proventriculus), and gizzards were removed and preserved in 70% ethanol. The contents of the organs were subsequently removed in the laboratory and identified to the lowest taxonomic level possible.

2.3 RESULTS

Aerial Surveys

Our aerial strip transects yielded density estimates of 18.6 birds per km^2 in January 1997 and 15.5 birds per km^2 in February 1998. The ducks were concentrated over the western fringes of the Nantucket Shoals, often over waters of 20 m depth. Extrapolating from our density estimates to the area of the Nantucket Shoals (2000 km^2) yielded estimates of 37,220 and 30,980 birds, respectively.

Diet Sampling

Of the nine Long-tailed Ducks collected in 1999, one was empty and the others contained the amphipod *Gammarus annulatus*. The mean number of amphipods per crop/proventriculus was 106.6, including the empty duck, with a mean biomass per bird of 0.6 g dry weight. Amphipods occurred in all ducks with non-empty stomachs. Trace amounts of sand and grit were found in the empty gullet, with one stomach having two small feathers. The diet of five Long-tailed Ducks collected in December 2006 also was dominated by the same species of amphipod. Two ducks had 7.8 and 34.6 ml food in the gullet, and this food was 99% amphipods wet weight. The other three, each with ~ 2 ml food, were also dominated by amphipods. Thus the diet off all ducks collected in either year was dominated by the same species of pelagic amphipod (Table 2.1).

Correlation with Sand Lance and Amphipods

Although both sand lance and Long-tailed Ducks increased during the 1970s, sand lance subsequently declined . Using the data available from Christmas Bird Counts and National Marine Fisheries Service between the years 1970-1986, we found a significant positive correlation in abundance between the two ($r_s = 0.55$, $p < 0.05$, $n=17$). We do not know whether Long-tailed Ducks were eating sand lance during that period, but a broad variety of other seabirds and whales in the Cape Cod and Nantucket area were (Payne et al. 1986, Payne et al. 1990,Veit and Petersen 1993, Hain et al. 1995, Weinrich et al. 1997). Using data from Avery et al. (1996) we found a negative correlation in abundance between amphipods and sand lance during 1978-1986 ($r_s = -0.73$, $p = 0.027$, $n=9$).

Thus our data, despite small samples, indicate that Long-tailed Ducks off Nantucket are taking amphipods and not sand lance, and, while the ducks may have been taking sand lance during the major increase in the 1970s, we have no evidence that this was the case.

2.4 DISCUSSION

Our aerial surveys yielded estimates of approximately 30,000 ducks, or only a tenth of those counted from shore. We have no explanation for this discrepancy, other than our surveys not covering sufficient area to locate all foraging concentrations. Our surveys were of broad enough scope to suggest the ducks concentrate on and around the Nantucket Shoals.

Despite uncertainties regarding estimates of the North American nesting population of Long-tailed Ducks (Robertson and Savard 2002, SDJV 2003), it is clear that a substantial proportion of these ducks winter in the vicinity of Nantucket, and feed on the Nantucket Shoals. Counts of commuting ducks taken during Christmas Bird Counts have several times exceeded 300,000 birds and the total number feeding in the area may be higher. Estimates of the North American breeding population range from 1,000,000 and up; there is an estimated world population of 10,000,000 or more, with 2,000,000 of those in the western Palearctic (del Hoyo et al. 1992). Thus the Long-tailed Ducks wintering around Nantucket may contain as much as 30% of the North American population.

Our recent data suggest that Long-tailed Ducks feed on amphipods, as do historical observations (J.C. Andrews, *pers comm*.) It is possible that Long-tailed Ducks select amphipods because of their nutritional content. Other prey such as blue mussels (*Mytilus edulis*) are certainly available in the area (Azarovitz and Grosslein 1987), and indeed are present in the particular area where we have seen rafts of foraging ducks. It may be either the accessibility of pelagic swarms of amphipods or their relatively high caloric content that make them especially attractive to Long-tailed Ducks. Amphipods have energy density of 5.9 kJ/g live mass (Brawn et al. 1968) compared to blue mussels with 1.92 kJ/g live mass (assuming 70% shell; Petersen 1981).

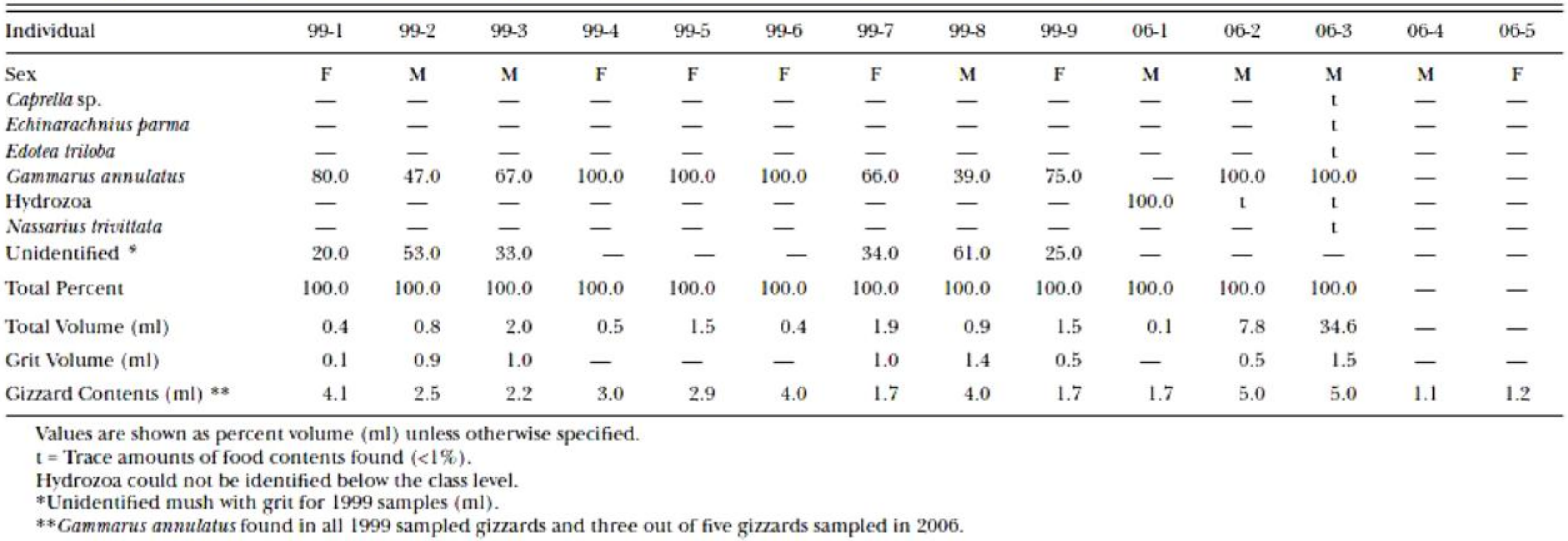
Long-tailed Ducks regularly dive to depths of 60 m (Cottam 1939, Schorger 1947). For this reason they may be especially adapted to feeding on a pelagic, schooling prey species such as amphipods. Avery et al. (1996) found that amphipods formed ‘densely packed’ clusters in the shallower (< 50 m) areas of the water column; depths in which we found aggregations of Long-tailed Ducks. Other vertebrate predators that feed on these amphipods or similarly sized zooplankton off southern New England include whales (*Megaptera novaeangliae*) and seabirds such as shearwaters (*Puffinus sp*.), gulls (*Larus sp*.), and terns (*Sterna sp*.) (Brown et al. 1981, Powers and Backus 1987, Macaulay et al 1995).

It is clear that a dramatic increase in Long-tailed Ducks at Nantucket occurred during the 1970s, despite their presence there in some numbers since the late 1800s. It is tempting to speculate that the major increase in sand lance at that time (Sherman et al. 1981) supported the increase in Long-tailed Ducks, but we have no evidence to support this notion. In recent years, places on Nantucket that used to be abundantly populated with sand lance are now populated with *gammarid* amphipods. For example, off the eastern end of the island, where large gulls used to feed on sand lance, Bonaparte’s Gulls now feed on amphipods (pers. obs.; CBC data). Many seabirds feed on sand lance (Fredericksen et al. 2007) and many species reached exceptional abundance in the Nantucket-Cape Cod area during the late 1970 and 1980s (Veit and Petersen 1993, Robards et al. 2000). Sand lance feed on amphipods as do other pelagic and demersal fish (Avery et al. 1996 , Robards et al. 2000), so it is possible that the increase in amphipods is related to the disappearance of predatory sand lance. In any event, it is now clear that Long-tailed Ducks off Nantucket are feeding on *gammarid* amphipods, and considering the numbers of ducks involved, this must represent a very major resource.

The concentration of such a large fraction of the North American population of any one species within a limited area implies critical need for conservation of Nantucket Shoals, Nantucket Sound and the surrounding waters. The area experiences heavy shipping traffic, which has been subjected to substantial oil spills (Powers and Rumage 1978, Teal and Howarth 1984), and recently is the proposed site of a major marine wind farm (Geo-marine Inc. 2004). Future work should focus on establishing seasonal variability in habitat use, diet selected by Long-tailed Ducks and in their susceptibility to development of the region.

Table

Table 2.1 Esophagus and proventriculus contents of non-empty Long-tailed Ducks collected during February 1999 and December 2006 at Nantucket, MA.



Individual	99-1	99-2	99-3	99-4	99-5	99-6	99-7	99-8	99-9	06-1	06-2	06-3	06-4	06-5
Sex	F	M	M	F	F	F	F	M	F	M	M	M	M	F
Caprella sp.	—	—	—	—	—	—	—	—	—	—	—	t	—	—
Echinarachnius parma	—	—	—	—	—	—	—	—	—	—	—	t	—	—
Edotea triloba	—	—	—	—	—	—	—	—	—	—	—	t	—	—
Gammarus annulatus	80.0	47.0	67.0	100.0	100.0	100.0	66.0	39.0	75.0	—	100.0	100.0	—	—
Hydrozoa	—	—	—	—	—	—	—	—	—	100.0	t	t	—	—
Nassarius trivittata	—	—	—	—	—	—	—	—	—	—	—	t	—	—
Unidentified *	20.0	53.0	33.0	—	—	—	34.0	61.0	25.0	—	—	—	—	—
Total Percent	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	—	—
Total Volume (ml)	0.4	0.8	2.0	0.5	1.5	0.4	1.9	0.9	1.5	0.1	7.8	34.6	—	—
Grit Volume (ml)	0.1	0.9	1.0	—	—	—	1.0	1.4	0.5	—	0.5	1.5	—	—
Gizzard Contents (ml) **	4.1	2.5	2.2	3.0	2.9	4.0	1.7	4.0	1.7	1.7	5.0	5.0	1.1	1.2

Values are shown as percent volume (ml) unless otherwise specified.
t = Trace amounts of food contents found (<1%).
Hydrozoa could not be identified below the class level.
*Unidentified mush with grit for 1999 samples (ml).
***Gammarus annulatus* found in all 1999 sampled gizzards and three out of five gizzards sampled in 2006.

Figures

Figure 2.1 Long-tailed Ducks counted during Nantucket Christmas Bird Counts 1956-2006 (r_p =0.87, $p<0.001$, n=50).

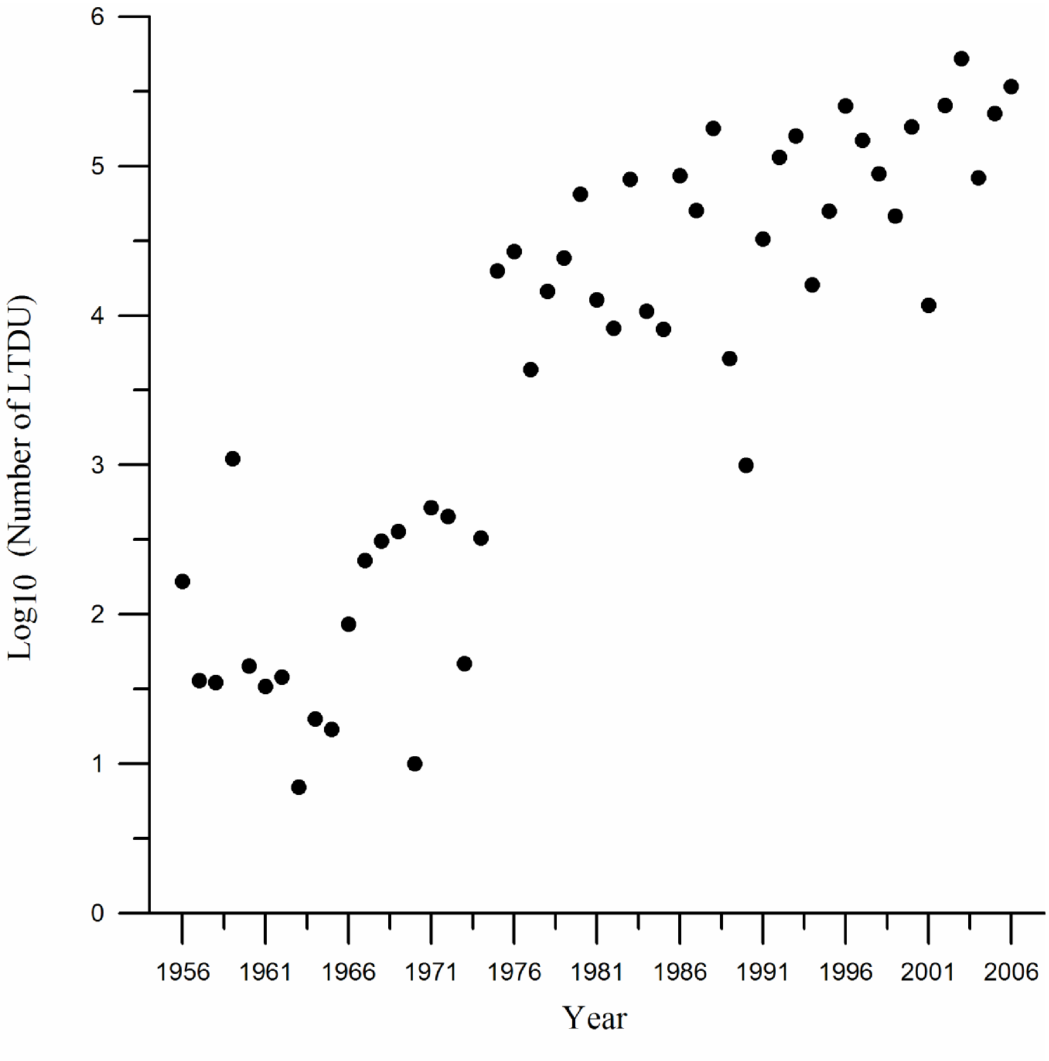
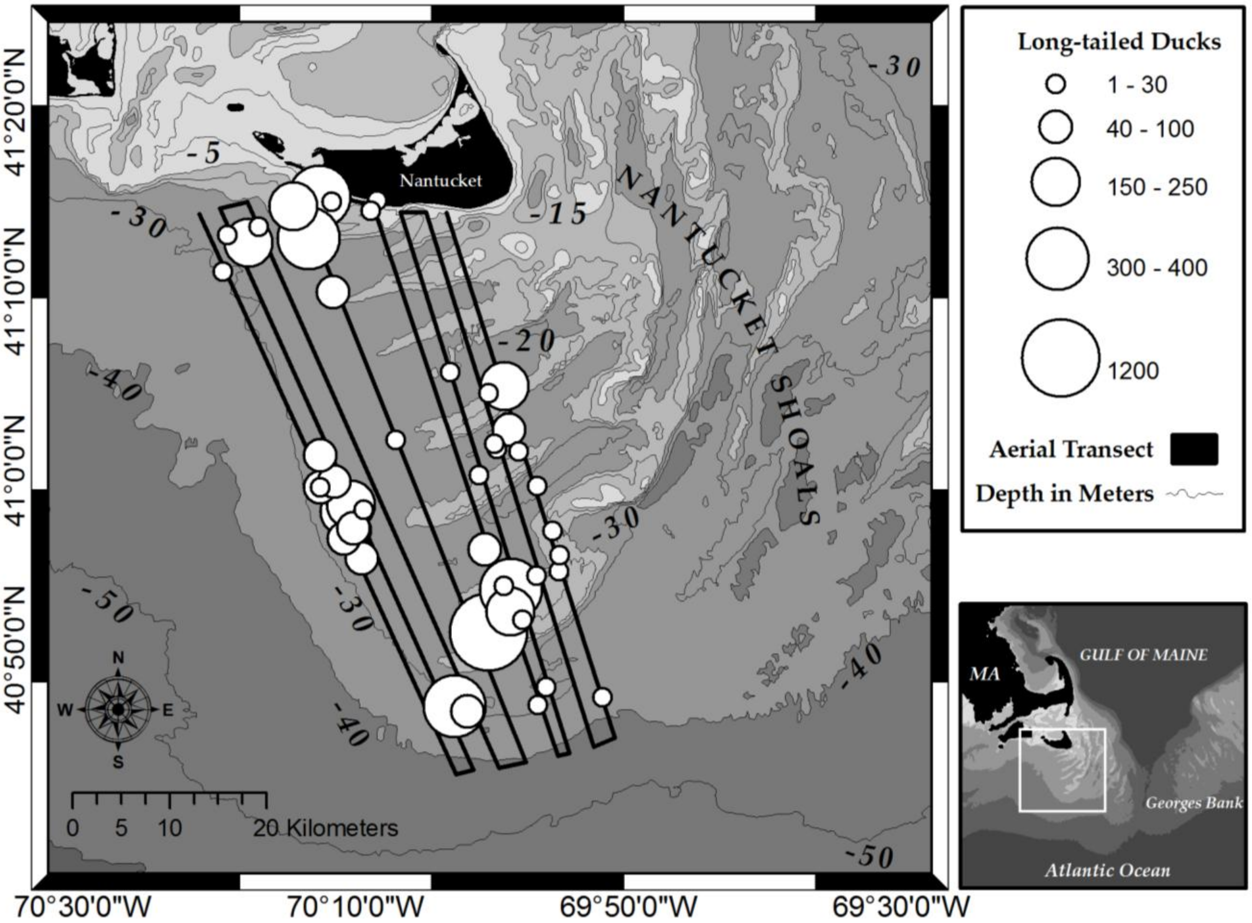


Figure 2.2 Distribution of Long-tailed Ducks off Nantucket as revealed by aerial surveys January 1997 and February 1998 (both years combined). Track lines approximate.



CHAPTER 3

Scale dependent spatial relationships in a predator-prey hotspot

Abstract

I conducted high-intensity aerial surveys to map the distribution and abundance of foraging sea ducks on Nantucket Shoals, MA in February 2008 – Spring 2011. For these surveys, west/east transect orientation ran perpendicular to bathymetric gradients, and covered a greater extent of Nantucket Shoals than did our preliminary surveys in 1997 and 1998. The preliminary surveys (1997/1998) provided a first glimpse into the offshore (depth < 50 m) distribution of Long-tailed Ducks, however, they were concentrated predominantly over the western fringes of Nantucket Shoals (Chapter 2). Current surveys covered both west and east Nantucket Shoals for comparative analysis. I examined the spatial dispersion of two numerically dominant sea ducks that forage on Nantucket Shoals in winter: Long-tailed Ducks (*Clangula hyemalis*) and White-winged Scoters (*Melanitta fusca*). Moreover, I related these findings to hotspots of potential prey (clams and pelagic amphipods), which are likely to influence the persistent at-sea foraging patterns of ducks. Results reveal core foraging areas for Long-tailed Ducks and White-winged Scoters overlapped over southwest Nantucket Shoals (mean foraging depth (m) ± SD: Long-tailed Ducks = 27.20 ± 8.25; White-winged Scoters = 29.8 ± 7.23), a zone where clams and pelagic amphipods are historically abundant. Overlapping duck distributions likely reflect a flexible foraging strategy, and to some degree, a mechanism of information transfer related to feeding facilitation. It is possible that social cues provided by feeding flocks contribute to spatial stability of this core foraging area offshore.

3.1 INTRODUCTION

Feeding Habits of Long-tailed Ducks and White-winged Scoters

Limited historical documentation exists concerning the winter feeding ecology and spatial organization of sea ducks in the vicinity of Nantucket Island and Cape Cod, MA. This region provides productive habitat for the largest concentration of wintering sea ducks on the eastern seaboard (Mackay 1891, 1892, Veit and Petersen 1993, Davis 1997, White et al. 2009). White-winged Scoters (*Melanitta fusca*), Surf Scoters (*Melanitta perspicillata*), Black Scoters (*Melanitta americana*),Common Eiders (*Somateria mollissima*), and Long-tailed Ducks (*Clangula hyemalis*) forage in the vicinity of Cape Cod and its outer islands (Veit and Petersen 1993, Perkins et al. 2005, White unpubl.). Offshore on Nantucket Shoals, Long-tailed Ducks were the numerically dominant duck species (Veit and Petersen 1993, Davis 1997, White et al. 2009). For Scoters spp., White-winged were dominant on Nantucket Shoals as determined by our preliminary aerial surveys (also see: Mackay 1891, Stott and Olson 1973, Veit, R.R. and Petersen 1993)

Long-tailed Ducks are known to take a high diversity of prey in the marine environment, and forage over a wide variety of benthic habitats (Mackay 1892, Cottam 1939, Stott and Olson 1973, Sanger and Jones 1984, Goudie and Ankney 1988, Stempniewicz 1995, Bustnes and Systad 2001, Zydelis and Ruskyte 2005)**.** Long-tailed Ducks select smaller-sized prey, < 16 mm (Bustnes and Systad 2001), when foraging for bivalves,. In the southern Baltic sea, they selected similarly sized bivalves ranging 11.0 - 11.6 mm, even though larger bivalves were available. This size class (ca. 11m) was likely optimum as a function of bill size and internal anatomy, despite larger bivalves having a greater energy content (Stempniewicz 1995). Prey size and burial depth are significant factors that influence prey availability to avian benthivores in marine environments (Richman and Lovvorn 2009). Although, infaunal and epifaunal bivalve prey were important to Long-tailed Ducks in the Baltic sea (consumption estimates = 6,350 tons) other prey taxa represented a significant proportion of their diet: fish (1,120 tons), crustaceans (400 tons), polychaetes (200 tons), and gastropods (125 tons) (Stempniewicz 1995). Long-tailed Ducks have a flexible feeding strategy, and likely specialize on crustaceans and non-mollusc prey due to high energetic demands, and in habitats where soft-bodied prey are abundant (Jamieson et al. 2001, Zydelis and Ruskyte 2005, White et al. 2009). On Lake Ontartio, Long-tailed Ducks favored amphipods and supplemented with zebra mussels (*Dreissna polymorpha*); here, shelled vs. non-shelled prey may be a deciding factor, since shells are unprofitable and not easily digested (Goudie and Ankney 1986, Richman and Lovvorn 2004, Ross et al. 2005, Schummer et al. 2008a). When feeding at polynas in Nunavut, CA, Long-tailed Ducks avoided blue mussels and preyed upon amphipods, sand lance and fish eggs; perhaps due to higher profitability and faster assimilation rates for these prey compared to mollusc prey (Jamieson et al. 2001). In the Baltic Sea on the Lithuanian coast, Zydelis and Ruskyte (2005) compared feeding ecology and body condition of Long-tailed Ducks in two disparate habitats, classified as hard bottom and soft bottom. Hard-bottom habitat, composed of stones and boulders, was dominated by blue mussels (~93%); soft-bottom-habitat was dominated by clams (~73%). However, in soft-bottom habitat, polycheates and crustaceans were abundant. In short, Long-tailed Ducks selected blue mussels in hard-bottom habitat, and crustaceans in soft-bottom habitat. The authors concluded that Long-tailed Ducks may have avoided infaunal bivalves in soft-bottom habitat as a function of burial depth, and instead fed upon crustaceans due to their high energy density, relative to clams. Moreover, body condition was good in both habitats, thus supporting evidence that Long-tailed Ducks possess a highly flexible foraging strategy. Foraging efficiency is likely greater for crustacean prey in terms of energetic value with minimal shell to digest and higher-energy density per unit mass compared to bivalve prey (Goudie and Ankney 1986, 1988). Moreover, shells provide little or no nutritional value, require time to grind, and occupy valuable space in the gut. Long-tailed Ducks are small-bodied diel foragers with high metabolic rates, and predicted to adopt an efficient foraging strategy that minimizes search and handling time in daylight hours in order to maximize foraging profitability (Goudie and Ankney 1986, Bolnick et al. 2003).

White-winged Scoters heavily consume bivalves in marine environments, although non-mollusc prey, e.g., crustaceans, polychaetes, fish and fish spawn may be underrepresented in diet studies due to bias against soft-bodied prey in collection methods (McGilvrey 1967, Bourne 1983, Vermeer and Bourne 1984, Fox 2003, Anderson et al. 2008, Palm et al. 2012). White-winged Scoters consume a broader size range and generally select larger bivalves than Surf Scoters, Black Scoters, and Long-tailed Ducks (Vermeer and Bourne 1984, Fox 2003, Anderson et al. 2008). Additionally, White-winged Scoters may buffer deteriorating weather and prey conditions more effectively than smaller sea ducks as a function of a larger body size, lower mass specific energy costs, greater fat reserves and lower thermal conductance (Goudie and Ankney 1986, Anderson and Lovvorn 2011). It is possible that smaller ducks may relocate to alternative foraging areas when conditions deteriorate, as they may lack the reserves and feeding flexibility of larger sea ducks to adapt to prolonged unfavorable conditions as winter progresses (Anderson and Lovvorn 2011).

Major sources of potential prey for Long-tailed Ducks and White-winged Scoters on Nantucket Shoals in winter are gammarid amphipods, infaunal bivalves, and sand lance (*Ammodytes spp*.). Specifically, the amphipod *Gammarus annulatus* is highly abundant on Nantucket Shoals and taken by Long-tailed Ducks in winter (Avery et al. 1996). For clams, the ocean quahog (*Arctica islandica*) and Atlantic surf clam (*Spisula solidissima*) (Cargnelli et al. 1999) are abundant, however, other potential-prey species are certainly available to diving ducks on Nantucket Shoals, e.g. Atlantic sea scallops *(Placopecten magellanicus),* razor clams (*Siliqua patula*), and also gastropods (Cottam 1939, McGilvrey 1967, Auster and Stewart 1986, Nelson and Ross 1991).

Locating prey at-sea

Sea ducks form gregarious feeding flocks in winter. This is exceptionally true for sea ducks in the vicinity of Cape Cod and Nantucket, where it is common to observe dense aggregations of foraging sea ducks numbering well above 10,000 individuals in a flock (Veit, R.R. and Petersen 1993, Davis 1997, White personal observ.)**.** Feeding aggregations are conspicuous at sea, and can serve as a visual cue to birds searching for prey (Pöysä 1992, Buckley 1996, Davoren et al. 2003a, Grünbaum and Veit 2003). This kind of public information is probably valuable to marine birds over “featureless” seascapes where resources are patchily distributed, ephemeral, and cryptic (Buckley 1996, Camphuysen and Webb 1999, Fauchald 1999, Davoren et al. 2003a)

Many taxa use publicly available information or cues from conspecifics and heterospecifics alike to assess the status of their environment (Stephens and Sutherland 1999, Seppänen and Forsman 2007, Weimerskirch et al. 2010, Ryan et al. 2012). Flocking over a food source may promote feeding facilitation, as birds searching for prey may join the flock to discern if habitat or a prey patch is profitable (Grünbaum and Veit 2003, Harrison and Whitehouse 2011). Diving ducks aggregate to abundant and profitable patches of prey (Nilsson 1972, Stott and Olson 1973, Guillemette et al. 1993, Schummer et al. 2008b). Foraging within a hierarchical patch of prey (a prey patch with nested spatial structures of patchiness and profitability) may promote "behavioral cascades" in which predators employ different behavioral mechanisms to locate and remain within the domain of profitability, e.g., local enhancement, area-restricted search, and memory (Kareiva and Odell 1987, Russell et al. 1992, Fauchald 1999, Davoren et al. 2003b, Silverman et al. 2004). Assuming a flock of diving ducks in the marine environment detected a profitable and persistent prey patch, the core feeding group may spatially stabilize the flock over a food resource by serving as a visual anchor to other members; perhaps to those resting at the periphery or displaced by currents (Mackay 1891, Clark and Mangel 1984, Haney et al. 1992, Guillemette et al. 1993). Diving ducks form large aggregations in the marine environment, and show high foraging site fidelity at some locations perhaps due to net benefits of social foraging behavior (Guillemette et al. 1993, Beauchamp et al. 1997). Moreover, it is possible that an increase in feeding flock size may also increase profitability by reducing search time for cryptic prey (Buckley 1996, Grünbaum and Veit 2003)**.**

Facilitation among individuals through positive density dependence is also referred to as Allee effects (Stephens et al. 1999, Courchamp et al. 1999). Unlike overcrowding or negative density dependence, facilitation through Allee mechanisms can result in net benefits to individual participants in a group as number or density increases (Courchamp et al. 2008). A formal definition of an Allee effect states a positive correlation with any component of an individual's fitness and density of conspecifics (Courchamp et al. 1999, Ryan et al. 2012). Similarly, through the mechanism of local enhancement and positive density dependence, foraging success may increase in likelihood provided that individuals searching for food locate and joins groups of successful foragers. Foraging in flocks may function as a component Alle effect, through which birds in the marine environment find food through positive density dependence (Guillemette et al. 1993, Davoren and Burger 1999, Stephens and Sutherland 1999, Davoren et al. 2002, Berec 2010). If foraging in groups during the non-breeding season increased the probability of survival, it is reasonable to postulate that reproduction may benefit from this seemingly positive feedback mechanism (Berec 2010, Ryan et al. 2012).

Mixed-species foraging flocks at sea can have variable characteristics and degrees of association among species. This may in part be a function of co-evolved interspecific associations and autecologies (Goudie and Ankney 1988, Harrison and Whitehouse 2011). Camphyusen and Webb (1999) documented feeding commensalism between sub-surface feeders and surface-feeding seabirds. Here, Black-legged-Kittiwakes (*Rissa tridactyla*) sought out groups of Razorbills (*Alca torda)* and Common Murres *(Uria aalge*) to take advantage of feeding opportunities that auks had created by corralling and driving fish to the surface. However, larger gulls used local enhancement to find and displace feeding kittwakes, a kleptoparasitic behavior. Buckley (1999) reported a similar finding between Turkey Vultures (*Cathartes aura*) and Black Vultures (*Coragyps atratus*) to patchily distributed carrion. Black Vultures used local enhancement as a mechanism to find carcasses by searching for groups of feeding Turkey Vultures. In this scenario Turkey Vultures were 'better' at finding food due to enhanced olfaction, whereas Black Vultures heavily relied on their visual acuities. Feeding interactions lead to competitive exclusion as increasing numbers of Black Vultures displaced Turkey Vultures at carcasses. Harrison et. al (1991) showed that Black-browed Albatrosses (*Thalassarche melanophrys*) initiates mixed-feeding flocks of seabirds that feed upon Antarctic krill (*Euphausia superba*). Similarly, Silverman et al. (2004) documented conspecific and heterospecific seabird associations with krill patches in the Antarctic.

Diving ducks form mixed-species feeding flocks in the marine environment (Goudie and Ankney 1986, 1988, Noel 2005). Foraging distributions of large and small sea ducks can overlap, however, there is little evidence of aggression-based competition among sympatric species (Goudie and Ankney 1988, Guillemette et al. 1993, Byrkjedal et al. 1997, Noel 2005, Schummer et al. 2008b). Larger sea ducks can take larger prey and are less sensitive to environmental variation than smaller ducks, who spend a greater fraction of their time feeding to maintain energy balance (Goudie and Ankney 1986, Systad et al. 2000, Anderson and Lovvorn 2011). Larger ducks may exploit different niches than smaller ducks, based on prey type and size. Black scoters and Long-tailed Ducks exploited similar habitats in Newfoundland, yet scoters fed on blue mussels and Long-tailed Ducks on amphipods, even though small blue mussels were available to Long-tailed Ducks (Goudie and Ankney 1986). White-winged Scoters in Kachemak Bay, Alaska primarily took bivalve prey, whereas, Long-tailed Ducks consumed crustaceans and fish and supplemented their diet with bivalves (Sanger and Jones 1984). While scoter spp., particularly White-winged Scoters, have a reputation as being "bivalve specialists", there is evidence to suggest that White-winged Scoters may supplement their diet with a greater proportion of fish and non-bivalve prey than previously reported (McGilvrey 1967, Zalakevicius et al. 1995, Palm et al. 2012).

In this study, I observed mixed-species foraging flocks of Long-tailed Ducks and White-winged Scoters on Nantucket Shoals. I examined the degree of spatial association between overlapping foraging distributions, and in relation to the spatial intensity of potential prey abundance - clams and pelagic amphipods. I postulate that the distribution and abundance of Long-tailed Ducks should track the distribution of pelagic amphipods more closely than would White-winged Scoters, primarily because Long-tailed Ducks are significantly smaller and should focus their foraging efforts on exploiting high quality prey where infaunal bivalves may be unprofitable due to size, shell, and burial depth restrictions (Goudie and Ankney 1986, Richman and Lovvorn 2009, Anderson and Lovvorn 2011). I predict that White-winged Scoters should generally track clam abundance more closely than pelagic amphipods, based on the following assumptions: 1) White-winged Scoters can access infaunal bivalves buried deeper in the sand than smaller ducks 2) can exploit a broader range of bivalve sizes and have a larger proportion of the bivalve prey field accessible to them 3) are not obligated to maintain energy balance by seeking out and exploiting high quality motile prey, due to a lower mass-specific metabolism than that of Long-tailed Ducks, and may have more reserve time to regulate energy balance independent of environmental conditions (Anderson and Lovvorn 2011). White-winged Scoters have a flexible diet and may consume non-mollusc prey. It is possible that the foraging distribution of Long-tailed Ducks and White-winged Scoters overlap in areas where these species share similar diets. Moreover, Long-tailed Ducks and White-winged Scoters may use interspecific social information (e.g., local enhancement) to locate prey patches on Nantucket Shoals during winter. A positive statistical association between Long-tailed Duck and White-winged Scoter abundance, across multiple spatial scales, would provide support for this hypothesis.

Densities of commuting Long-tailed Ducks often peak in early winter and decline as winter progresses as commuting Long-tailed Ducks are seldom observed during March (NAB 2012, TPW unpublished data). Similarly, the Nantucket Shoals gammarid amphipod population has a bimodal seasonal cycle as it peaks in November and subsequently declines as winter progresses until May, when it then peaks again (Avery et al. 1996). The lack of a foraging commute by Long-tailed Ducks to Nantucket Shoals in late winter may indicate a movement away from the Shoals to find prey elsewhere. If Long-tailed Ducks predominantly prey upon pelagic amphipods on Nantucket Shoals, and White-winged Scoters on clams, then Long-tailed Duck abundance may reflect a decline in amphipod abundance as winter progress. Furthermore, White-winged Scoter abundance should be relatively stable throughout winter, assuming clam abundance is similarly stable. I test this hypothesis by comparing the seasonal abundance of Long-tailed Ducks and White-winged Scoters on Nantucket Shoals.

3.2 METHODS

Aerial surveys and data collection

We conducted aerial surveys to record the distribution and abundance of sea ducks south of Nantucket Island over Nantucket Shoals. These were conducted offshore (inshore of the 60m isobath) on a seasonal basis from late fall (December) through early spring (March/April) in years 2008 - 2011, approximately once per month, when weather conditions permitted (Table 3.1).

We recorded distribution, abundance, and behavioral data of all bird taxa encountered along transects within an area delimited by the following geographic coordinates: 41.18 N and 40.77 N; 70.38 W and 69.40 W. The survey design included six east-west transects aligned in parallel approximately 90 km in length and 9 km intervals. However, on occasion, we deviated from design described above (the one most frequently surveyed) primarily due to the addition of exploratory transects, or a reduced version of the design due to deteriorating and unsafe weather conditions. For example, we surveyed 4 east-west transects during the maiden survey in February 2008, and added transects to subsequent surveys upon discovering major concentrations of Long-tailed Ducks and White-winged Scoters on the southern transects. I also modified the March 2008 survey design to include an additional transects between the standard 9 km intervals. I considered this an exploratory design and surveyed it only once.

We conducted surveys over Nantucket Shoals at an altitude of 61m using a high-fixed wing aircraft. However, we flew two surveys at 152m due to the pilot’s personal safety preference. Two observers concurrently recorded density data within a 200 meter strip-width by referencing calibrated marks on the wing struts, while observing from starboard and port sides (Tasker et al. 1984, Certain et al. 2007)**.** All taxa were identified all taxa to species level when possible.

Density estimation

We (2 observers) recorded and transcribed data (observations and aerial track) on independent computers using voice/GPS software **(**USFWS 2003). A typical voice recording constituted species identification and numerical estimation of individual birds observed within the 200-meter strip-width. We also recorded an index of relative observation conditions within the survey strip, e.g. glare intensity, sea state. We restricted surveys to wind speeds ≤ 15 knots, and used a scale from 1 through 5 to classify the general quality of conditions that might influence our ability to see birds: an index of 1 represented least optimal conditions (e.g., high glare, high wind), and an index of 5 represented most optimal conditions (e.g. overcast sky, low wind). I omitted data collected with conditions ≤ 2 from density estimates.

Density estimates for all species were calculated using the following formula:

$$\text{Density} = \text{number of birds} / \text{area surveyed} \qquad (1)$$

I calculated the area parameter in equation 1 by multiplying the survey track length by the survey width. I binned density estimates along-track to 3km segments for individual surveys. I chose this scale as a tradeoff between a fine-scale spatial resolution with high autocorrelation amongst short distance classes, and coarse-scale spatial resolution, which can confine spatial associations and reduce sample size. Reports of scale-dependent associations between sea ducks and schooling prey are virtually absent from the literature. However, the strength of predator-predator and predator-prey associations can be scale dependent (Piatt 1990, Rose and Leggett 1990). Burger et al. (2004) suggested that scales between 1 -10km are appropriate for predator-prey analyses and habitat mapping. Schneider and Piatt (1986) found positive associations between subsurface foraging birds and schooling fish at spatial scales 2-6 km. Birds sitting on the water can visually track the behavior of other birds up to 4.5 km away, as estimated by Haney et al. (1992); also see Davoren et al. (2003). Here I assumed that Long-tailed Ducks and White-winged Scoters can cue the activities of conspecifics and heterospecifics within a distance of 4.5 km. I considered this a reasonable assumption considering the two species form large gregarious feeding flocks. Therefore the 3 km scale I use here is within the suggested range of appropriate spatial scales for predator-predator and predator-prey spatial analysis.

Potential Prey: Amphipod and Clam data

National Marine Fisheries Service (NMFS) collected a 32-year time series (1977-2009) of gammarid amphipod distribution and abundance for the U.S. continental shelf. Full details of collection methods used are described in Jossi et. al (1983), and Kane (2003). The Marine Resources Monitoring, Assessment, and Prediction program (MARMAP) and Ecosystems Monitoring program (EcoMon) broad-scale surveys ranged shelf-wide from Cape Hatteras, NC, USA to Nova Scotia, CAN. These surveys assessed seasonal and annual zooplankton stocks throughout continental shelf waters (Figure 3.11). Amphipod density is calculated as the number of individuals per 100 m^3.

I created an index of winter gammarid amphipod abundance using kernel density estimation (Silverman 1986) and mapped this composite within all EcoMon and MARMAP surveys between Cape Hatteras and Nova Scotia to determine if and where multiple amphipod hotspots were located on the shelf. I also mapped this composite index at the scale of Nantucket Shoals to determine where gammarid amphipods were abundant and persistent on Nantucket Shoals, and to relate this index to local intensity of sea duck distribution and abundance. I used a temporal and spatial subset of amphipod density (November – April; 42 N 38 N : 72 W and 68 W) to account for the wintering period when Long-tailed Ducks and White-winged Scoters occupy Nantucket Shoals.

Kernel density estimation is a nonparametric function as the data suggest the shape rather than a preselected probability density distribution (Silverman, 1986). In general, a smooth kernel is centered and weighted at each observation to estimate density at the location. Total kernel density was calculated by summing overlapping distributions of individual kernels for the area or cell (Silverman, 1986). Density estimation is sensitive to the search distance of the kernel (i.e., smoothing parameter). A small window size may illuminate compact local densities, whereas a larger window may generalize intensity over a given area. However, too large a window can over-smooth data and blur local variability (Seaman and Powell 1996, Silverman 1986). The kernel estimator I used was weighted by amphipod density as determined by 32 years of net hauls. I mapped a second kernel within the Nantucket Shoals area using a more recent subset of amphipod density (Nov-April, 1999 – 2009) to determine if the areas of local intensity as revealed by the 32-year time series, occurred at similar locations. I considered an area to be an amphipod hotspot if local areas of amphipod abundance were spatially persistent, high in density, and concordant at disparate temporal scales. I chose the value of the smoothing parameter based on the distance between bongo stations, which ranged from 8 km – 35 km (Kane 2007). I applied a maximum 15 km search radius because at larger distances the kernel interpolated density into Nantucket Sound, an area not sampled for amphipods by NMFS, and also outside the survey extent of this study.

I analyzed and mapped the benthic data set using the same criteria as in the amphipod data with the exception of a temporal subset. I mapped the distribution and abundance of clams, as well as the composite abundance index as descried above, using all data collected on and within the vicinity of Nantucket Shoals, for years 2005-2008. I did not analyze a temporal subset of the clam data, because there were too few tows in any one year to provide an even composite index for Nantucket Shoals. Therefore, I used all tows collected across three survey years to create the clam abundance index.

Comparing west/east densities

I used density estimates of Long-tailed Ducks, White-winged Scoters, gammarid amphipods and clams to test for differences in abundance between western and eastern Nantucket Shoals. I did this to determine if there was a broad-scale spatial coherence among predators and potential prey, due to my prediction that western Nantucket Shoals should have high biodiversity and overall abundance of these taxa due to the unique oceanography at that location (chapter 4). I used the 3km binned bird densities to compare west-east abundance estimates. I analyzed gammarid amphipod and clam abundance at the scale of a station, i.e., abundance estimated from hauls at one at-sea sampling station. The purpose of the scale related analysis was to “narrow down” where significant areas of aggregations of potential prey and birds spatially co-occured. I first analyzed data at a broad-scale (west/east), then at a fine-scale (local intensity) in order to determine if and where hotspots of ducks, amphipods, and clams occured and possibly co-occured on Nantucket Shoals.

I first partitioned the survey area in to equal halves to represent western and eastern Nantucket Shoals. Each half encompassed an area of approximately 2000 km^2. An equal number of 3km bird bins were distributed in both areas given the survey was completed in full, which was not always the case due to adverse weather conditions. I selected gammarid amphipod and clam abundance data within the same west/east boundaries.

I used a nonparametric bootstrap Monte Carlo simulation (Efron and Tibshirani 1994, Manly 1997) to test individual null hypotheses of no mean difference in abundance between western and eastern areas for Long-tailed Ducks, White-winged Scoters, scoter spp., and gammarid amphipods. To clarify, I’ve included a scoter spp. group (all scoters combined) because a proportion of scoters were not identified to the species level. However, I assumed the majority of these unidentified scoters were White-winged, based on my previous and ongoing aerial and ship-based surveys of seabirds on Nantucket Shoals. Benthic samples were predominantly concentrated over western Nantucket Shoals, therefore I used descriptive statistics and kernel density estimation to compare abundance between west and east areas.

The statistic evaluated is the difference of mean densities between west and east Nantucket Shoals. I tested the observed mean difference against a simulated distribution of the mean difference using a nonparametric bootstrap test. The final bootstrapped mean difference population was sampled with replacement from the pooled empirical data 9,999 times. I determined the Monte-Carlo p-value (evidence against the null hypothesis, given the null hypothesis is true) by calculating the number of times the absolute value of the observed sample statistic was as extreme or more extreme than the mean difference values in the simulated distribution, divided by the number of bootstrap randomizations. I also created plots of the observed mean difference with bias-corrected-and-accelerated (BC_a) bootstrapped confidence intervals to compare abundances between west and east areas.

Seasonality and interannual variability

I compared seasonal occupation of Nantucket Shoals by Long-tailed Ducks, White-winged Scoters, and scoter spp. by first classifying seasons in to categories: 1) winter (December- February), 2) early spring (last days of March - first days of April). I divided the seasons this way because the gammarid amphipod population on Nantucket Shoals declines as winter progresses, after the autumn peak. The aerial surveys were concentrated in early and mid-winter, and then again in spring (~ 1 April). I tested if densities of Long-tailed Ducks and White-winged Scoters decline from winter to spring, similar to that of the amphipod population. I used the same bootstrap procedure for testing seasonal differences in mean abundance as I did with testing differences between west/east densities. Since the Clam surveys were conducted in summer only, I did not test for seasonal variability. However, I assumed that clam density on Nantucket Shoals was stable and did not significantly decline throughout winter and spring.

I assessed interannual variability of winter gammarid amphipod density on Nantucket Shoals over years 1977–2009, by comparing annual mean densities (no. / $100m^3$) with bootstrap BC_a 95% confidence intervals randomized 9,999 times, with replacement.

Spatial interactions, species assemblages, and patch classification

I tested if species assemblages of Long-tailed Ducks, White-winged Scoters and gammarid amphipods were spatially associated at similar patch scales on Nantucket Shoals with a randomized multivariate Mantel test (Bjørnstad et al. 1999, Legendre and Legendre 2012). This statistic measures the degree of spatial association between multiple variables through (dis-) similarity matrices. The original matrices were geographic coordinates (X /Y - as meters); also bird, amphipod, and clam abundance (X_{ij}/Y_{ij} - for bird density and indices represented amphipod and clam abundance). The null hypothesis of the Mantel test stated no spatial association between species pairs. I tested the hypothesis of no spatial association by randomizing distance matrices 9,999 times for each species pair in order to create a simulated distribution (null) of the test statistic, with which to compare the sample test statistic (observed) at all distances (i.e. spatial units) – here a distance increment was 3km or the distance interval between bins.

I qualitatively compared results of the Mantel tests to the mapped distributions of sea ducks and amphipods. I mapped the most intense areas using kernel density utilization isopleths 10% and midrange 50% quantiles of the kernels (utilization areas).

The 10% isopleths delineated high intensity areas of abundance (weighted by density) while the 50% isopleths delineated the core area of utilization. I compared the spatial extent of significant patches classified by Mantel tests (positive patch structure and size of patches were cross-correlations above the abscissa), with those patches (areas of high intensity) classified by kernel density estimation.

Bivalve and gastropod abundance on Nantucket Shoals

NMFS collected bivalve and clam data on bottom trawl surveys designed to assess the spatial distribution and population abundance of Atlantic surf clams and Ocean quahogs (Cargnelli et al. 1999). These surveys occured every three years during summer, and I analyzed bottom trawl data collected south of Nantucket Island in years 2005, 2008, 2011. I reported total abundance and percent frequency of occurrence for all taxa in (Table 3.2).

3.3 RESULTS

We conducted aerial surveys in winter and early spring in years 2008 - 2011. Most surveys were conducted at 61 m, and covered a mean area of 173 km^2 or 451 linear km of ocean (Fig. 3.1.; Table 3.1).

West / East Nantucket Shoals Abundance Comparisons

Long-tailed Ducks were numerically dominant on Nantucket Shoals (Figs. 3.3, 3.4). And White-winged Scoters were more abundant than other scoter species. The following is the taxonomic proportion of scoters calculated in all 3 km binned samples:

63.1% White-winged Scoters, 29.5% unidentified scoters, and 7.4% Black and Surf Scoters.

West and east Nantucket Shoals significantly differed in abundance estimates of all sea duck taxa and amphipods, as determined by nonparametric bootstrap tests (Fig. 3.2). All taxonomic groups were significantly more abundant in the western area of Nantucket Shoals than in the eastern area, in both winter and early spring, as revealed by sample means and 95% bootstrap BC_a confidence intervals (Fig. 3.3).

Seasonality and interannual variation of sea duck and amphipods

Abundance estimates of Long-tailed Ducks, White-winged Scoters, and scoter spp. showed considerable interannual and seasonal variation over the course of this study (Fig 3.4). Long-tailed Ducks were more abundant than White-winged Scoter except in April 2009 and December 2010. In March 2011, Long-tailed Duck and scoter densities did not differ. All taxonomic groups were organized in to large feeding aggregations at sea. Wide 95% confidence intervals resulted from many bins with zero abundance, and few bins with high densities. This reflects the highly patchy distribution of forging sea ducks at sea.

Winter gammarid amphipod population on Nantucket Shoals also showed strong interannual variability and episodic events as revealed by 32 years of nets hauls (Fig. 3.5). Similar to sea ducks, gammarids were patchily distributed on Nantucket Shoals and wide bootstrap 95% confidence intervals were attributed to many net hauls with zero catches and few hauls with large catches. The population appeared to exhibit “boom-and-bust” periods. During the mid to late 1980s, gammarids were super abundant on Nantucket Shoals, followed by several years of low abundance, then a return to a anomalously high abundance in 1999 (Fig 3.5)

Seasonal variability

White-winged Scoter abundance was stable across seasons, based on nonparametric bootstrap results (Fig 3.6): White-winged Scoters (p =0.40), combined Scoters group (p=0.67). Scoters were highest in April 2009, December 2009, and December 2010 (Fig 3.4). However, Long-tailed Ducks had a tendency to disperse from Nantucket Shoals as winter progressed, although evidence was not strong (p = 0.09) (Fig.3.6). Long-tailed Duck density declined substantially from winter to early spring in three of four survey seasons in 2008, 2009, 2011. In the 2010 season, Long-tailed Duck density moderately declined, then stabilized from midwinter through spring.

The scoter population showed seasonal fluctuations, however, densities were fairly stable compared that of Long-tailed Ducks. Scoter density was highest in April 2009, December 2009 and December 2010 (Fig 3.4).

The Nantucket Shoals gammarid amphipod population had two distinctive seasonal peaks in abundance that occur in spring and fall (Fig. 3.7). Following the fall peak, gammarid densities declined as winter progresses until an abrupt increase in spring. It is possible that gammarid amphipods breed twice annually, and synchronize production with phytoplankton blooms. Results here are similar to those reported by Avery et al. (1996)

Patch-scale characteristics of sea ducks and potential prey

Two broad-scale patches were revealed on Nantucket Shoals between sea duck species, and also between ducks and potential prey, as determined by multivariate Mantel tests (Figs 3.8 – 3.10). Correlations were above the abscissa twice for all spatial correlograms, revealing ~ 15 – 30 km significant patch scales of association among the near distance classes, and weaker, non-significant patch scales at farther distances (Figs. 3.8 - 3.10). Long-tailed Ducks and White-winged Scoters were significantly associated in space up to 15 km (Fig 3.8). This significant patch of Long-tailed Ducks and White-winged Scoters was interrupted by a 50 km zone of negative spatial association (areas where the two species were not associated). A small-scale, weak, and non-significant patch of long-tailed ducks and White-winged Scoters formed in the far distance classes (Fig 3.8).

Long-tailed Ducks and amphipods were spatially associated within an approximate 20 - 30 km zone. Long-tailed Ducks and clams shared a similar significant spatial association in an approximate 30 km zone. However, Long-tailed Ducks were slightly more correlated with amphipods than with clams in near distance classes (Fig. 3.9). Mantel tests produced similar results for White-winged Scoters and potential prey, however, White-winged Scoters were slightly more correlated with clams than with amphipods in near distance classes (Fig. 3.9). White-winged Scoters and potential- prey showed a significant spatial association at a patch scale of ~ 30km. Similar to that of Long-tailed Ducks, White-winged Scoters showed negative association with potential prey at ~ 45km before a weak and a non-significant patch is revealed in the farthest distance classes (Fig 3.9).

For all combinations (Fig. 3.10), a concordant significant patch structure took form in a zone that is approximately ≤ 35 km. This strong patch was followed by an approximate 45 -55km area of negative spatial association, after which, another weak non-significant yet positive patch occured (Fig. 3.10). West and east areas of Nantucket Shoals were sampled heavily for birds (3km samples west: n=890; 3km samples east: n=799) and amphipods (tows west: n= 186; tows east= 139). Western Nantucket Shoals appeared adequately sampled to form general conclusions regarding clam intensity and spatial dispersion (n=20), however the eastern area was sampled one-quarter as much (n=5).

High intensity areas (50% and 10% kernel isopleths weighted by abundance) of Long-tailed Ducks, White-winged Scoters, gammarid amphipods and clams (Atlantic surf clam and ocean quahog, combined) were located along the west and southwestern areas of Nantucket Shoals (Figs. 3.11 - 3.15). The Long-tailed Duck kernels appeared to overlap more generally with the amphipod core than with the clam core. Moreover, the White-winged Scoter core appeared to align more so with the clam cores than with the amphipods core (Fig 3.14). These findings were strengthened by Mantel test results confirming a slightly stronger spatial relationship between Long-tailed Ducks and amphipods, compared to that of White-winged Scoters, which had a slightly stronger affinity for the clam area (Fig 3.9). The distance between amphipod kernels on west and east Nantucket Shoals was approximately 50km. These results supported Mantel results by showing two patches roughly 50km apart (Figs 3.9, 3.14).

Co-located peaks and troughs of bird, amphipod and clam abundance also suggested similar areas of habitation on Nantucket Shoals in winter (Fig. 3.16). The highest density bird bins were located on western Nantucket Shoals: Long-tailed Ducks > 5000 birds km^{-2} (February 2008); White-winged Scoters > 1000 birds km^{-2} (December 2010) (Fig. 3.15).

Surf Clam and Ocean Quahog survey data (benthic hauls)

NMFS performed 75 tows south of Nantucket Island and Martha's Vineyard between 2008 -2011: 33% (n=25) were within the sea duck study area; 27% (n=20) in the western area, and 7% (n=5) in the eastern area. Sixty-seven percent (n=50) of hauls were conducted outside of the sea ducks study area, yet in the vicinity of Nantucket Shoals (Fig. 3.13; Table 3.2). Ocean quahogs and Atlantic surf clams were the most dominant bivalve species collected inside the sea duck study area, (81% and 14%, respectively). Ocean quahogs and sea scallops (96% and 1.5%, respectively) were most abundant outside the study area yet in the vicinity of Nantucket Shoals. A wide diversity of mollusc, crustacean and echinoderm species were collected and recorded in samples (Table 3.2). Ocean quahogs and Atlantic surf clams were large (Table 3.2). The smallest clams were within the upper size limits that White-winged Scoters are known to consume. These are not accessible to Long-tailed Ducks as they are limited to smaller bivalves. However, it is possible that the sampling gear selected larger clams: "Mechanically, the bar spacing with the 2" liner creates a bar spacing of about 1/2" to 3/4"." (V. Nordahl personal communication) (Table 3.2).

3.4 DISCUSSION

My primary objectives were to map the spatial dispersion of sea ducks in winter on Nantucket Shoals, and to determine if and where diving ducks had a tendency to aggregate in relation to potential-prey drivers - primarily pelagic gammarid amphipods and clams (Atlantic Surf Clams and Ocean Quahogs). Long-tailed Ducks and White-winged Scoters were numerically dominant on Nantucket Shoals in winter. However, Long-tailed Duck density was far greater than White-winged Scoter density, on most surveys (Fig 3.4). We surveyed west and east areas of Nantucket Shoals with equal effort (Fig 3.1), and observed intense spatial overlap of foraging Long-tailed Ducks and White-winged Scoters in some areas, chiefly along the southwestern corner of Nantucket Shoals (Figs. 3.14, 3.15). In winter and early spring 2008 - 2011, Long-tailed Ducks and White-winged Scoters foraged over a mean depth of ~ 30 m, in areas where pelagic amphipods and clams are historically abundant and highly aggregated (Fig. 3.14). In this area, Long-tailed Ducks and White-winged Scoters formed interspecific foraging associations at spatial scales between 15 -20 km (Figs. 3.8, 3.14, 3.15). They both tracked potential prey intensity at larger spatial scales, up to ~30 km (Figs. 3.9, 3.10). However, at smaller spatial scales, predator-prey spatial associations were stronger between Long-tailed Ducks and amphipods, as well as between Long-tailed Ducks and clams. In contrast, spatial associations between White-winged Scoters and clams were stronger at smaller spatial scales than between White-winged Scoters and amphipods (Figs. 3.9, 3.10). Small-scale predator-prey spatial correlations suggested that Long-tailed Ducks focus on tracking amphipod abundance closely, while White-winged Scoters track clam abundance. The data suggested that Long-tailed Ducks and White-winged Scoters track prey types similar to those reported by other winter feeding ecology studies in soft-bottom habitat (Mackay 1891, Sanger and Jones 1984, Vermeer and Bourne 1984, Goudie and Ankney 1986, Fox 2003, Ross et al. 2005, Zydelis and Ruskyte 2005, Schummer et al. 2008, Anderson et al. 2008, White et al. 2009).

Previous studies characterized the Long-tailed Duck as an opportunist with a malleable foraging strategy, likely more carnivorous based on gut morphology, and who seeks out high-quality soft bodied prey to manage high mass-specific energy costs (Nilsson 1972, Stott and Olson 1973, Sanger and Jones 1984, Goudie and Ankney 1986, Stempniewicz 1995, Jamieson et al. 2001, Zydelis and Ruskyte 2005). Long-tailed Ducks may forgo infaunal inaccessible bivalve prey in relation to burial depth in sediment (Zydelis and Ruskyte 2005). Richmond and Lovvorn (2009) showed how a combination of clam size, clam burial depth, and threshold densities can influence profitability for diving ducks. For Lesser Scaup, (a small diving duck similar in size to a Long-tailed Duck, however larger), clams buried deeper than 5 cm were unprofitable when sizes > 12 mm long. However, for the larger White-winged Scoter, clams size > 18 mm was profitable at lower densities buried deeper than 5cm. White-winged Scoters, unlike smaller ducks, can profit by selecting broader bivalve sizes, and taking infaunal bivalves buried too deep for smaller ducks (Richman and Lovvorn 2008). It is possible that White-winged Scoters can select more lower-quality prey than Long-tailed Ducks in winter as a function of having greater flexibility in terms of energy balance, and reserve time to adjust their activities (Goudie and Ankney 1986, 1988, Anderson and Lovvorn 2011).

White et al. (2009) found that Long-tailed Ducks fed principally of *Gammarid annulatus* on Nantucket Shoals, however, they did not find evidence of bivalve prey. If Long-tailed Ducks supplement their diet with infaunal bivalves on Nantucket Shoals, they may select a size range and burial depth similar to those described for Lesser Scaup (Richman and Lovvorn 2008). Hard-bottom habitat composed of rock and boulders supports growth and proliferation of epifaunal bivalves, however, Nantucket Shoals is composed of sandy habitat and lacks this type of macrozoobenthos (Table 3.2 ; Backus and Bourne 1987). Long-tailed Ducks have smaller bodies, higher mass-specific energy costs, and may have less reserve time than White-winged Scoters, thus productive foraging time is crucial for these diel-foraging birds. Soft-bodied prey, though motile and patchily distributed, is likely valued by Long-tailed Ducks for its higher energy content and digestibility, compared to that of shelled prey (Goudie and Ankney 1986, 1988). The Nantucket Shoals ecosystem is a major winter foraging location for Long-tailed Ducks specifically due to its abundant and persistent amphipod stock (White et al 2009). These results also suggested a potential for niche overlap between Long-tailed Ducks and White-winged Scoters in an area where prey was persistently abundant (i.e., a predator-prey hotspot).

Spatial Overlap, Competition, and Threshold Densities

While foraging in the marine environment intra- and interspecific diving ducks appear to generally coexist with limited competitive exclusion through aggression (Goudie and Ankney 1988, Lovvorn et al. 2013). Many studies claim to provide evidence for interspecific competition, however, conclusions are oftentimes circumstantial (Wiens 1989). Assembling strong evidence to test interspecific competition among marine animals while at sea is fraught with many challenges, particularly when the organisms under study are sub-surface feeders. However, knowledge of species' natural history, feeding ecology, habitat use, combined with high – quality spatial data sets on distribution and abundance, may provide strong circumstantial evidence to support an inference of competition or lack thereof (Wiens 1989, Legendre and Legendre 2012).

Body size and bill morphologies closely relate to the feeding habits and energy status of Long-tailed Ducks and White-winged Scoters (Anderson, E.M. et al. 2008). As I have shown throughout this paper, numerous studies conducted in the Nearctic and Western Palearctic have demonstrated that Long-tailed Ducks consumed a substantially higher fraction of soft-bodied prey than do White-winged Scoters, which take mainly bivalves. A study by Sanger and Jones (1984) in Kachemak Bay, AK, is the only study to my knowledge that has directly compared the diets of these two species. In the bay, Long-tailed Ducks primarily foraged in soft-bottom habitat and consumed a wide variety of prey, however, predominantly soft-bodied, which included 24 % sand lance. White-winged Scoter foraged over hard-bottom and primarily consumed bivalve prey, and a small proportion of soft-bodied prey. Bivalve lengths taken by both ducks differed significantly – longer for White-winged Scoters (blue mussels ≥ 50-69 mm; clams ≥ 10 - 49 mm); shorter for Long-tailed Ducks (clams and blue mussels < 10 mm). However, White-winged Scoters are flexible to forage on alternative prey (i.e. fish and non-mollusc prey) (McGilvrey 1967, Zalakevicius et al. 1995, Palm et al. 2012). The occurrence of such prey species is likely to have been underreported in many diet studies due to sampling bias (Anderson, E.M. et al. 2008). In winter on Nantucket Shoals, the feeding habits of Long-tailed Ducks and White-wined Scoters may be concordant with feeding trends as reported elsewhere for soft-bottom habitat, and as suggested by results here. However, the data here show a substantial and significant area of spatial overlap of Long-tailed Ducks, White-winged Scoters, pelagic amphipods and clams in relatively deep water (~30 m) and approximately 40 + km offshore. In these areas of overlap, it is possible that Long-tailed Ducks and White-winged Scoters utilized their flexible foraging strategies and interacted through mutualism or commensalism in areas where soft-bodied prey are abundant (Hoffman et al. 1981).

Sea ducks may associate with flocks to reduce search costs and time at the bottom (Guillemette et al. 1993, Lovvorn et al. 2013)**.** Foraging success here is likely dependent on flock size, in other words, positive density dependence through local enhancement, an Alle-like mechanism (Stephens et al. 1999, Courchamp et al. 1999, Stephens and Sutherland 1999, Grünbaum and Veit 2003, Gardner 2004, Ryan et al. 2012)**.** Long-tailed Ducks and White-winged Scoters are not uniformly dispersed over Nantucket Shoals, however, dense aggregations of diving ducks concentrated over small-scale high intensity areas of potential prey (Fig. 3.15). By locating persistent small-scale, high-density patches, diving birds may reduce search time and increase profitability (Fauchald 1999, 2009, Fauchald et al. 2000). Long-tailed Ducks and White-winged Scoters likely use a combination of local enhancement (cueing in on the distribution of other feeding birds rather than directly to prey) and memory to locate patches of prey at sea (Pöysä 1992, Davoren et al. 2003a, Grünbaum and Veit 2003, Buckley 2009). Marine birds may also cue in on distant birds traveling to feeding patches or to feeding groups (Hoffman et al. 1981). Diving Ducks on Nantucket Shoals form massive feeding flocks. Sitting birds may perceive the foraging activities of feeding birds up to 4.5 km away (Haney et al. 1992), hence, direct and indirect visual connectedness between flocks may serve to stabilize core feeding aggregations of birds over a larger area where prey is abundant and persistent.

Prey threshold effects may also influence the distribution and abundance of vertebrates (Van Baalen et al. 2001). Predators may exploit and aggregate to prey above a perceived prey-density threshold, until it is no longer profitable to increase search effort for prey (Hassel and May 1974, Piatt and Methven 1992, Robards et al. 1999). This relationship can be sigmoidal, as predators may concentrate where prey is above some minimum abundance threshold (Piatt 1990, Piatt and Methven 1992).

Threshold effects may be related to how Long-tailed Ducks and White-winged Scoters perceive and formulate decisions about prey patches on Nantucket Shoals. Potential prey densities are lower in the eastern Shoals, markedly along the southeast corner (Figs 3.3, 3.14, 3.16). Since predators are not omniscient and lack complete knowledge of the prey field, prey patches are often missed by predators (Sih and Christensen 2001, Lewis et al. 2007, Anderson and Lovvorn 2012). The White-winged Scoter population was stable throughout winter, suggesting abundant and accessible bivalve prey, if they are indeed foraging for clams (Fig. 3.6). The gammarid amphipod population decreases on Nantucket Shoals as winter progresses (Avery 1993, Avery et al. 1996). Long-tailed Ducks have a tendency to disperse from Nantucket Shoals later in the season, and it is tempting to speculate if this is related to a decreasing amphipod density threshold for ducks (Figs. 3.6, 3.7). Long-tailed Ducks may disperse from the Shoals in some years to alternative foraging areas (Oppel et al. 2009). Predators can increase foraging efficiency if they use prior knowledge of successful foraging locations rather than a randomly searching the environment (Gende and Sigler 2006, Benoit-Bird et al. 2013), and might abandon a prey patch before depletion if prey density thresholds drop to unfavorable levels (Lovvorn et al. 2013).

Future work could further test these hypotheses by collecting Long-tailed Ducks and White-winged Scoters in areas of overlap and non-overlap along southwest Nantucket Shoals to test how strong my assumptions hold. The prey field should also be sampled in these areas with plankton nets and grab samples to test for seasonal variability in prey abundance and density threshold effects.

TABLES

Table 3.1 – Survey dates, area sampled, and altitude of individual surveys.

Year	Month/Date	Linear km	Area (km^2)	Altitude (m)
2008	February 15, 16	468	187	61
2008	February 20 *	440	176	61
2008	March 30	642	256	61
2009	February 7	516	206	61
2009	February 11 *	261	104	61
2009	April 1	547	219	61
2009	December 31 ¥	327	131	152
2010	January 10	453	181	152
2010	February 18,22	517	207	61
2010	February 27,28*	260	104	61
2010	March 27	520	208	61
2010	December 18 ‡	521	104	61
2011	February 7	517	207	61
2011	February 11*	259	104	61
2011	March 30	519	208	61

* Replicate transects
¥ Adverse weather conditions, i.e. fog, snow, prevented portions of transects to be completed
‡ White was the only observer on survey

Table 3.2 –Molluscs, crustaceans, and echinoderms collected south of Nantucket Island in years 2005, 2008, and 2011. WSA = within sea duck survey area; OSA = outside sea duck survey area.

Strata	Species	Percent frequency of occurrence	Total number of individuals collected with strata	Mean (SD) length (mm) of ocean quahogs and surf clams
WSA (n_{stations} = 25)	Atlantic rock crab	0.351405622	7	106.88 (30.90), n = 1,912
	Atlantic surf clam	**14.45783133**	288	
	boreal asterias	0.301204819	6	
	hermit crab	0.803212851	16	
	Jonah crab	0.200803213	4	
	lady crab	1.004016064	20	
	northern cyclocardia	0.050200803	1	
	northern moonsnail	1.104417671	22	
	ocean quahog	**81.52610442**	1624	
	razor and jackknife clam	0.050200803	1	
	smooth asarte	0.15060241	3	
OSA (n_{stations} = 50)	Atlantic rock crab	0.043535046	6	84 (27.26), n = 13,308
	Atlantic surf clam	0.195907706	27	
	boreal asterias	0.551443912	76	
	false quahog	0.065302569	9	
	hermit crab	0.137860978	19	
	Jonah crab	0.253954433	35	
	lady crab	0.058046728	8	
	northern cyclocardia	0.07255841	10	
	northern horse mussel	0.116093455	16	
	northern moonsnail	0.348280366	48	
	ocean quahog	**96.36482368**	13281	
	sea scallop	**1.509214918**	208	
	sea star/ brittle star	0.007255841	1	
	smooth asarte	0.22493107	31	
	Simon’s whelk	0.007255841	1	
	waved whelk	0.043535046	6	

FIGURES

Figure 3.1 – Survey intensity: Aerial survey transect represented by parallel horizontal lines (9km intervals). Cell length = 3km spatial bins.. Color scale = survey frequency of cell. Some transects were surveyed more intensely than others due to replication.

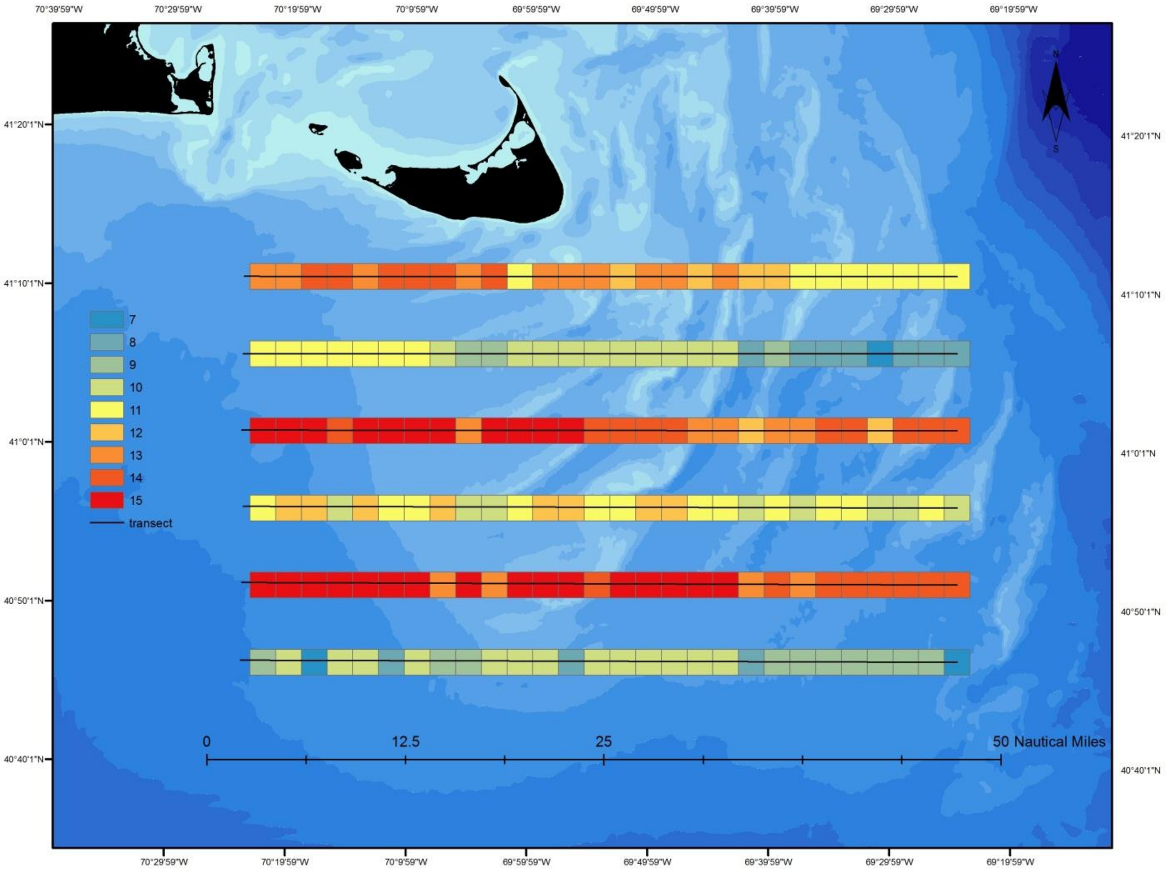


Figure 3.2 - Hypothesis tests of no mean difference in abundance between west and east Nantucket Shoals. Abundance of all taxa differed significantly between west and east Nantucket Shoals. A Monte Carlo p-value was computed by drawing 9,999 bootstrap replicates of the data. Vertical red lines represent the observed sample statistic (mean difference).

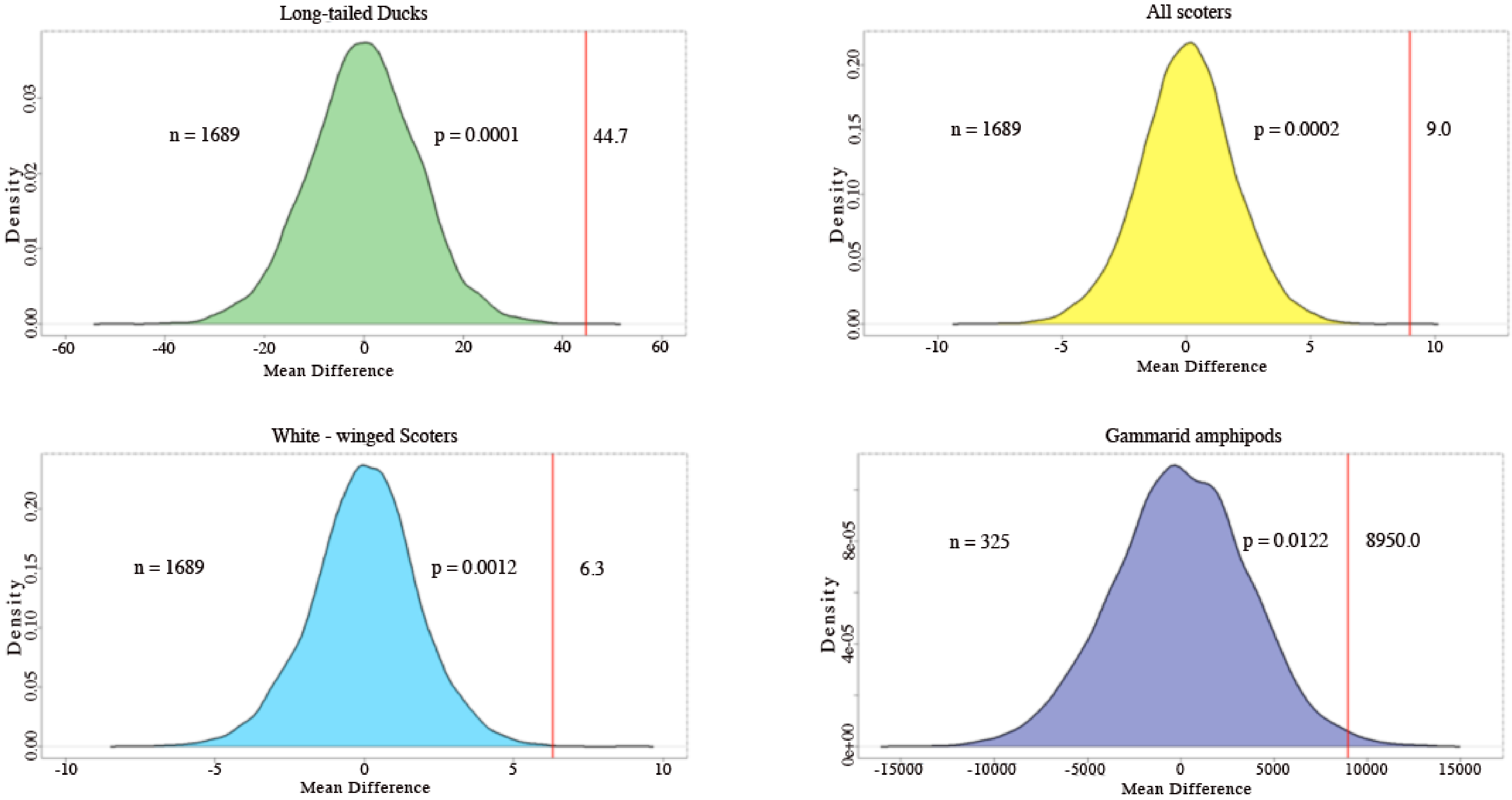


Figure 3.3 - Means and 95% bootstrap confidence intervals in west (n=890) and east (n= 799) areas of Nantucket Shoals for Long-tailed Ducks, White-winged Scoters, and the combined scoters spp.; gammarid amphipods west (n=186) and east (n=139).

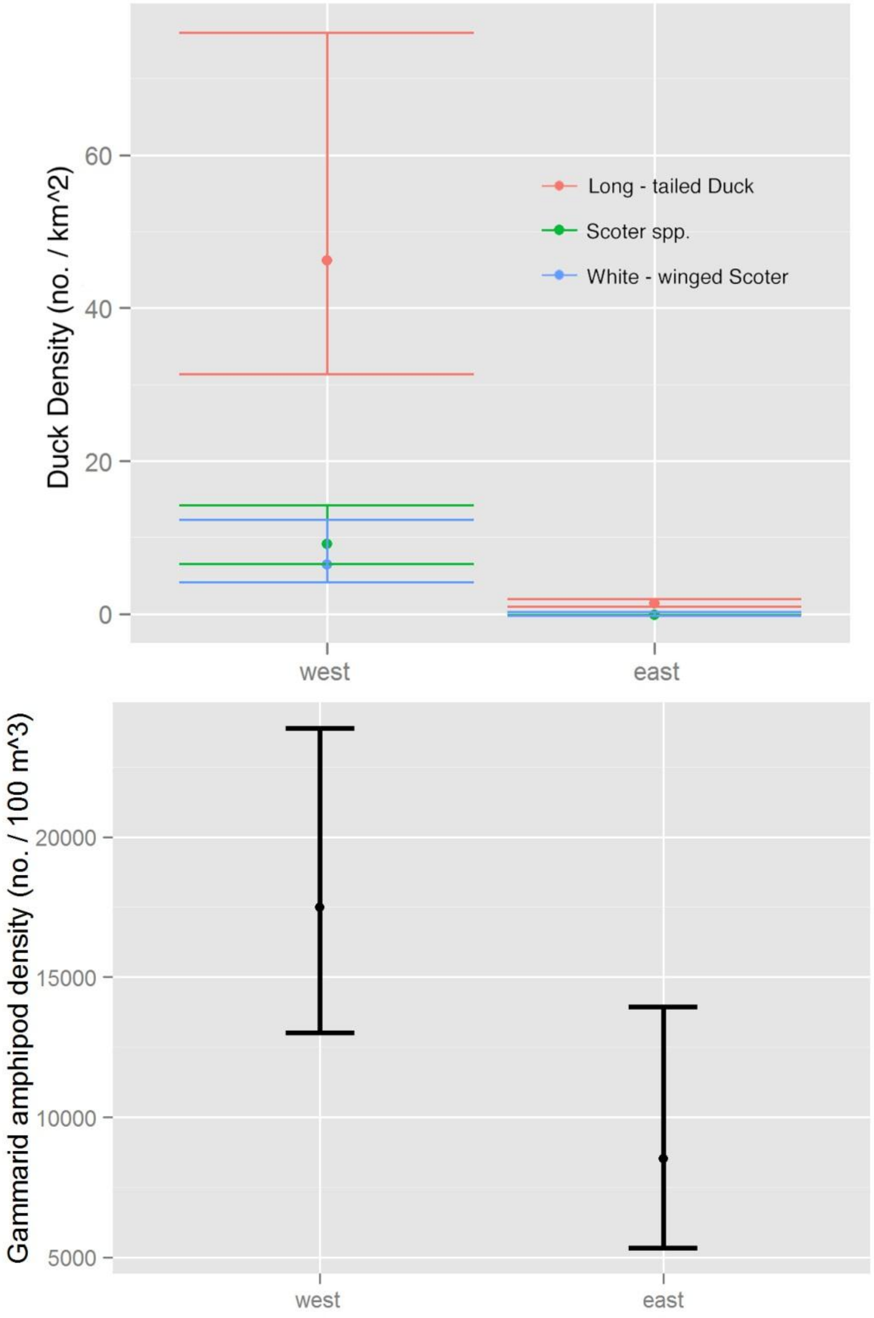


Figure 3.4 - Mean abundance and 95 % bootstrap confidence intervals of Long-tailed Ducks, White-winged Scoters, scoter spp. (December – April 1, 2008 – 2011).

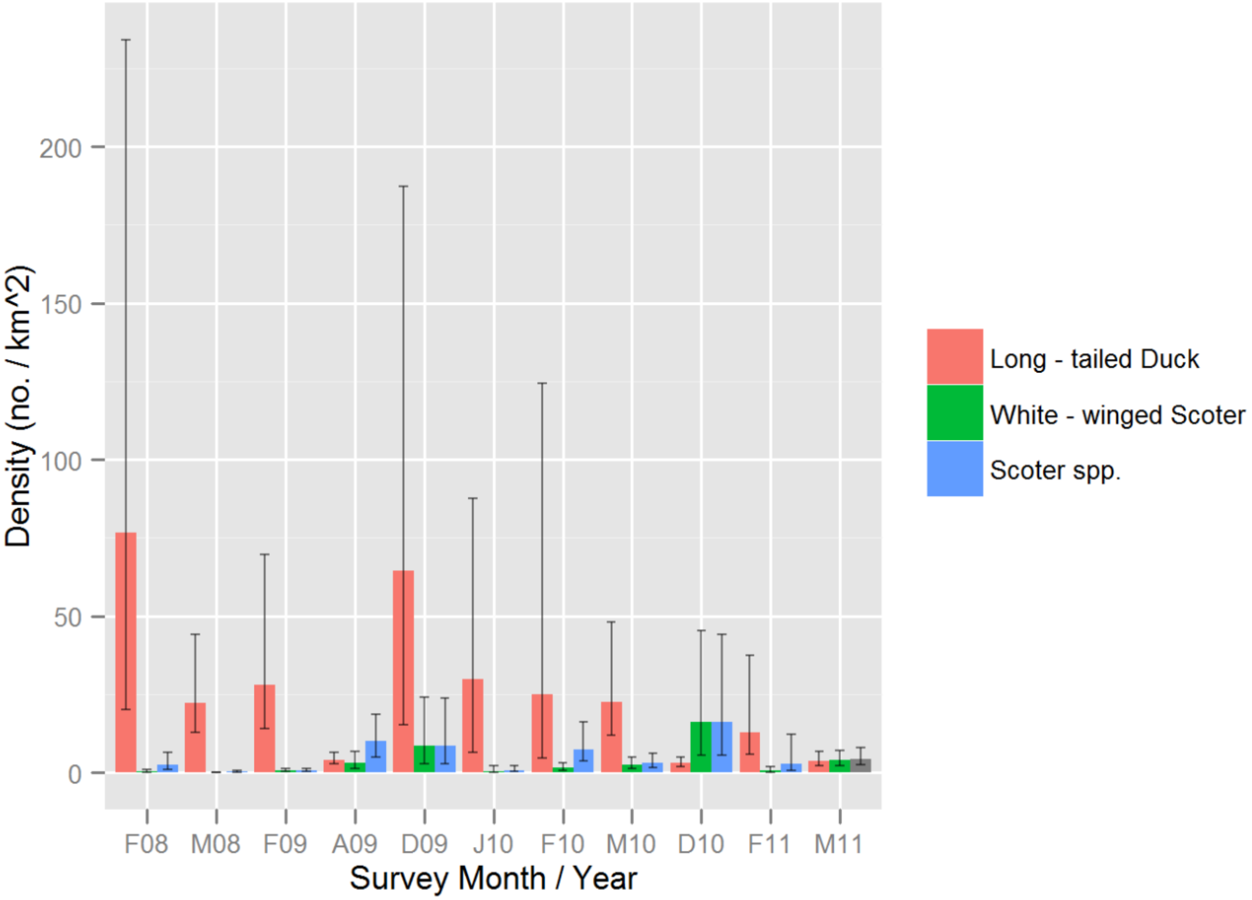


Figure 3.5 – Winter delta-mean abundance of gammarid amphipods with 95 % bootstrap confidence intervals. All tows were conducted on Nantucket Shoals between years 1977 – 2009.

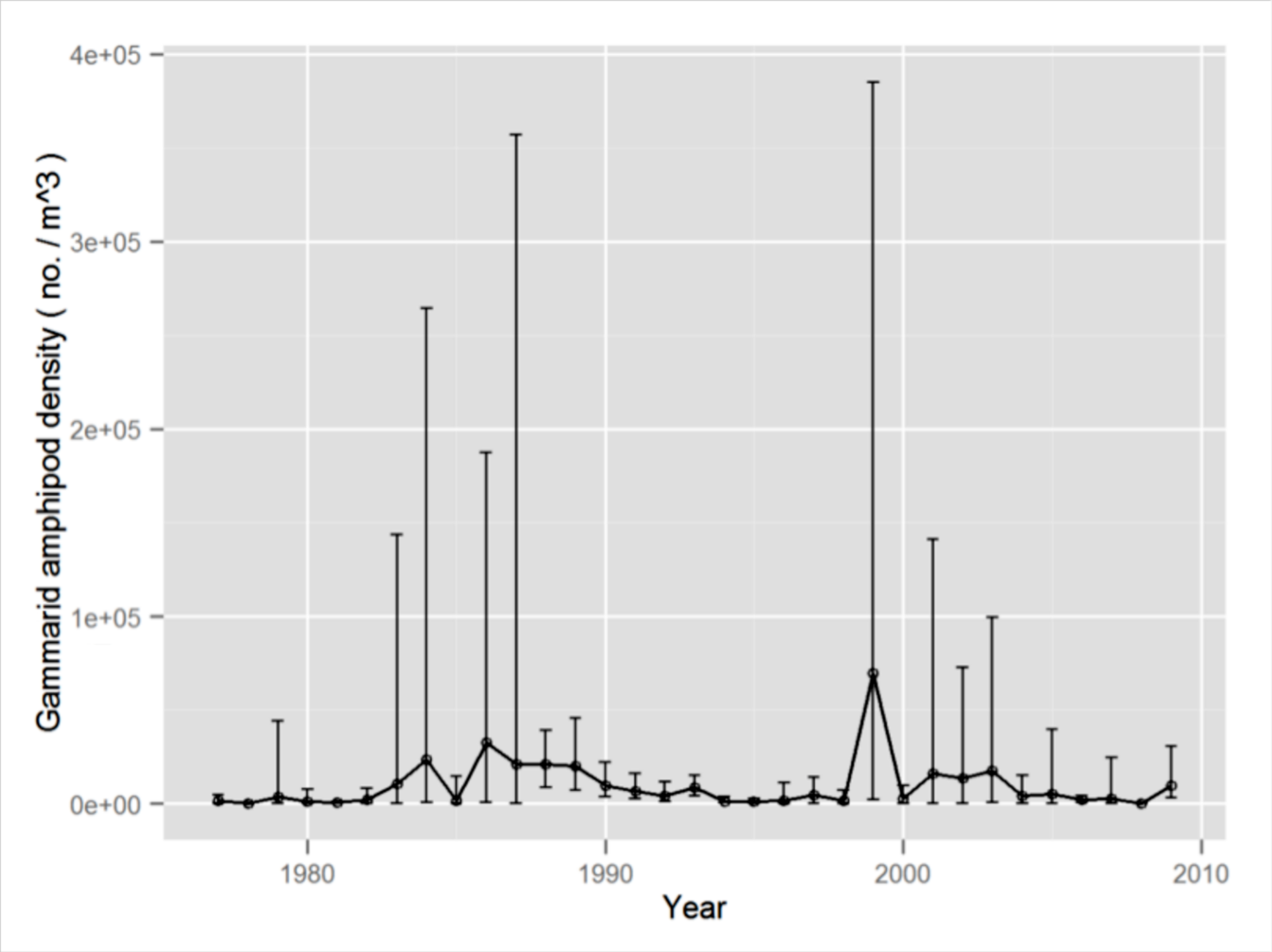


Figure 3.6 - Mean difference in abundance or seasonal occupation of Nantucket Shoals (early/midwinter [n=1101] vs. late winter/early spring [n=588]) for Long-tailed Ducks, White-winged and scoter spp.

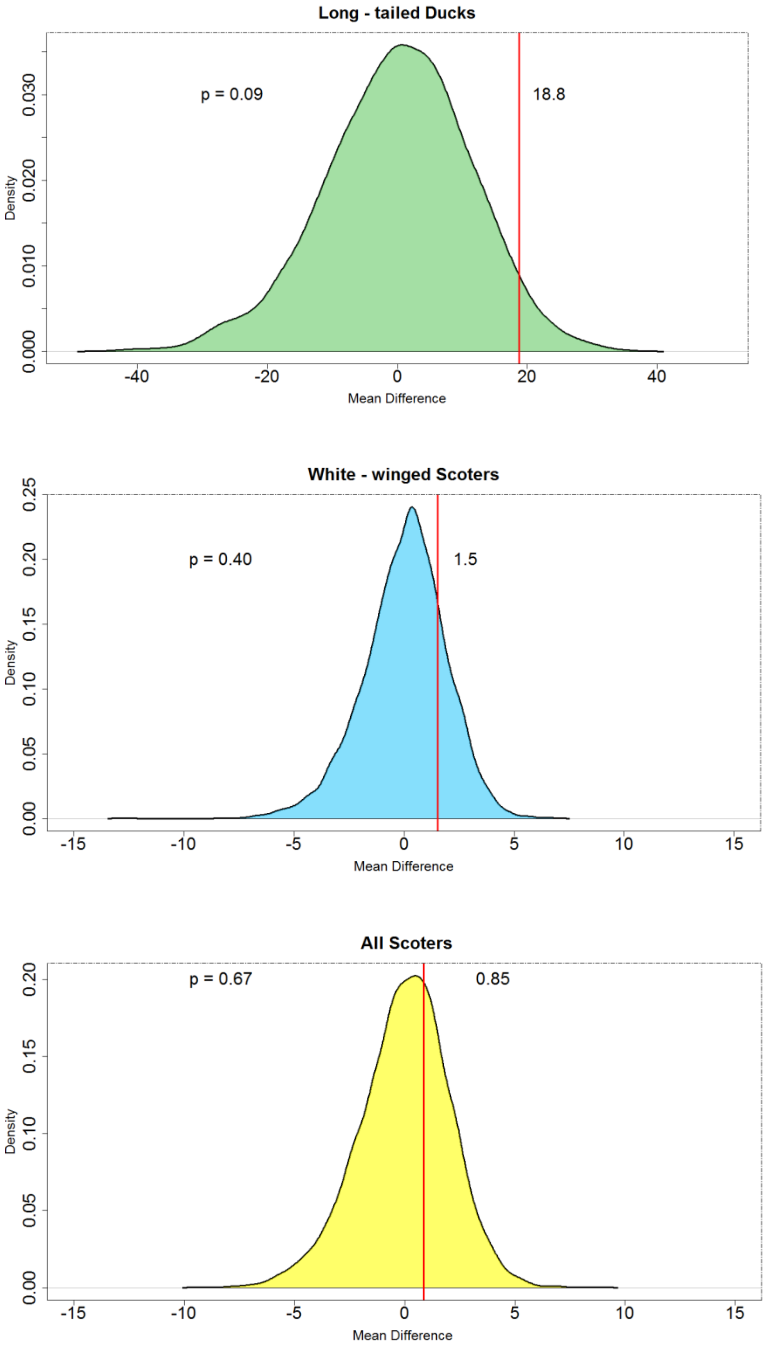


Figure 3.7 – Delta-mean monthy abundance with 95% bootstrap confidence intervals, of gammarid amphipods on Nantucket Shoals in winter (1977-2009).

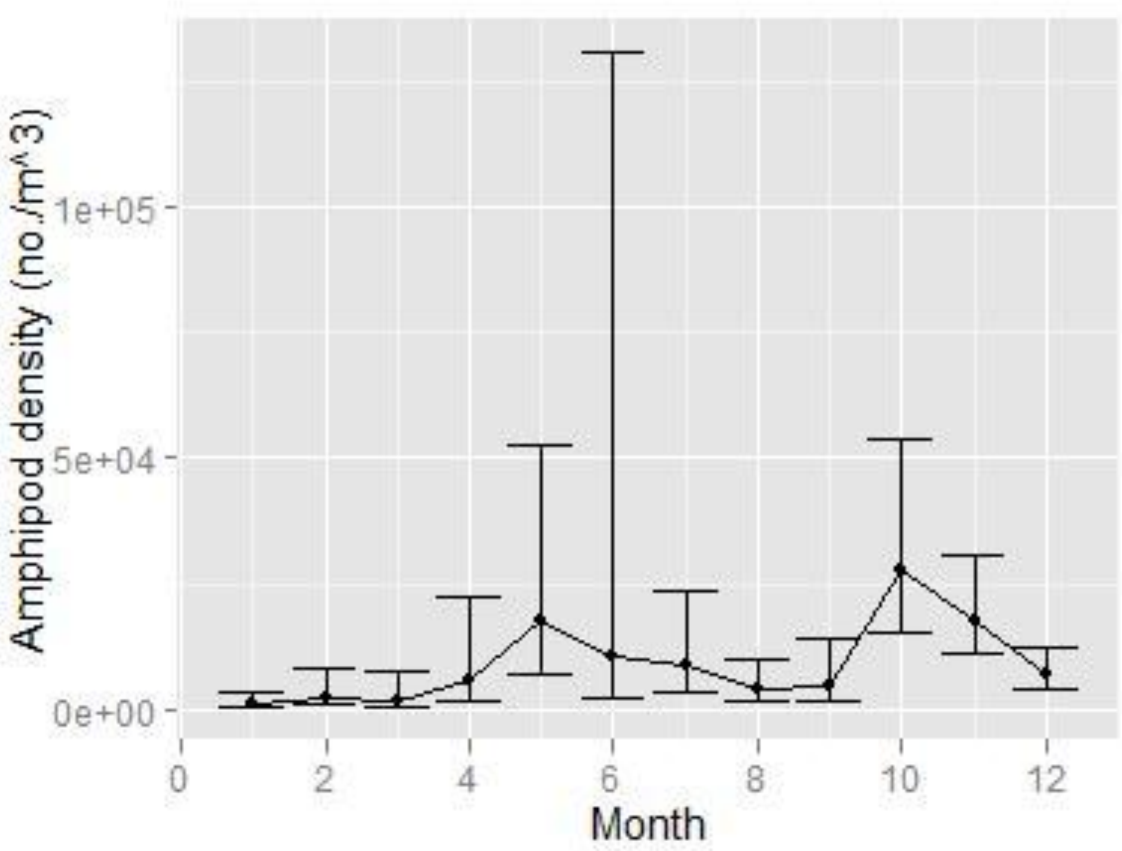


Figure 3.8 - Mantel cross-correlation between Long-tailed Duck density (no./km^2) and White-winged Scoter density (no./km^2)

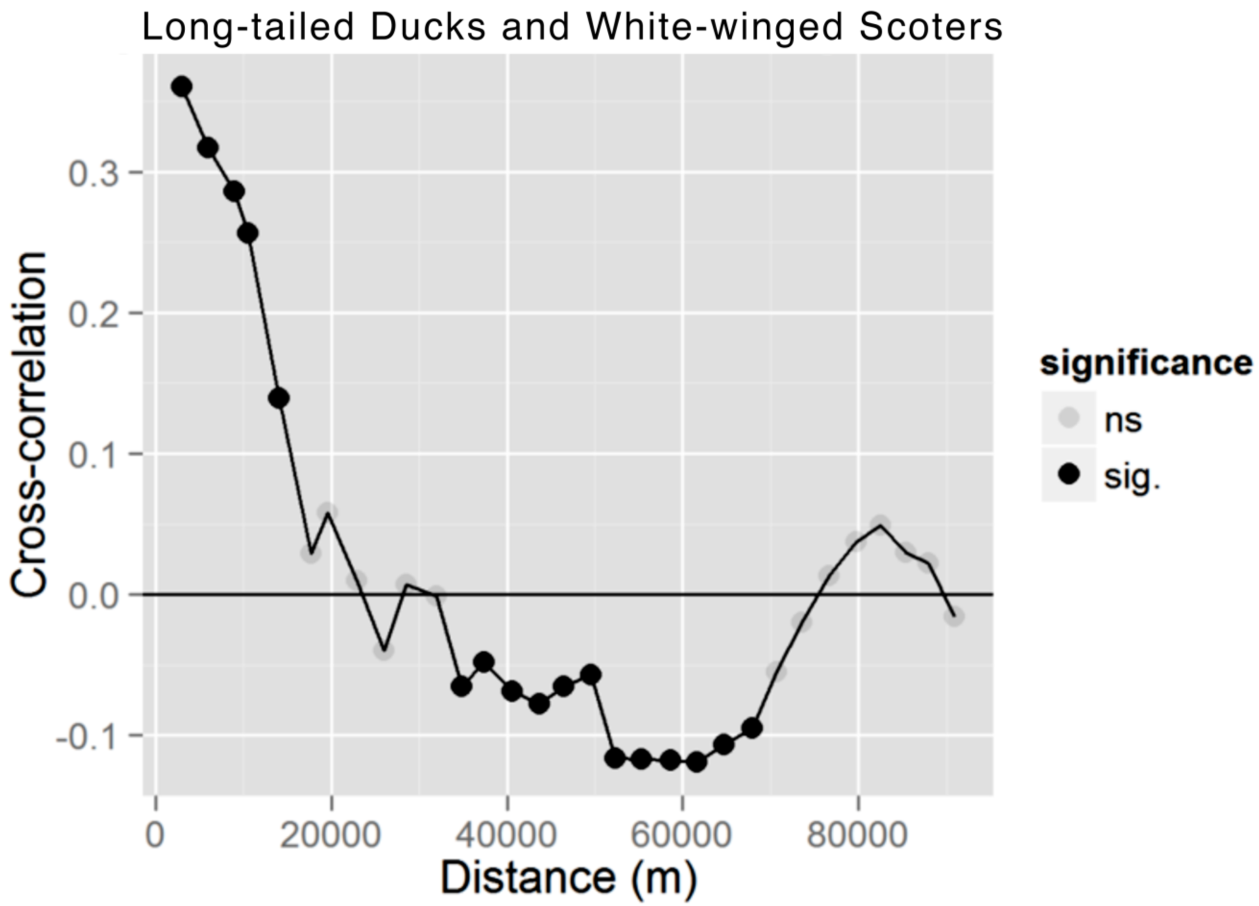


Figure 3.9 – Cross-correlation between (top) Long-tailed Duck density and potential prey and (bottom) White-winged Scoter density and potential prey.

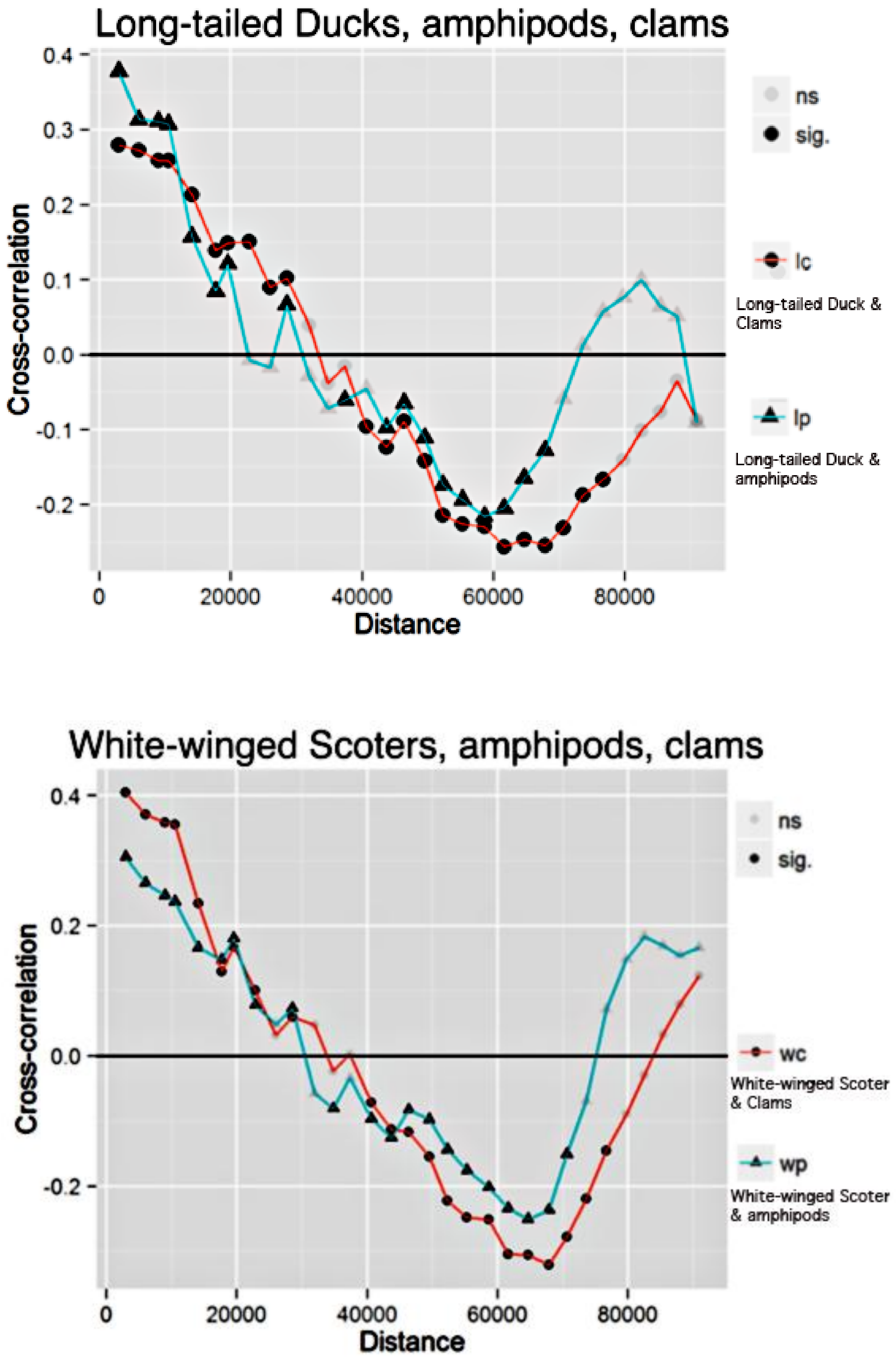


Figure 3.10 - Mantel spatial cross-correlation results testing interactions between: Long-tailed Ducks and White-winged Scoters (lw); Long-tailed Ducks and amphipods (lp); Long-tailed Ducks and clams (lc); White-winged Scoters and amphipods (wp); White-winged Scoters and clams (wc).

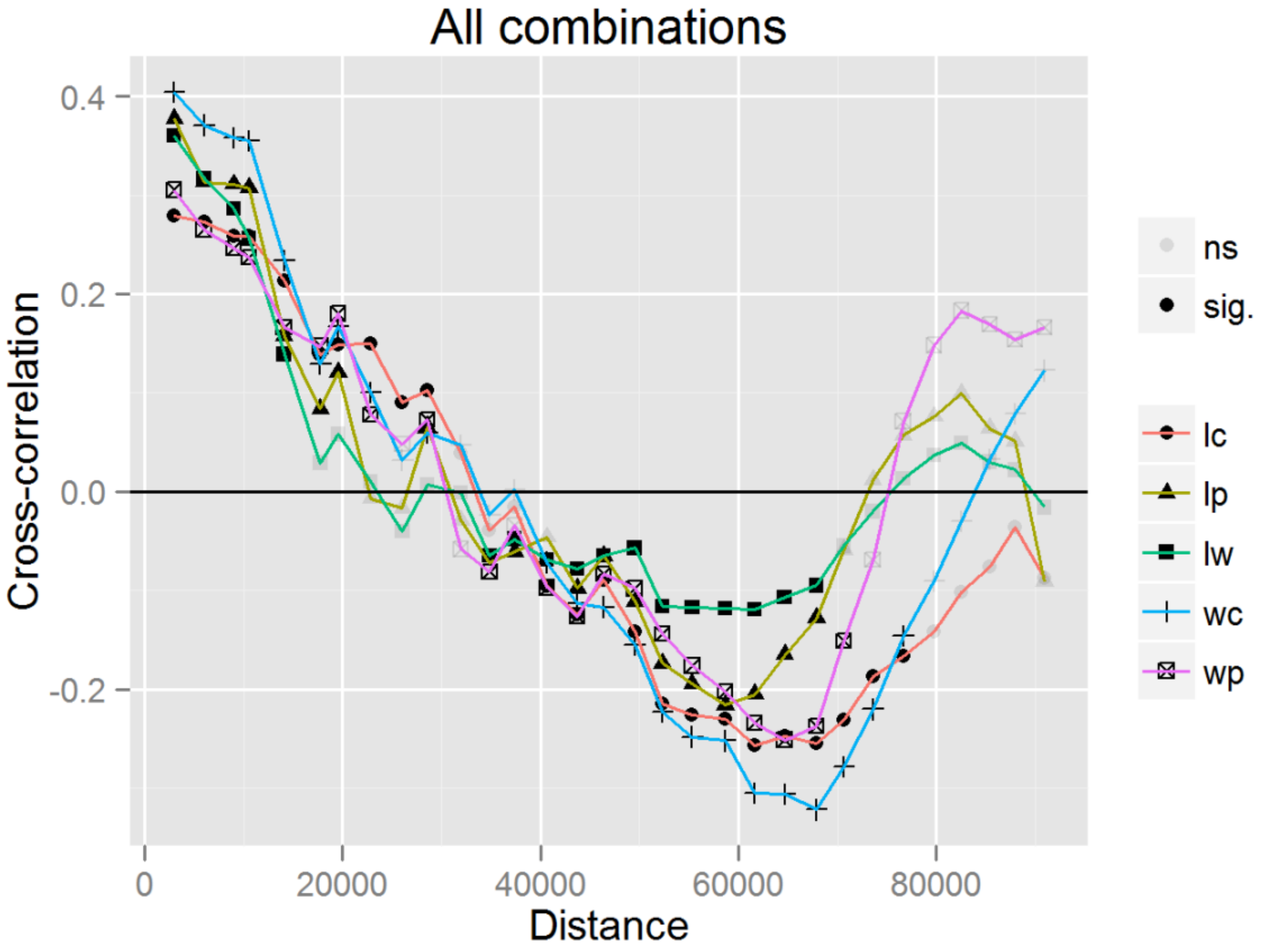


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Figure 3.11 – Locations of zooplankton bongo tows (top) and kernel density of gammarid amphipods (bottom) on the continental shelf (1977-2009).

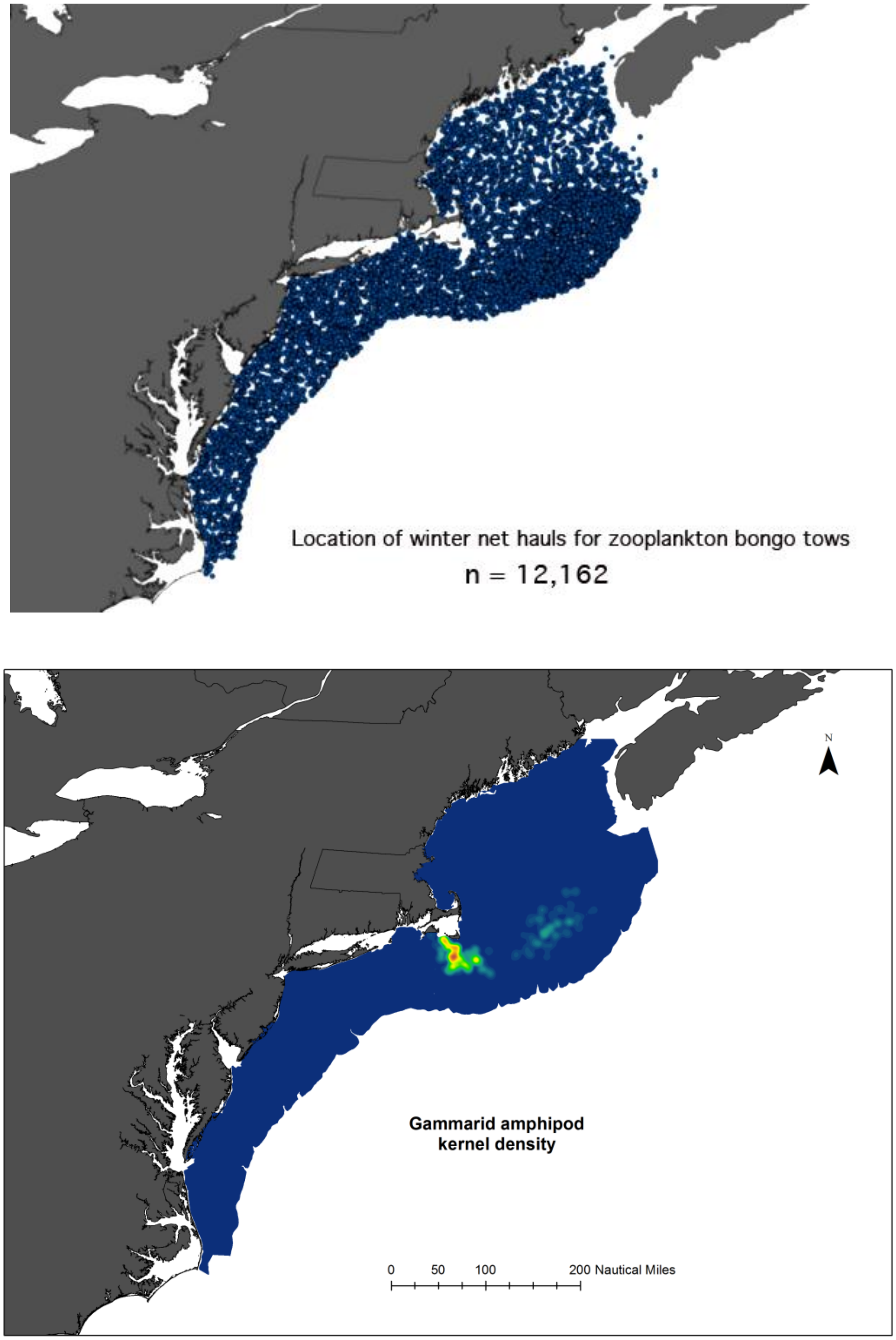


Figure 3.12a – Gammarid amphipod density on Nantucket Shoals (1977-2009). Black dots represent tows; warm colors= high density areas; cool colors = low density areas). Black frame delimits sea duck aerial survey area.

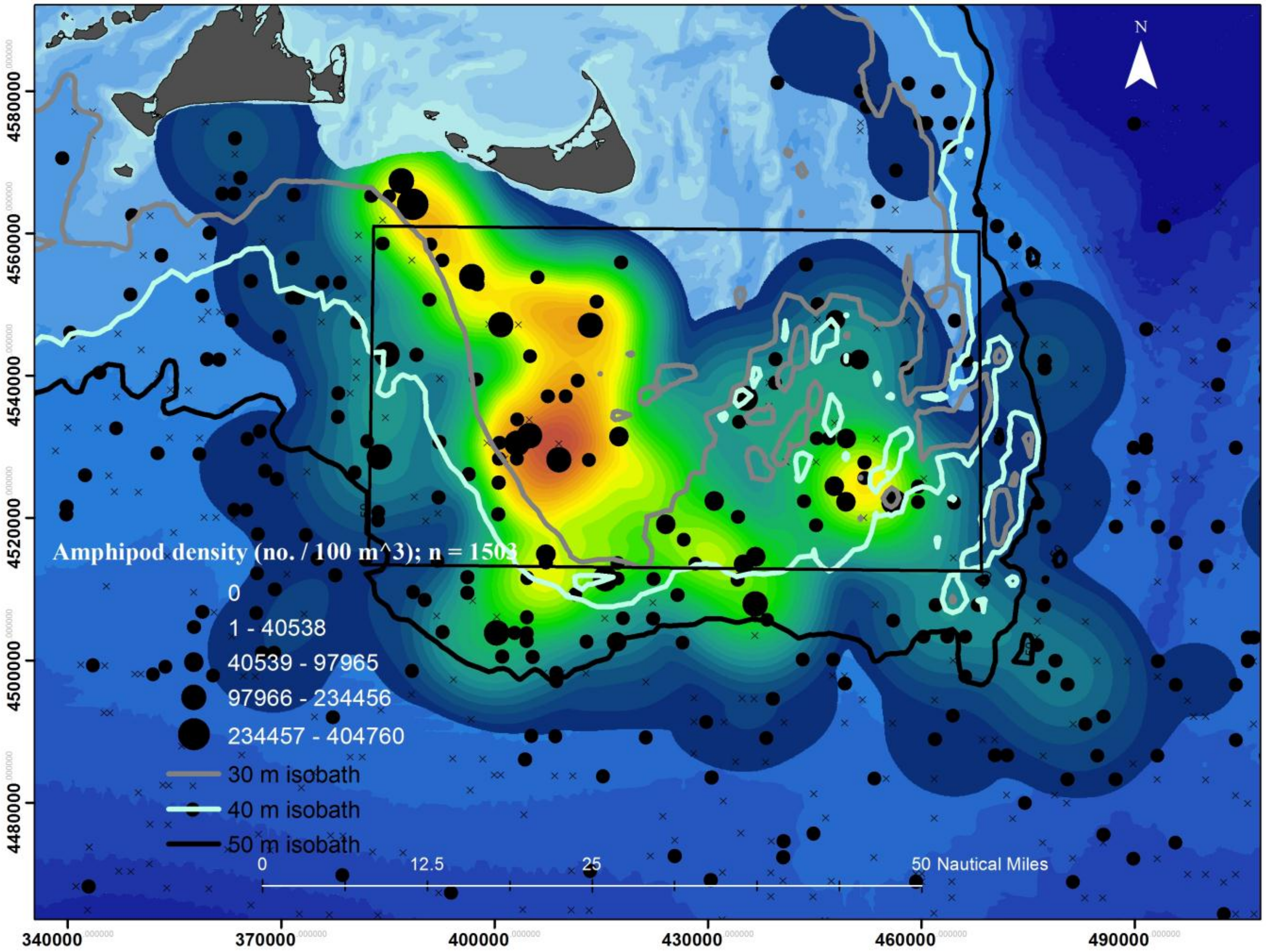


Figure 3.12b – Gammarid amphipod density on Nantucket Shoals (1999-2009). Black dots represent tows; warm colors= high density areas; cool colors = low density areas). Black frame delimits sea duck aerial survey area.

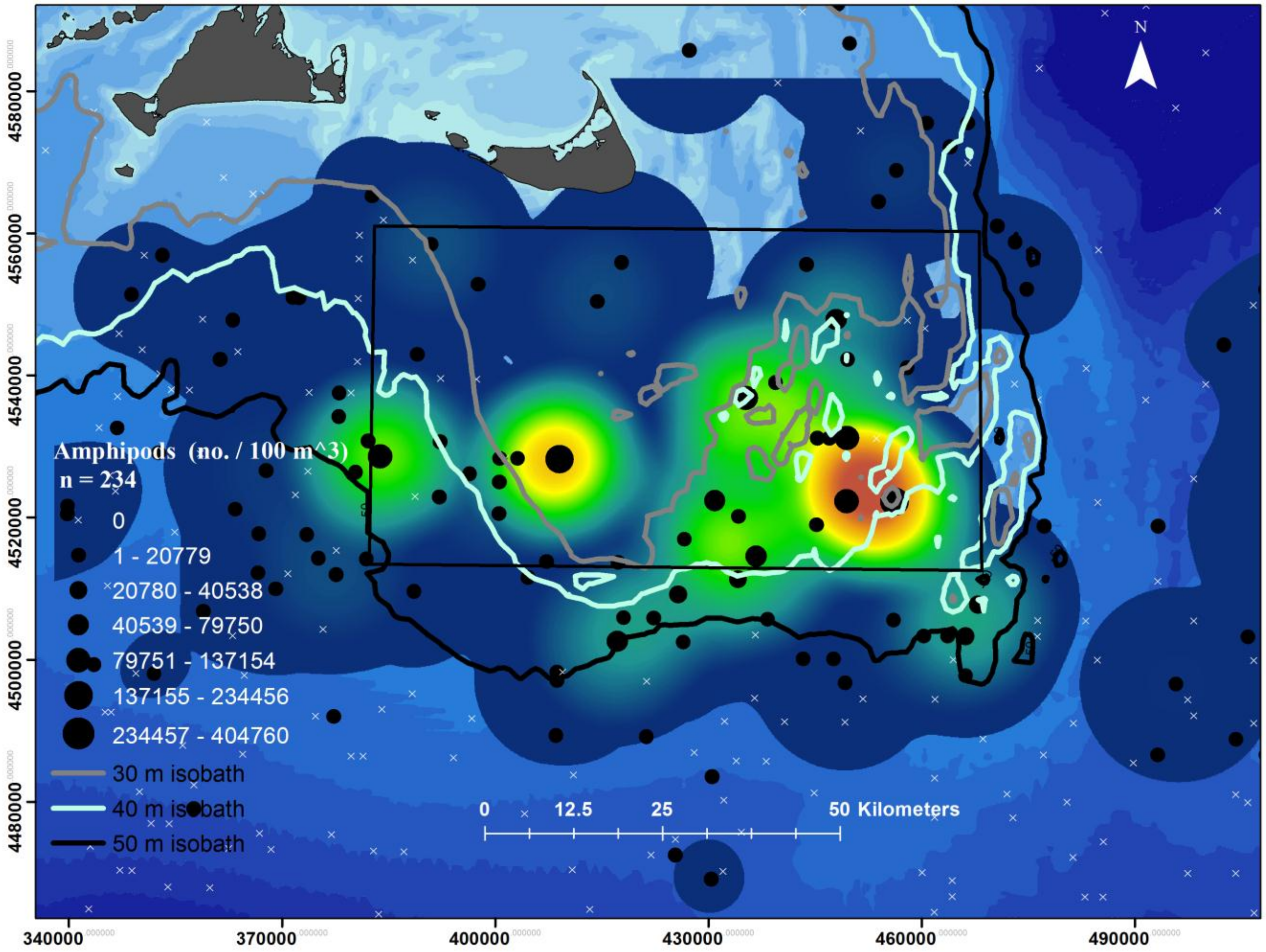


Figure 3.13 – Clam (Ocean quahogs and Atlantic surf clams) abundance (black dots represent tows) and kernel density interpolation (warm colors= high density areas; cool colors= low density areas). Border delimits survey area.

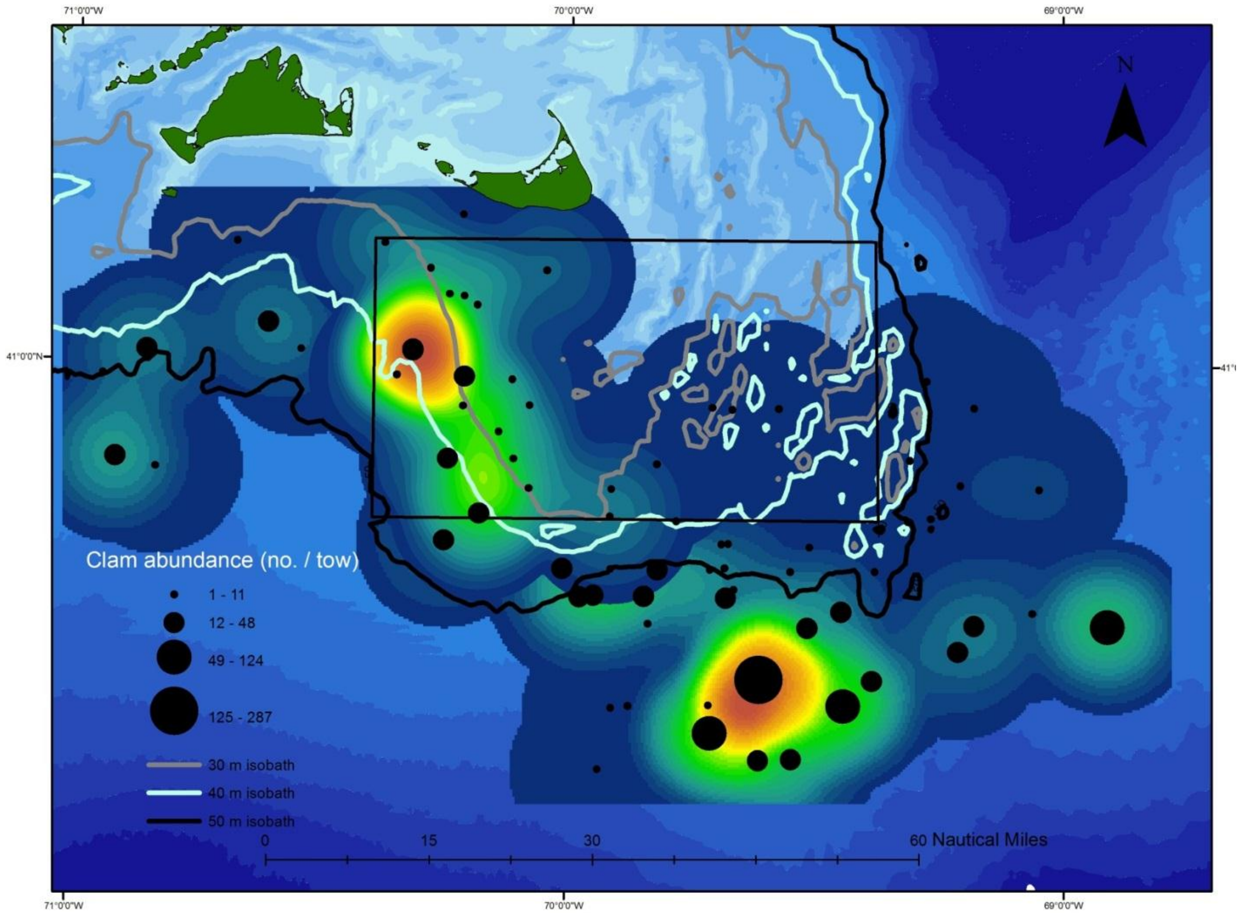


Figure 3.14 – Kernel density core area (intensity) of clams, ducks, and gammarid amphipods.

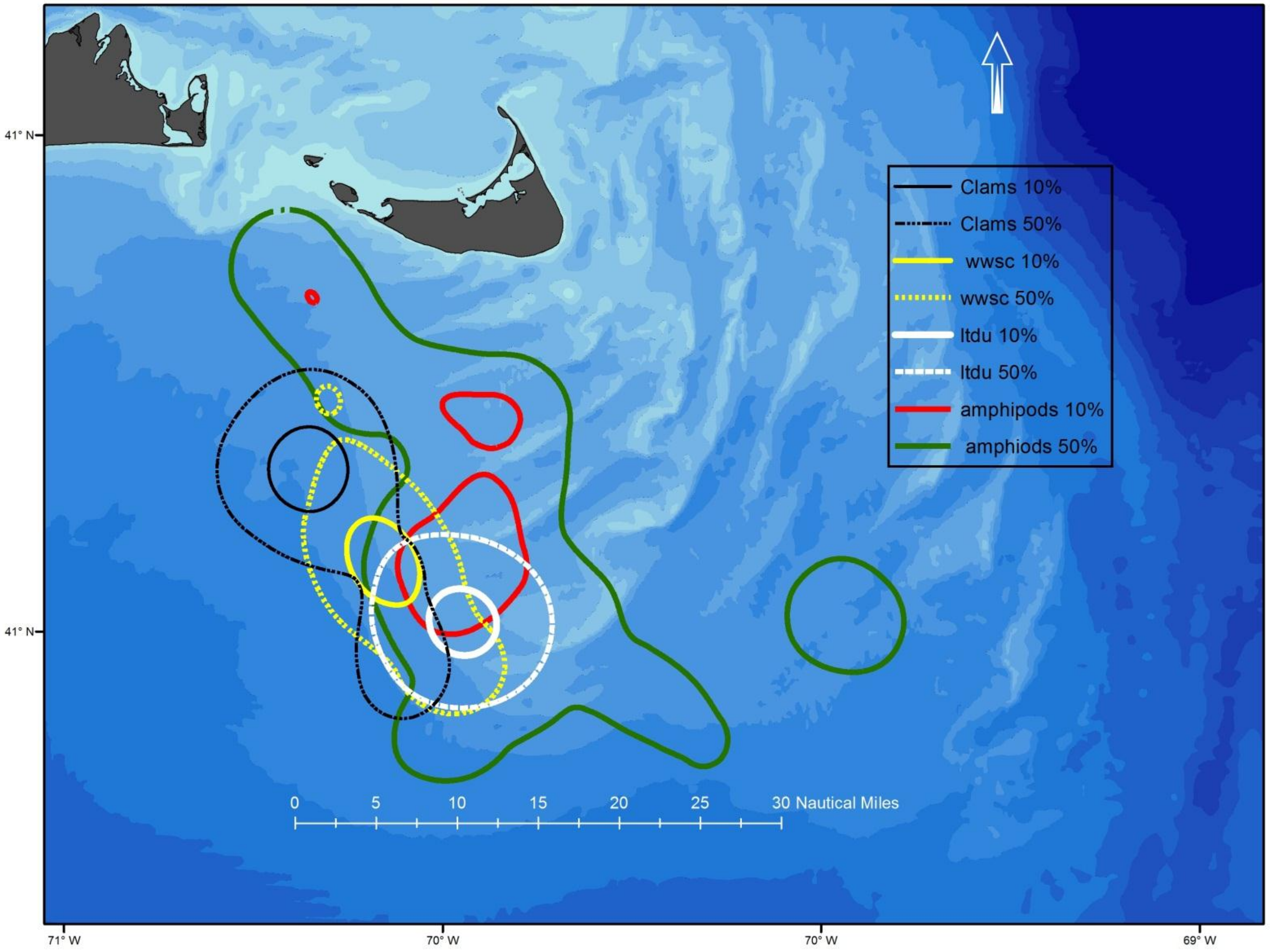


Figure 3.15 - Locations of the highest density bins for Long-tailed Ducks and White-winged Scoters (density = no.birds / km^2) with their core utilization isopleths (10%, 50%). All east/west 3km bins plotted in background as transect reference.

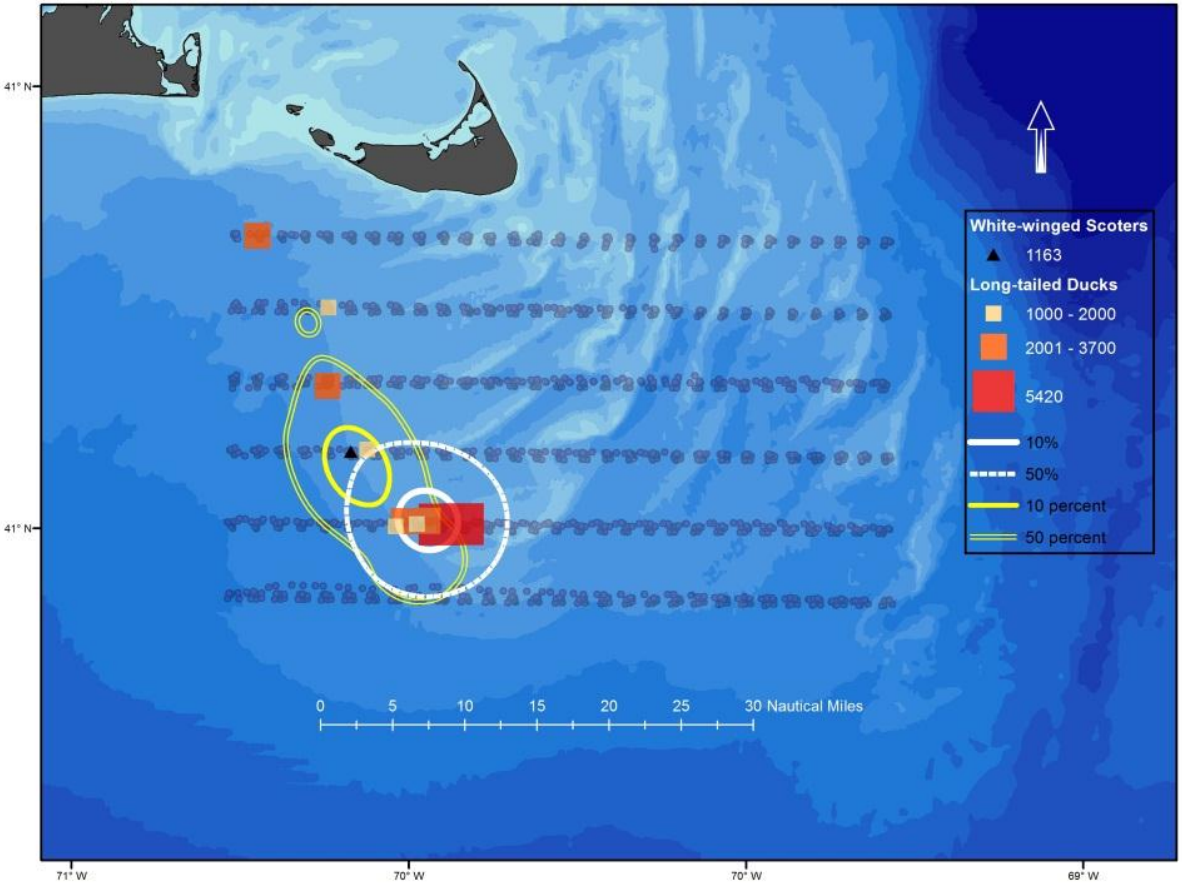
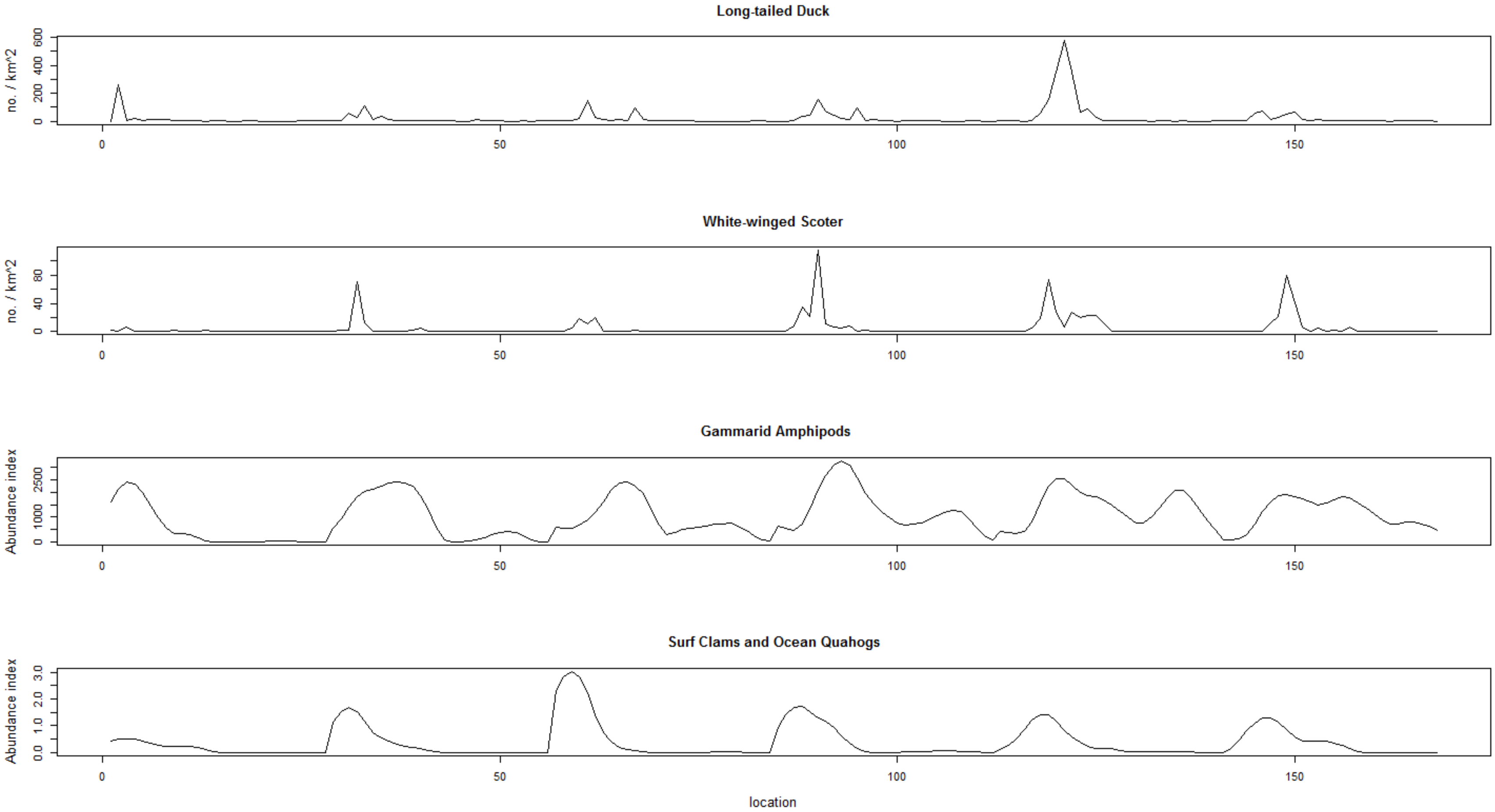


Figure 3.16 - Co-located 3km density bins of Long-tailed Ducks (top), White-winged Scoters (second), amphipods (third), surf clams and ocean quahogs (bottom) sampled on Nanucket Shoals.



CHAPTER 4

A Foraging Hotspot for Diving Ducks and Prey at a Winter Front on Nantucket Shoals

4.1 INTRODUCTION

Resources available to marine birds at sea are patchily distributed, and is inherently reflected in highly aggregated at-sea foraging distributions of marine birds (Birt et al. 1987, Piatt 1990, Nevitt 2000, Davoren et al. 2003c, Bost et al. 2009). Hydrographic mechanisms can induce spatial structure in predator-prey associations by concentrating prey within zones that are predictable to marine predators. Predator-prey associations at sea are oftentimes scale-dependent in relation to hydrographic mechanisms that influence prey availability. Tidal rips form at a temporal scale of hours, and can force prey within the foraging domain of surface feeding birds. (Safina and Burger 1985, Cairns and Schneider 1990, Hunt Jr. et al. 1998). Here, predators and prey are likely associated at small spatial scales since predators may exploit prey constrained by forcing mechanisms until tidal flow slackens. By contrast, when prey have fewer environmental constraints imposed upon their dispersion, the strength of predator-prey associations will likely be weaker at smaller spatial scales (Schneider et al. 1987, Sih 2005).

Tidal fronts associated with shallow banks probably fall somewhere in between these two scenarios. In these zones, tidal flow is probably not violent enough to overwhelm the swimming capabilities of most prey species, however, upwelling and convergent flow nurture local stocks of primary and secondary production that support productive ecosystems (Wolanski and Hamner 1988, Perry et al. 1993, Durazo et al. 1998, Ainley et al. 2009). Predators may aggregate to these areas where prey abundance is enhanced and spatially predictable (Irons 1998, Davoren et al. 2003a, Etnoyer et al. 2004, Gende and Sigler 2006).

In winter, Long-tailed Ducks and White-winged Scoters aggregated along the western fringes of Nantucket Shoals in areas where invertebrate density was high, and also where a prominent tidal front and horizontal flow has been documented (Lough and Manning 2001, Ullman and Cornillon 2001, Chen et al. 2011). It is possible that the flow field induces substantial mixing, inducing high phytoplankton densities and a passive aggregation of organic suspended matter, which are favored by phytoplanktivores and sessile suspension feeders e.g., pelagic amphipods and clams, respectively (O'reilly et al. 1987, Thouzeau et al. 1991, Avery 1993, Avery et al. 1996). Diving ducks prey upon clams and pelagic amphipods in the marine environment and in Nantucket Shoals in winter.

Tidal fronts and zooplankton

Nantucket Shoals is an ecosystem dominated by tidal-mixing, similar to that of Georges Bank, a productive fishing ground to its northeast. They are both productive shallow banks with tidal-mixing fronts at their gradually sloping flanks (Lough and Manning 2001, Ullman and Cornillon 2001b, Wiebe et al. 2002, Townsend et al. 2006, Wilkin 2006, Belkin et al. 2009, Chen et al. 2011). Tidal frontal zones are associated with both current flow and production. Such physical and biological interactions produce narrow areas within the vicinity of the tidal-mixing front that support complex trophic interactions (Hyrenbach et al. 2000, Etnoyer et al. 2004, Genin et al. 2005). Upwelling (divergence) and downwelling (convergence) mechanisms promote enhanced densities of phytoplankton and zooplankton production as tidal flux impinges upon sloping topography and subsequently function to upwell and aggregate nutrients and production. Elevated primary production can propagate up the food chain to higher trophic level predators (e.g., fish, marine mammals, birds) through secondary production (Genin et al. 2005). Convergent flow can serve as accumulation zones for passive organisms such as phytoplankton and zooplankton. Many species of zooplankton exhibit diel vertical migration and maintain depth by swimming counter to vertical flow (Pingree et al. 1974, 1975, Franks 1992,Genin et al.

2005). Zooplankton may also swim counter to flow in order to remain within vicinity of high food production and conspecifics, which may offer breeding opportunities and swarming mechanisms for predator dilution. Nevertheless, swimming against vertical flow in convergent zones promotes high aggregations of zooplankton (Genin et al. 2005). Nantucket Shoals, similar to Georges Bank, has a prominent tidal frontal zone and topographically rectified currents (anticyclonic flow) around their sloping flanks (Lough and Manning 2001, Ullman and Cornillon 2001, Chen et al. 2011). Benthic suspension feeders (e.g. bivalves) proliferate in zones where topography steers productive currents (Thouzeau et al. 1991, Genin 2004).

Currents and tide-topography interactions

Nantucket Shoals is awash in nutrient-rich waters flowing from the Gulf of Maine at its north, and embedded in the coastal current pathway, which extends from Labrador, CAN to Cape Hatteras, NC, and (Limeburner and Beardsley 1982, Beardsley et al. 1985, Hu et al. 2008). The coastal current, steered by topography, flows south past the coast of Maine and splits east off Cape Cod. A branch flows east and circumnavigates Georges Bank, while the southward-flowing branch follows topography around Nantucket Shoals, where current velocity is strong, approximately 10cm/s (Limeburner and Beardsley 1982, Shcherbina and Gawarkiewicz 2008, Manning et al. 2009). Limeburger and Beardsley (1982) hypothesized that nutrients upwell from the northeast region of Nantucket Shoals from the Gulf of Maine and advect to the southwest regions of Nantucket Shoals around its outer flanks, inshore of the 30m isobath, a strong tidal wave impinges upon Nantucket Shoals from the southwest and propagates across to the northeast. The tidal-mixing front on western Nantucket Shoals is seemingly the area where massive feeding aggregations of diving ducks coalesce in winter (White et al. 2009, Chen et al. 2011; see Chapter

3). A signature of the tidal-mixing front is revealed by abrupt gradients in water temperature (colder) and phytoplankton densities (enhanced) as a function of mixing. Although the tidal-mixing fronts are strong in summer when waters are warm and stratified outside the mixing zone, they also exist in winter (Perry et al. 1993, Lough and Manning 2001, Ullman and Cornillon 2001).

In winter, Long-tailed Duck, White-winged Scoter and invertebrate prey densities are high in the southwest region of Nantucket Shoals in close proximity to the 30m isobath (Chapter 3). The tidal-mixing front was located within the vicinity of the 30m isobath, as were high densities of gammarid amphipods and benthic organisms (clams)**.** On Georges Bank, Perry et. al (1993) found high densities of the amphipod *Gammarus annulatus* at mid-depths in less than ~30 m, and were strongly associated with the tidal-mixing front where chlorophyll concentrations were high. Avery (1993,1996) conducted feeding experiments with *Gammarus annulatus* and concluded that this amphipod can exclusively graze upon phytoplankton for survival in areas of high phytoplankton concentrations. Long-tailed Ducks feed upon *Gammarus annulatus* on Nantucket Shoals (White et al. 2009). Furthermore, benthic organisms, i.e. clams, are suspension feeders that filter phytoplankton and feed at the same trophic levels as amphipods.

I tested if the distribution and abundance of Long-tailed Ducks and White-winged Scoters was influenced by the tidal-mixing front on Nantucket Shoals. I refer to the Georges Bank tidal-mixing front as a mode, due to a similar topography and flow-field where primary and secondary production are high, and where similar prey for diving ducks are located in high abundance (Perry et al. 1993). I used oceanographic data derived by satellites (sea-surface temperature and chlorophyll a) to determine the location of the tidal front and to test if this is a good predictor of Long-tailed Duck and White-winged Scoter abundance. I also used bathymetric data (depth, slope) and the distribution and abundance of potential prey (amphipods , clams) to test which of these are reliable predictors of Long-tailed Duck and White-winged Scoter spatial distribution and abundance on Nantucket Shoals.

4.2 METHODS

Survey area and transects

We conducted aerial surveys for the purpose of recording the distribution and abundance of sea ducks south of Nantucket Island over Nantucket Shoals. We surveyed offshore within the 60 meter isobath on a seasonal basis from late fall (December) through early spring (March/April), 2008 - 2011 and approximately once per month, when weather conditions permitted. Details of survey methodology can be found in Chapter 3.

Oceanographic Data

Nantucket Shoals is an area known for its complex topography, unique flow field, and year-round high phytoplankton abundance due to vertical mixing and localized upwelling (Cornillion, 1996; Limeburer and Beardsley 1982; Hu et al. 2008). On Georges Bank, Perry et al. (1993) determined that high densities of *Gammarus annulatus* were associated with the tidal front: a well-mixed area characterized by high chlorophyll a densities (a proxy of phytoplankton density), and sharp sea-surface temperature (SST) gradients and flow gradients induced by bottom topography. Nantucket Shoals and Georges Bank are hydrographically very similar. I selected similar variables to explain Long-tailed Duck and White-winged Scoter density and distribution on Nantucket Shoals as those explaining *Gammarus annulatus* density on Georges Bank, because *Gammarus annulatus* has been shown by Perry et al. (1993) to be a good indicator of the tidal-mixing zone.

Sea-surface temperature (SST) and Chlorophyll a (Chl) concentration were measured by Moderate Resolution Imaging Spectroradiometer (MODIS). Chl concentration was also measured by Sea-viewing Wide Field of view Sensor (SeaWiFS), through December 2010, when the mission ended. SST and Chl were processed to 1 kilometer bins (i.e. 1km^2 pixels) using SeaDAS 6.1 software; standard flags were employed to mask clouds and low-quality data (Ocean Color Biology Group, http://oceancolor.gsfc.nasa.gov). Daily images of SST and Chl coincided with the survey period, December through April. I averaged daily images of SST and Chl to create monthly composites. I averaged individual monthly composites of SST imagery and Chl imagery across years to create two climatologies: an SST climatology and a Chl climatology. I then sampled both climatologies across individual survey transects at 3 km sampling intervals to coincide with the spatial scale of the averaged 3km bird bins; the Nantucket Shoals tidal-mixing front is identifiable at this spatial scale (Ullman and Cornillion, 2001). I applied these samples to statistical tests and modeling.

Satellite derived SST fronts and bottom topography

The Cayula-Cornillion edge detection algorithm (CCA) classified hydrographic SST fronts in 1 km^2 monthly SST images (Cayula and Cornillion 1992, 1996; Roberts et al. 2011). The CCA employs an iterative moving-window approach to sample SST pixels across an image using a pre-defined window size, stride length, and SST gradient threshold. CCA flags the spatial location and orientation of the gradient (front) when a significant bimodal threshold of SST was detected. I calibrated the CCA algorithm to detect strong SST gradients ≥ 0.5 ^{0} C/km (default gradient detection is 0.375 ^{0} C/km), using a moving-window area of 32km^2, stride length of 16 km^2 and a 1km^2 pixel size for SST.

I used bathymetric data provided by GEBCO **(http://www.gebco.net/)** to characterize the complex topography of Nantucket Shoals by calculating slope and depth.

Non-parametric tests and statistical models

I chose a generalized additive modeling framework (GAM) (Wood, 2006) to determine which combination of explanatory variables significantly influenced Long-tailed duck and White-winged Scoter abundance on Nantucket Shoals. GAMs are an extension of general linear models (GLMs) (Wood, 2006) and are commonly used in species distribution modeling due to their flexibility fitting non-linear relationships (Guissan et al. 2007; Zuur et al., 2009; Wood, 2006). GAMs are considered to be semi-parametric smoothing models in that a probability distribution is specified for the response variable and non-parametric smoothers can be applied to explanatory variables (Wood, 2006).

Long-tailed Duck and White-winged Scoter counts included many zero bins, and also few bins with very large counts. The high variance-to-mean ratio was likely due to the highly aggregative nature of feeding sea ducks. I chose a negative binomial distribution for GAMs to model the response variables in order to account for overdispersion (high variance-to-mean ratio) in the bird density data (Hilbe 2007, Wood 2006, Zuur et al. 2009). The application of a Gaussian or Poisson distribution was considered inappropriate here because the distribution of birds counts (response) did not conform to these assumptions as they are non-normal and variance-to-mean ratios were unequal (Zuur et al. 2009).

The information-theoretic approach governed GAM model selection (Burnham and Anderson 2002). The most parsimonious models – those that best fit the data amongst a group of candidate models - had the lowest Akaike Information Criteria (AIC) scores. I tested if serious collinear relationships existed among explanatory variables with a stepwise variance inflation factor analyses (VIF). I did not include an explanatory variable in models if it was determined to have VIF value ≥ 3 (Montgomery and Peck 1992, Zuur et al. 2009). I also eliminated non-significant ($p \leq 0.02$) explanatory variables in GAM models using a backwards selection approach (Zuur et al. 2009, Wood 2006). Cubic regression splines were used as smoothers to model main effects in GAM models and tensor splines were used for interaction terms. Optimal smoothing was determined by generalized-cross validation (GCV) **(**Wood 2006), and model residuals were examined for significant autocorrelation. Since my objective was to determine those mechanisms in the data set that most strongly influence Long-tailed Duck and White-winged Scoter distribution and abundance, I excluded geographic coordinates even though it was a good predictor, because space was collinear on many of the explanatory variables, i.e. the system exhibited a high degree of spatial structure. Geographic location is not a driver in and of itself, however, it can serve as a proxy for indirect mechanisms that influence patchiness in seabird abundance (e.g. SST fronts); unmeasured variables (e.g. currents); or direct drivers (e.g. prey abundance) (Guisan and Zimmermann 2000, Guisan et al. 2006, Guisan and Graham 2007)**.**

Scale

I tested if Long-tailed Ducks and White-Winged Scoters were associated at five spatial scales: 200 m, 500 m, 1000 m, 2000 m, 3000 m, using GAM analysis (Figs. 4.8 – 4.12).

4.3 RESULTS

Density

The highest averaged density bins of Long-tailed Ducks and White-winged Scoters were located along the southwest Nantucket Shoals, and in close proximity to the 30m and 40 m isobaths, and also in areas of high gammarid amphipod and clam abundance (Figs. 4.1, 4.2, 4.3) This area is characterized by moderate southwest slope, high phytoplankton abundance and cold SST fronts (Fig. 4.1).

Fronts

Locations of significant SST fronts classified by the CCA - those delineating strong frontal gradients $\geq 0.5\ ^{0}$ C / km - were distributed along the western and southwestern area of Nantucket Shoals along areas were Long-tailed Ducks and White-winged Scoters foraged (Figs 4.4, 4.5). Chl and SST showed a strong negative relationship on Nantucket Shoals in winter ($r_{s\,=}$ - 0.84, $p < 0.001$ (Fig.4. 6), and was suggestive of tidal-mixing zone on the western side of Nantucket Shoals.

Models

Spearman-rank correlation revealed Long-tailed Ducks and White-winged Scoters were positively associated at a spatial scale of 3km – this relationship was also revealed in spatial cross-correlations in Chapter 3. Both duck species shared a similar degree of association with potential prey and habitat covariates (Table 4.1). However, collinearity among predictor variables was high as determined by VIF analysis. Duck distribution, potential-prey distribution and habitat showed significant spatial structure (Fig. 4.7). For GAMs, I included duck density, Chl and SST, because some variables were collinear, and this combination of explanatory variables had a VIF < 3. It seems logical to use these variables for modeling because the interaction, Chl and SST, should be good proxy of the tidal-mixing front. The top GAMs (those having the lowest AIC scores among candidate models) that best explained Long-tailed Duck and White-winged Scoter distribution and abundance, included a combination of White-winged Scoter density (as predictor of Long-tailed Duck abundance), Long-tailed Duck density (as a predictor of White-winged Scoter abundance) and an interaction term between Chl and SST (Tables 4.2 and 4.3). The most parsimonious models of Long-tailed Duck and White-winged Scoter abundance explained 69.4% and 79.2% of the deviance, respectively.

I also included prey and bathymetry in additional GAMs, because this combination of variables along with SST and Chl showed VIF slightly greater than 3. I did not consider this set of explanatory variables to be highly correlated. Some studies included variables if VIF ≤ 10, so I considered variables having VIF scores slightly over 3 to be marginal and satisfactory to be included in GAMs. GAMs with highest explanatory power included the following: interspecific duck associations, prey, phytoplankton density, interaction term between slope and distance to thermal fronts (Tables 4.4, 4.5).

GAMs of relationships between ducks and proximity to satellite derived fronts were significant, and the deviance explained was moderate: White-winged Scoters (deviance explained = 51.6%%, p-value < 0.0001, n=168; Long-tailed Ducks (deviance explained = 48.7%, p-value < 0.0001, n=168) (Fig. 4.13).

GAMs with an interaction term between SST and Chl, including an additive term for duck density, provided a good prediction of the location and relative abundance of Long-tailed

Ducks and White-winged Scoters on Nantucket Shoals compared to empirical densities (Tables 4.2, 4.3; Figs. 4.14, 4.15). The models predicted both ducks species in the western regions of Nantucket Shoals at similar locations and proportions compared to the empirical densities. The models had a tendency to under-predict density, however, not by much. GAMs have a tendency to over fit as a result of overloading the model with many covariates, so the results here were encouraging because, at most, a model had only 3 variables from which to predict both location and abundance of ducks.

Drifter Buoys

All buoys set adrift at sea in the Gulf of Maine were collected on the western side of Nantucket Shoals (Manning et al. 2009)**.** Two drifters released in northern Gulf of Maine followed the coastal current: drifter 200004393 was released in western Gulf of Maine coastal current, and drifter 36381 was released in the eastern Gulf of Maine coastal current (Fig 4.16-4.18). Both drifter paths coincided east of Cape Cod. Drifter 200004393 subsequently followed the western branch of the current around Nantucket Shoals, while drifter 36381 was guided by the eastern branching current around Georges Bank. Drifter 86091 was released in the southeast area on Nantucket Shoals, and drifted south almost to the shelf-break, then back to Nantucket Shoals, presumably guided by currents. All drifters were ultimately guided around Nantucket Shoals by currents associated with the 30m - 50m isobaths. Ten drifter paths on the western side of Nantucket Shoals intersected with the distribution of Long-tailed Ducks and White-Winged Scoters, between the 30m and 40m isobaths. These paths were very similar to the location of winter SST fronts classified by the CCA in the vicinity of western Nantucket Shoals (Figs 4.4, 4.5).

Scale

Long-tailed Ducks and White-winged Scoters were significantly associated in patches at all spatial scales (Figs 4.8 – 4.12).

4.4 DISCUSSION

Long-tailed Ducks were associated with the western frontal zone on Nantucket Shoals where clam and amphipods are an abundant available food resource. The thermal fronts classified by the CCA algorithm were likely a manifestation of vertical and horizontal flow induced by tidal flux and topographically rectified currents. In this zone, amphipods and clams likely proliferate under similar conditions of high phytoplankton densities and suspended organic matter. Long-tailed Ducks and White-winged Scoters were associated at all spatial scales, however, in patches. These species tend to feed on disparate prey, however they were at times observed in mix-species flocks, perhaps feeding upon similar prey, as they both have flexible foraging strategies.

Marine birds aggregate to hydrographic frontal zones in search of prey (Hunt et al. 1999). While mechanisms that function to enhance prey at frontal zones vary (e.g. salinity, temperature, current velocity, primary production), the unifying measure that defines a frontal zone is the magnitude of its gradient. Marine birds forage more often over strong gradients rather than weak gradients (Schneider et al. 1987). Strong frontal zones are areas where nutrients and organisms can aggregate in relatively narrow zones, however, areas of strong flow do not always support high local production (Hunt Jr. et al. 1998). In coastal areas, tidal currents impinge upon abrupt topography and can physically force mobile prey to surface regions within the foraging domain of marine birds (Safina and Burger 1985, Genin et al. 2005). For ecosystems with tidal-mixing fronts, upwelling and convergence enhance primary and secondary production, which propagate up the food chain, thus promoting complex trophic interactions (Schneider et al. 1990, Perry et al. 1993, Durazo et al. 1998, Hyrenbach et al. 2000).

The southwest region of Nantucket Shoals harbors a persistent population of gammarid amphipods, which are major winter prey for Long-tailed Ducks. This significant concentration is likely related to the region’s strong hydrography and productive tidal front (Perry et al. 1993). Pelagic amphipods likely remain in the vicinity of the tidal front due to the supply of high concentrations of food (phytoplankton) (Perry et al. 1993). Swarms can form here as a behavioral response to maintain depth in upwelling and convergent flow (Genin et al. 2005). Nantucket Shoals, similar to that of Georges Bank, is a productive ecosystem having a well-mixed area and supports a standing stock of benthic and pelagic organisms (Avery 1993, Avery et al. 1996). High concentrations of Long-tailed Ducks and White-winged Scoters aggregate within the vicinity of the western tidal-mixing front on Nantucket Shoals. This is likely related to the positive effects that vertical and horizontal flow have on the local production of potential prey (Perry et al. 1993). In the southwest region where Long-tailed Duck and White-winged Scoter densities are persistently high, strong SST gradients align with tightly converging bathymetric gradients. It is in the southwest region where a tidal wave impinges upon topography and propagates to the northeast forming a tidal mixing front (Chen et al. 2011). Ullman and Cornillion (2001) hypothesized that Ekman transport could occur at southwest Nantucket Shoals induced by prevailing northwest winds in winter.

In the southwest area of Nantucket Shoals there is spatial concordance in hotspot overlap of Long-tailed Ducks and White-winged Scoters, with gammarid amphipods and bivalves (Chapter 3). These spatial relationships between predators and potential prey are directly influenced by the western frontal zone. Very few studies have reported on amphipod behavior and habitat use, although they are a vitally important prey for many fish species in the northwest Atlantic. Dickinson et al. (1980) and Dickson and Wigley (1981) reported on the distribution and abundance of gammaridean amphipods in the mid-Atlantic Bight and Georges Bank from data collected between 1953-1965. They found high densities of *G. annulatus* in the Nantucket Shoals region, and only a single specimen on Georges Bank. It is unclear why they missed *G. annulatus* on Georges Bank, however, *G. annulatus* is patchily distributed and episodic (Avery 1993, Avery et al. 1996 Kane 2007, Chapter 3). Perry et al. (1993) reported high densities of *G. annulatus* on Georges Bank at the tidal front with a signature of enhanced chlorophyll concentrations, and strong gradients of salinity, temperature, and nitrate. At some stations *G. annulatus* was the numerically dominant species. They sampled 6 depth strata with BIONESS, and determined that *G. annulatus* occurred in mean depths of 31m (day) and 28m (night). Although Dickinson and Wigley (1980) did not report on water column sampling (e.g. SST, chlorophyll concentrations), they found *G. annulatus* most abundant between 30m - 40m anc\d concluded that *G. annulatus* might be both pelagic and epibenthic. Avery et al. (1996), reported gammarid amphipod were highly abundant and densely packed in the water column ≤ 30m on Nantucket Shoals and Georges Bank. My results, along with these reports confirm that gammarid amphipods (probably the pelagic species *G. annulatus)* are not distributed uniformly over Nantucket Shoals but rather concentrated in the vicinity of the tidal front.

This productive zone may provide high-quality habitat for a diverse community of pelagic and benthic organisms. A fourth hotspot in the southwest area of Nantucket Shoals consists of bivalve clams, ocean quahogs and Atlantic surf clams (Chapter 3). In addition to the vertically flowing tidal current, a strong topographically rectified current flows around the flanks of Nantucket Shoals. This current may also advect nutrients and phytoplankton to the southwestern/western regions thus providing enhanced food to pelagic and benthic filter feeders. On Georges Bank, suspension feeders are the dominant benthic organisms and this is associated with high levels of phytoplankton. Currents and mixing enhance year-round phytoplankton densities and promote suspension of organic matter, augmenting growth and recruitment of benthic communities (Thouzeay et a. 1991). Surf Clams (Spisulla soildissima) were 4 to 5 times more abundant in areas of high phytoplankton concentrations on Georges Bank (O’reilly et al. 1987). Clams are an important food item for White-winged Scoters and Long-tailed Ducks – however, White-winged Scoters may have more flexibility to select larger bivalves than Long-tailed Ducks since bivalve size and energy content are related. Nevertheless, even if Long-tailed Ducks and White-winged Scoters have unlimited access to a wide range of bivalve size classes, and also assuming that other species of benthic and epibenthic potential prey are available to them on Nantucket Shoals (e.g. razor clams and sand lance), it is likely that the “whirlwind” of mechanisms that coincide at the southwestern/western area of Nantucket Shoals clearly form a biophysical coupling of primary, secondary and top trophic level predators (Long-tailed Ducks and White-winged Scoters) in relation to unique topography.

This relatively small winter foraging hotspot for Long-tailed Ducks and White-winged Scoters is connected to physical processes at a larger scale. Nutrients that fuel phytoplankton growth on Nantucket Shoals advect in from the Gulf of Maine transported by the costal current and tidal flux. A tidal wave from the southwest creates a productive tidal front bordering the western margins Nantucket Shoals. Benthic and pelagic organisms thrive in these narrow productive zones, and provide prey to hundreds of thousands of arctic breeding diving ducks in winter when resources are limited.

The wintering Long-tailed Duck population show strong interannual variability, which might be reflective of the episodic gammarid amphipod population. However, population estimates of ocean quahogs and Atlantic surf clams have sharply declined over the last decade (Program 2009). It is possible that large-scale climatic drivers influence the population dynamics of pelagic and benthic organisms on Nantucket Shoals, however, the mechanisms remain unclear. It is easy to imagine the devastating effects a major oil spill could have on this system, and on the highly concentrated duck foraging aggregations, especially if it occurred within close proximity to flow field leading to Nantucket Shoals. The Nantucket Shoals is a unique ecosystem in the ocean that provides high quality habitat and a predictable prey field to diving ducks in winter, and forms a predator-prey hotspot through unusual hydrography and biophysical coupling

TABLES

Table 4.1 - Spearman rank correlation tests of duck density with potential prey, and habitat: r_s (p-value).

Covariates	Long-tailed Duck Density	White-Winged Scoter Density
Amphipod density	0.58 (< 0.0001)	0.57 (< 0.0001)
White-Winged Scoter Density	0.63 (< 0.0001)	–
Long-tailed Duck Density	–	0.63 (0.0001)
SST	-0.51 (< 0.0001)	-0.55 (< 0.0001)
Chl	0.65 (< 0.0001)	0.63 (< 0.0001)
Distance to SST Fronts	-0.55 (< 0.0001)	-0.56 (< 0.0001)
Slope	0.30 (< 0.0001)	0.30 (< 0.0001)
Depth	0.27 (0.00036)	0.30 (< 0.0001)
Clam Abundance	0.57 (< 0.0001)	0.70 (< 0.0001)

Table 4.2 - Individual GAM models with predictors of Long-tailed duck abundance on Nantucket Shoals.

White-winged Scoter density	SST	Chl	te(SST,Chl)	AIC	% Deviance
x			x	955.5985	69.4%
x	x	x		982.619	65.7%
	x			1132.888	38.9%
	x	x		1033.329	56.3%
		x		1039.947	53%
x				1156.403	35.3%

Table 4.3 - Individual GAM models with predictors of White-winged Scoter abundance on Nantucket Shoals.

Long-tailed Duck density	SST	Chl	te(SST,Chl)	AIC	% Deviance
x			x	484.9153	79.2%
x	x	x		516.9366	70.2%
x				543.8397	63.6%
		x		567.1467	58.4%
	x	x		671.515	41.1%
	x			699.3208	35.9%

Table 4.4 - Individual GAM models with predictors of Long-tailed Duck abundance on Nantucket Shoals.

White-Scoters	Gammarid amphipod density	Chl	Slope	Distance to SST thermal fronts	te (slope, distance to fronts)	AIC	% Deviance
x	x	x			x	469.2	81.6
x	x	x		x		473.3	80.3
x		x			x	480.7	76.4
x		x				489.2	74.8
	x	x	x	x		491.7	76.3
	x	x			x	495.5	78.1
x	x					513.3	71.3
x						543.9	63.6
		x				567.2	58.4
					x	588.2	60.7
				x		607.5	53.1
	x					672.5	40.9
			x			721.3	33.3

Table 4.5. Individual GAM models with predictors of White-winged Scoter abundance on Nantucket Shoals.

Long-tailed Ducks	Gammarid amphipod density	Chl	Slope	Distance to SST thermal fronts	te (slope, distance to fronts)	AIC	% Deviance
x	x	x			x	931.7	75.5
x	x	x	x	x		938.5	72.8
x	x	x		x		941.6	71.2
x	x				x	945.5	72.0
	x	x			x	950.2	69.7
	x	x	x	x		951.1	69.2
x	x		x	x		953.8	69.1
x		x	x	x		957.9	67.8
x	x				x	958.3	68.1
x		x			x	959.5	67.8
x	x			x		967.2	66.1
x	x					1000.6	60.5
	x					1061.3	49.7
		x				1040.0	53.0
				X		1067.6	48.7
x						1156.4	35.3
					x	1239.4	23.1

Figure 4.1 - Composite plots of oceanographic variables, sea duck abundance, and amphipod abundance across individual transects.

The most northerly transect is 1, and most southerly is 6.

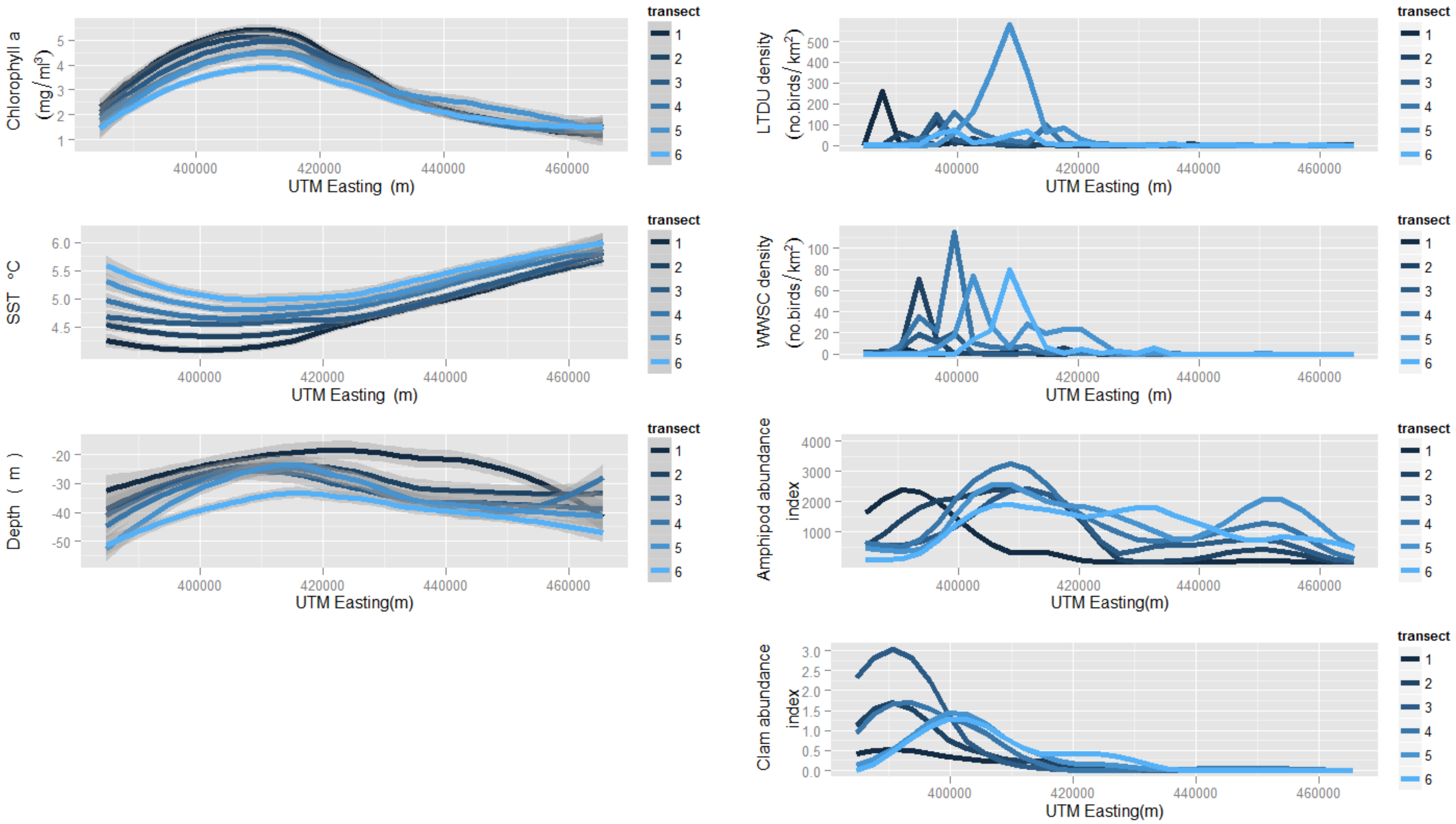


Figure 4.2 - Composite density (averaged density bins) and distribution of Long-tailed Ducks (no./km^2) on Nantucket Shoals.

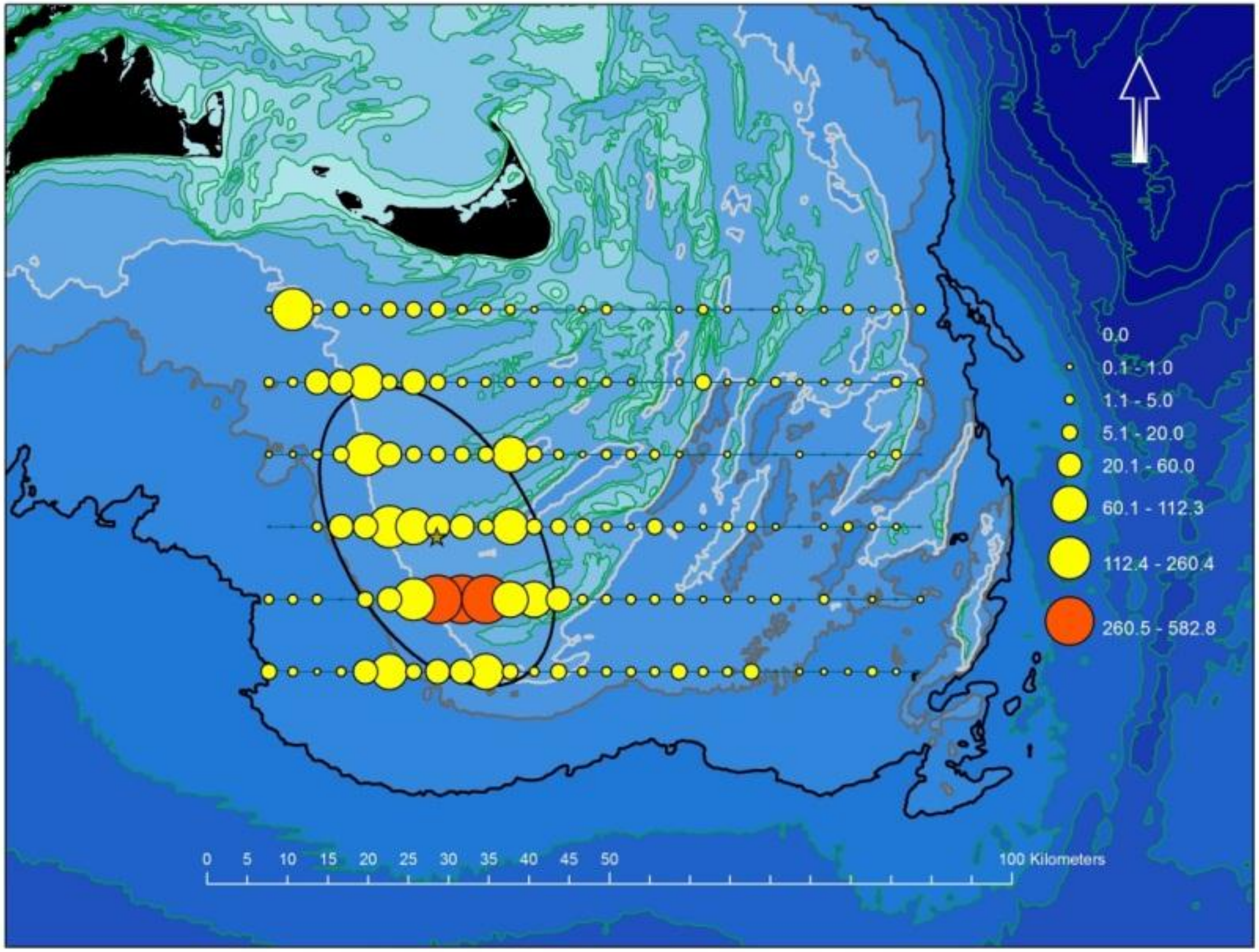


Figure 4.3 - Composite density (averaged density bins) and distribution of White-winged Scoters (no./km^2) on Nantucket Shoals.

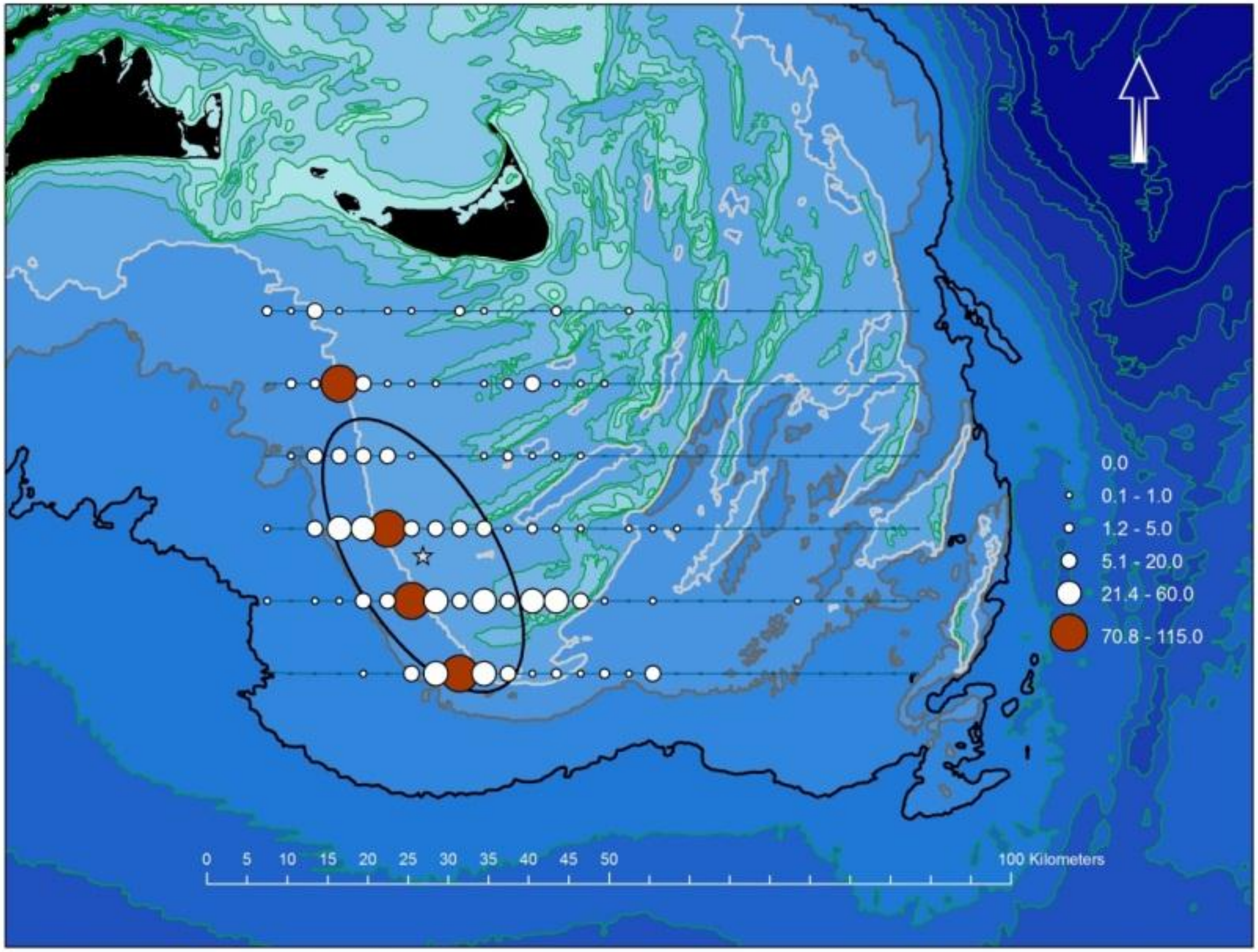


Figure 4. 4 - Location of significant SST composite fronts (≥ 0.5°C / km) (green "ribbons") and Long-tailed Duck density (no./km^2).

Star symbol = geographic mean center of Long-tailed Duck distribution; directional ellipse, 1 standard deviation from mean center.

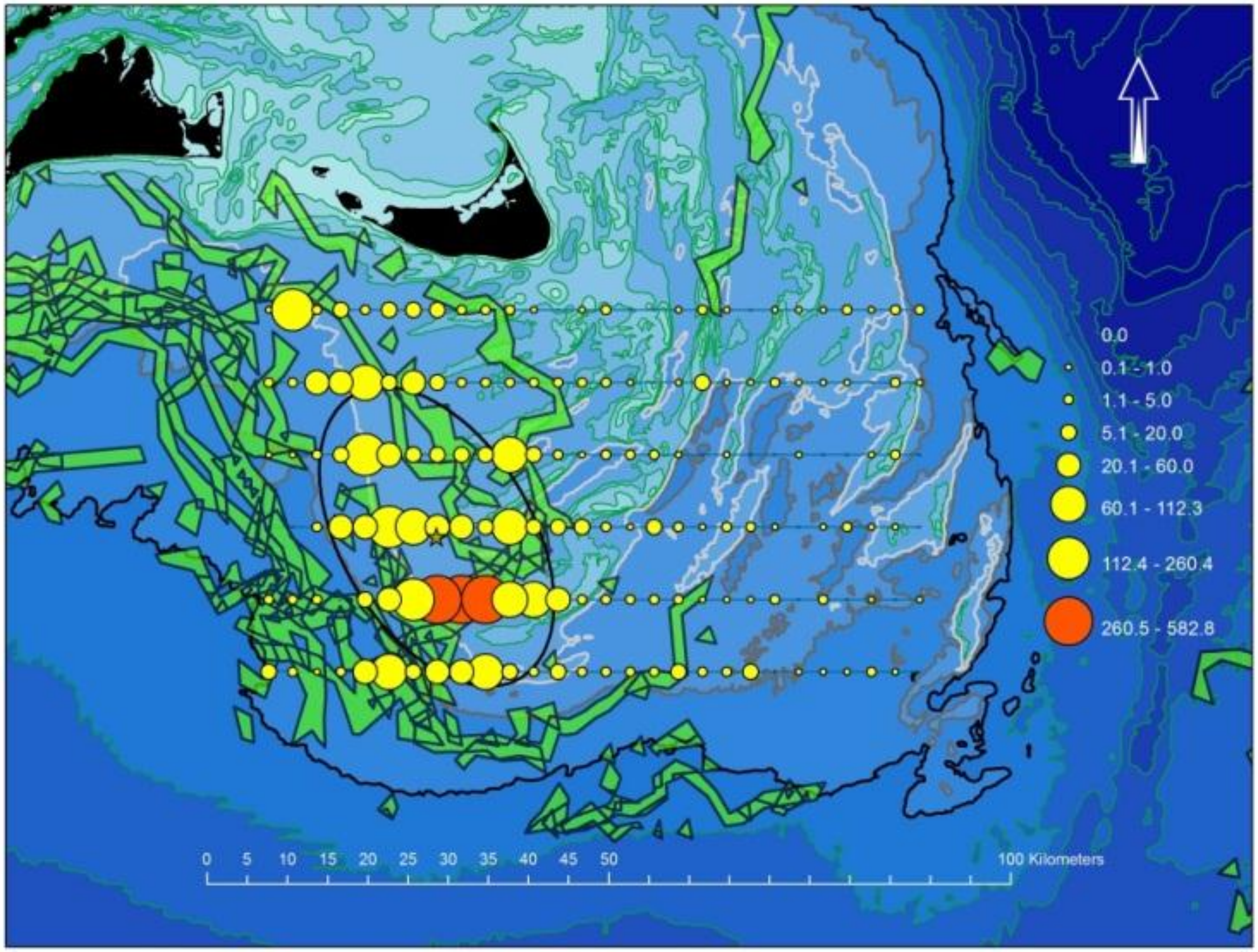


Figure 4. 5 - Location of significant SST composite fronts (≥ 0.5°C / km) (green “ribbons”) and White-winged Scoter density (no./km^2). Star symbol = geographic mean center of White-winged Scoter distribution; directional ellipse, 1 standard deviation from mean center.

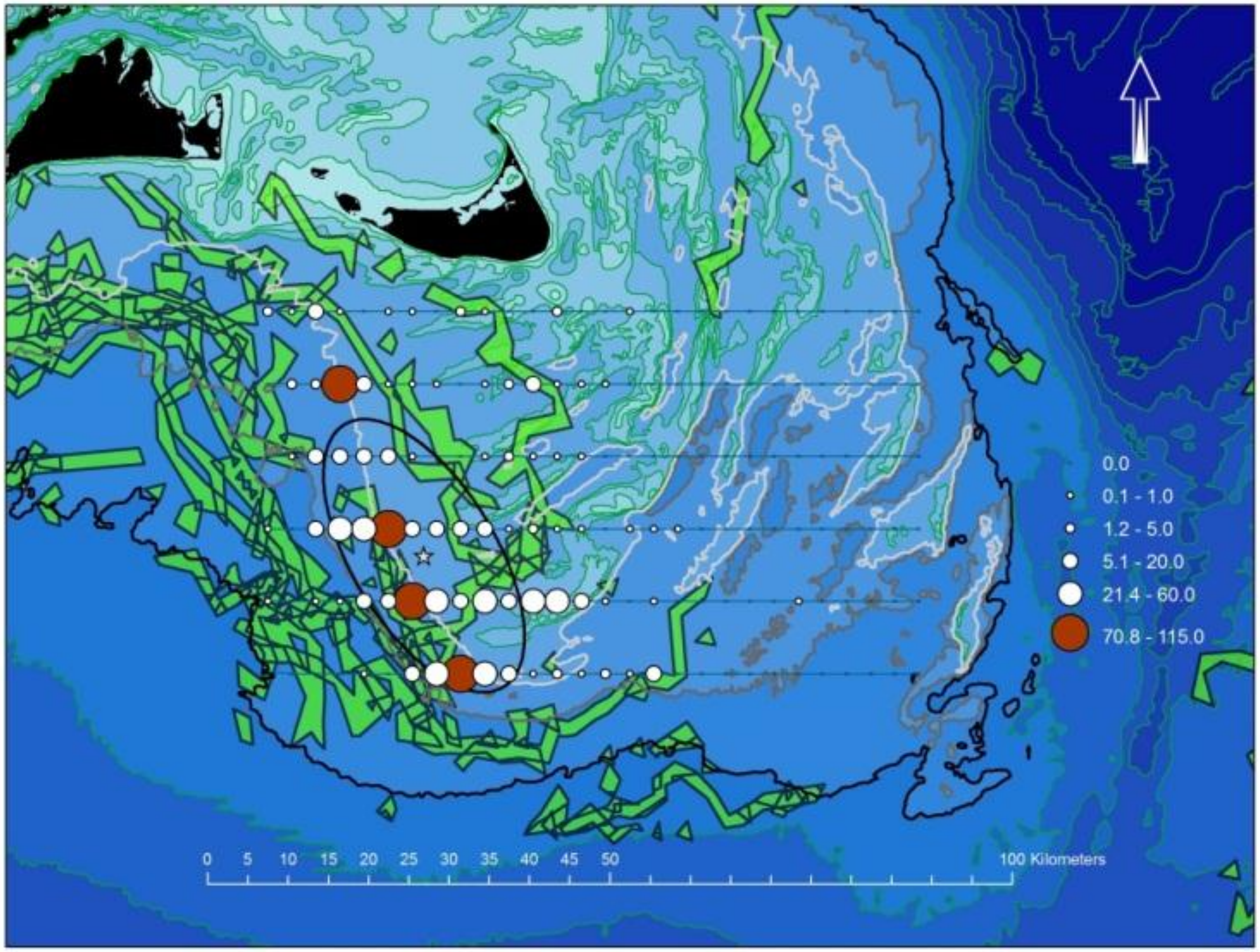


Figure 4.6 - Winter monthly average SST and Chl on Nantucket Shoals, 2008 - 2011.

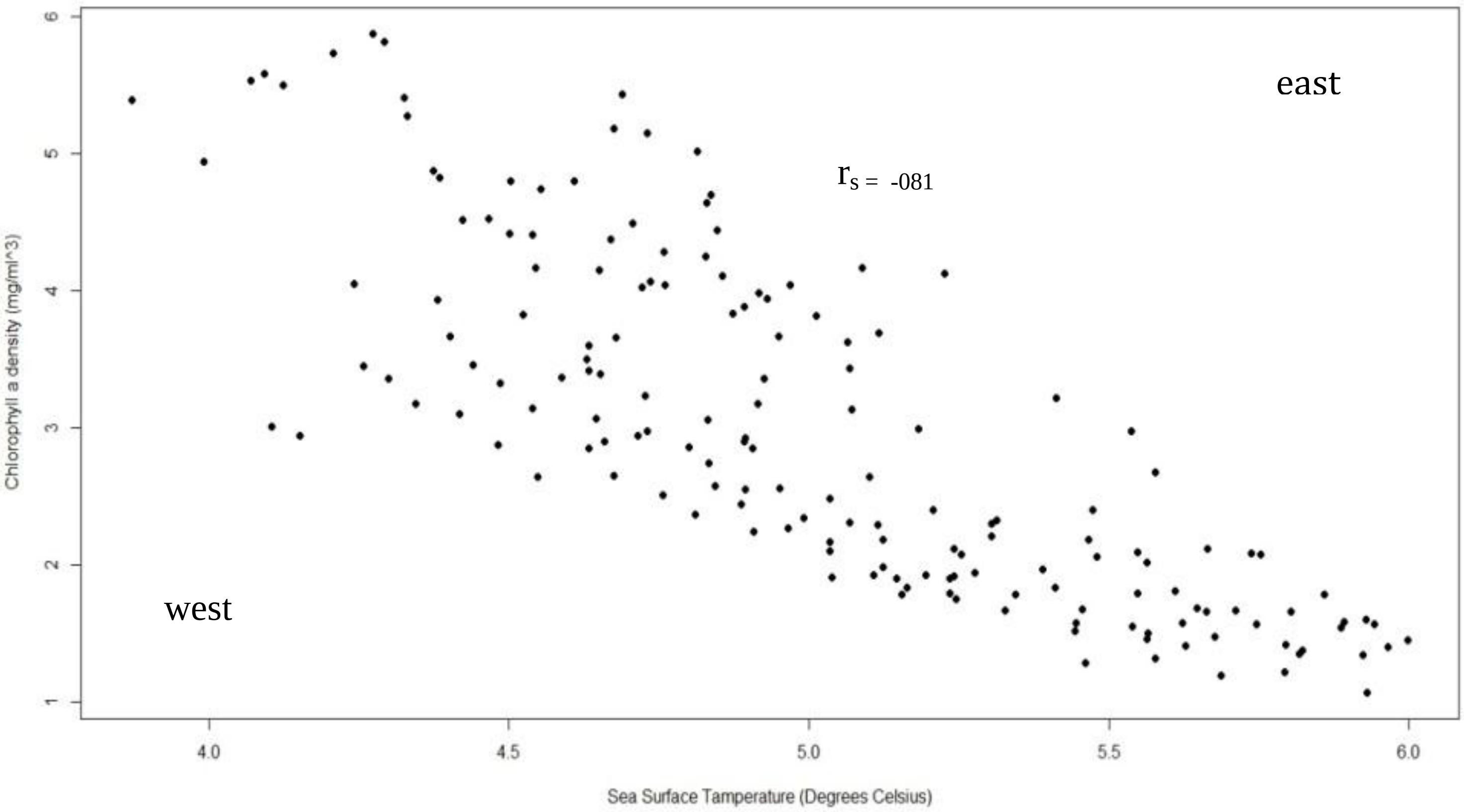


Figure 4.7 – Spatial GAM models of duck, potential prey, and habitat distribution going from west to east Nantucket Shoals.

LTDU = Long-tailed Duck; WWSC = White-winged Scoter

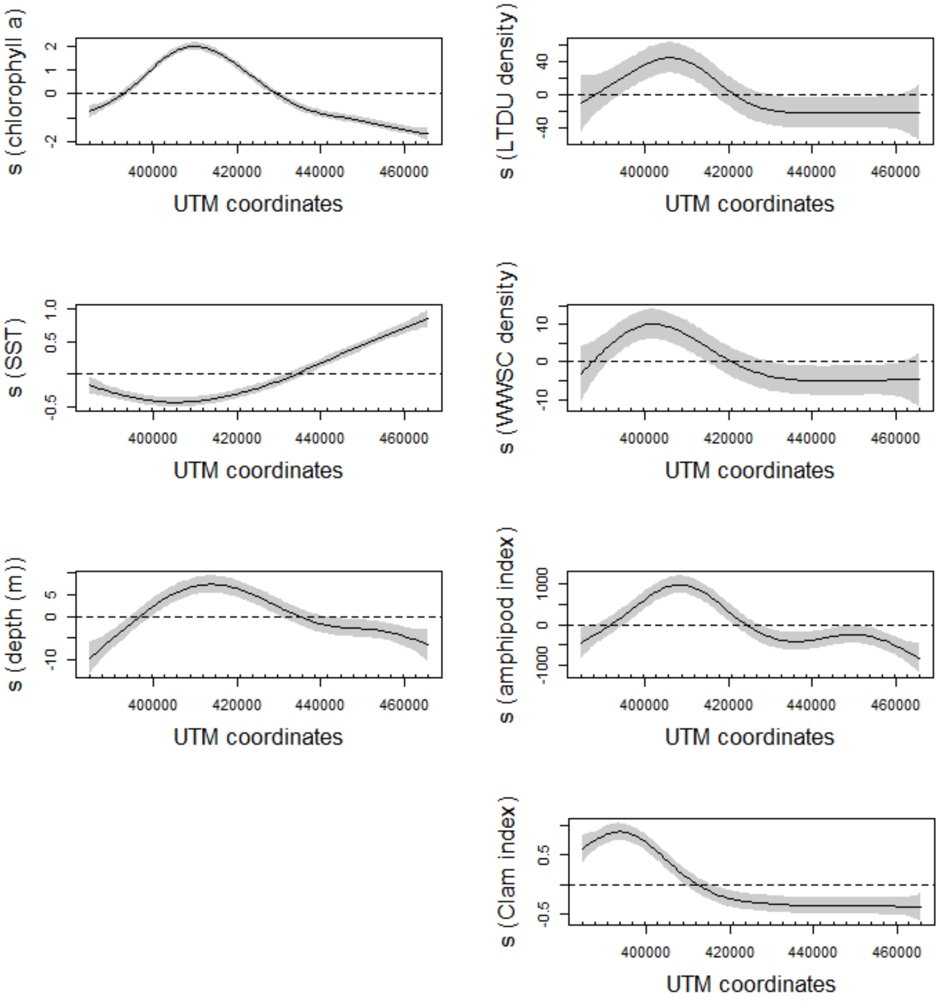


Figure 4.8 – GAM models of interspecific association between Long-tailed Ducks and White-winged Scoters at a spatial scale of 200m.

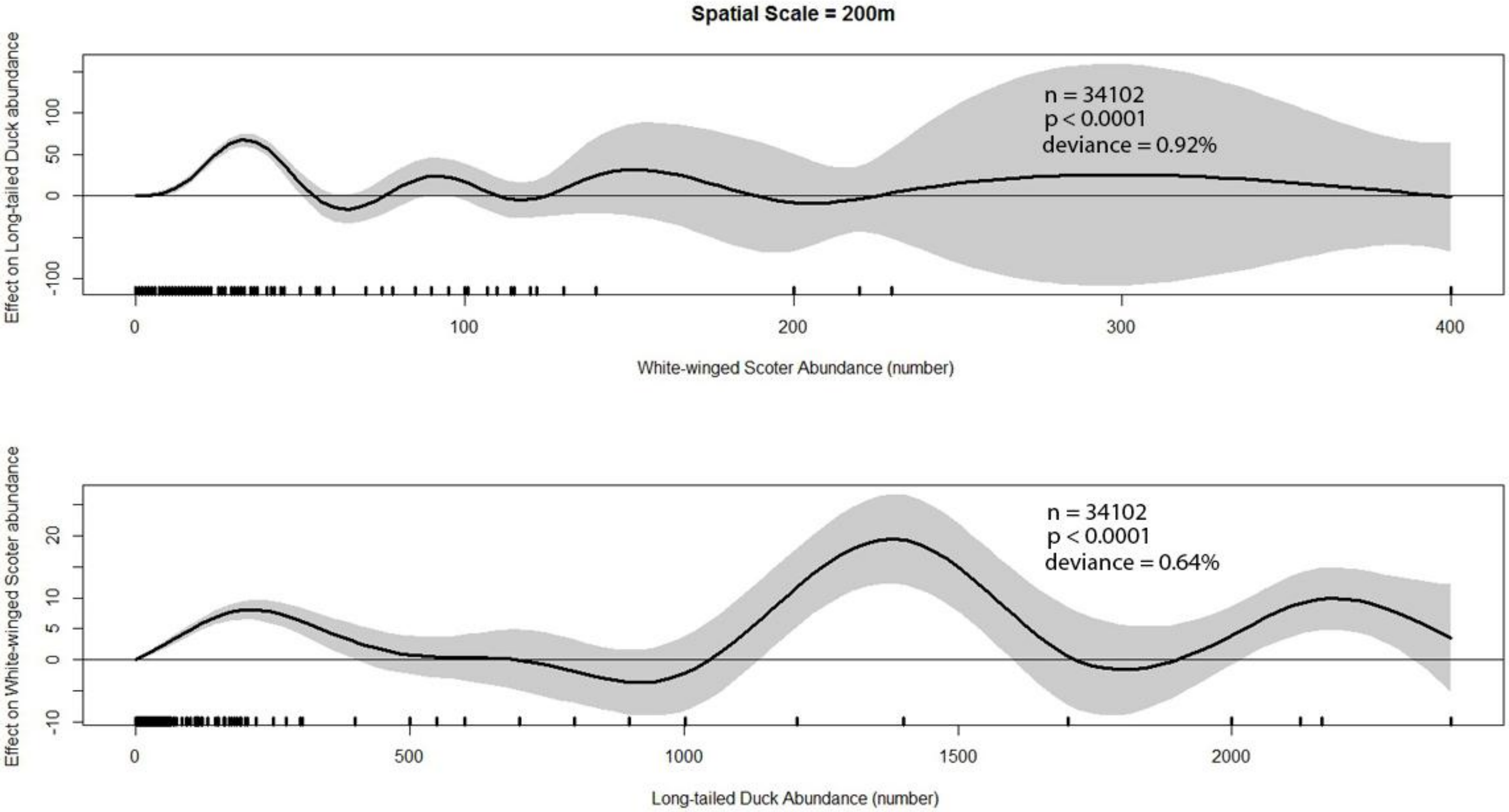


Figure 4.9 – GAM models of interspecific association between Long-tailed Ducks and White-winged Scoters at a spatial scale of 500m.

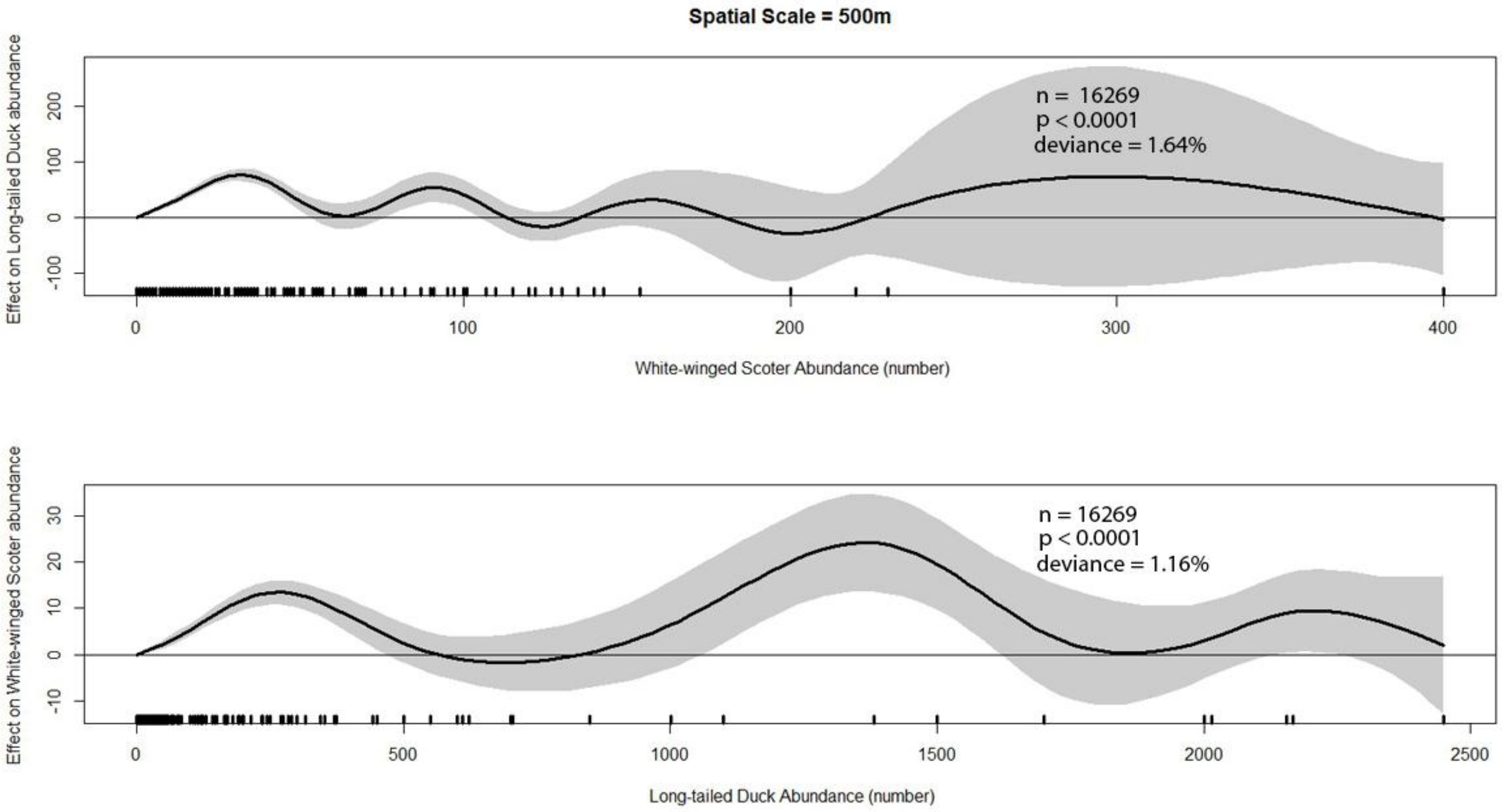


Figure 4.10 – GAM models of interspecific association between Long-tailed Ducks and White-winged Scoters at a spatial scale of 1000m.

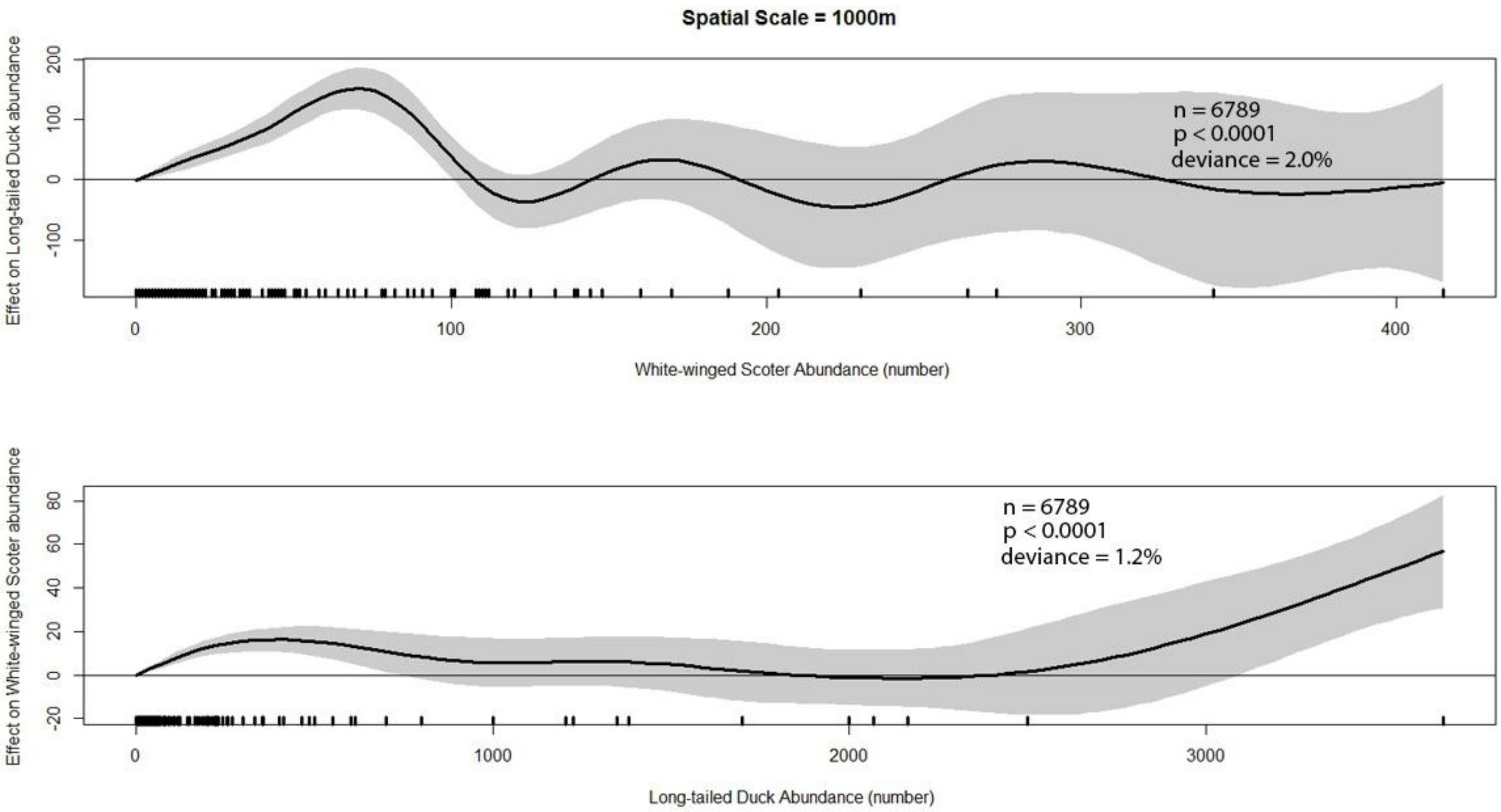


Figure 4.11 – GAM models of interspecific association between Long-tailed Ducks and White-winged Scoters at a spatial scale of 2000m.

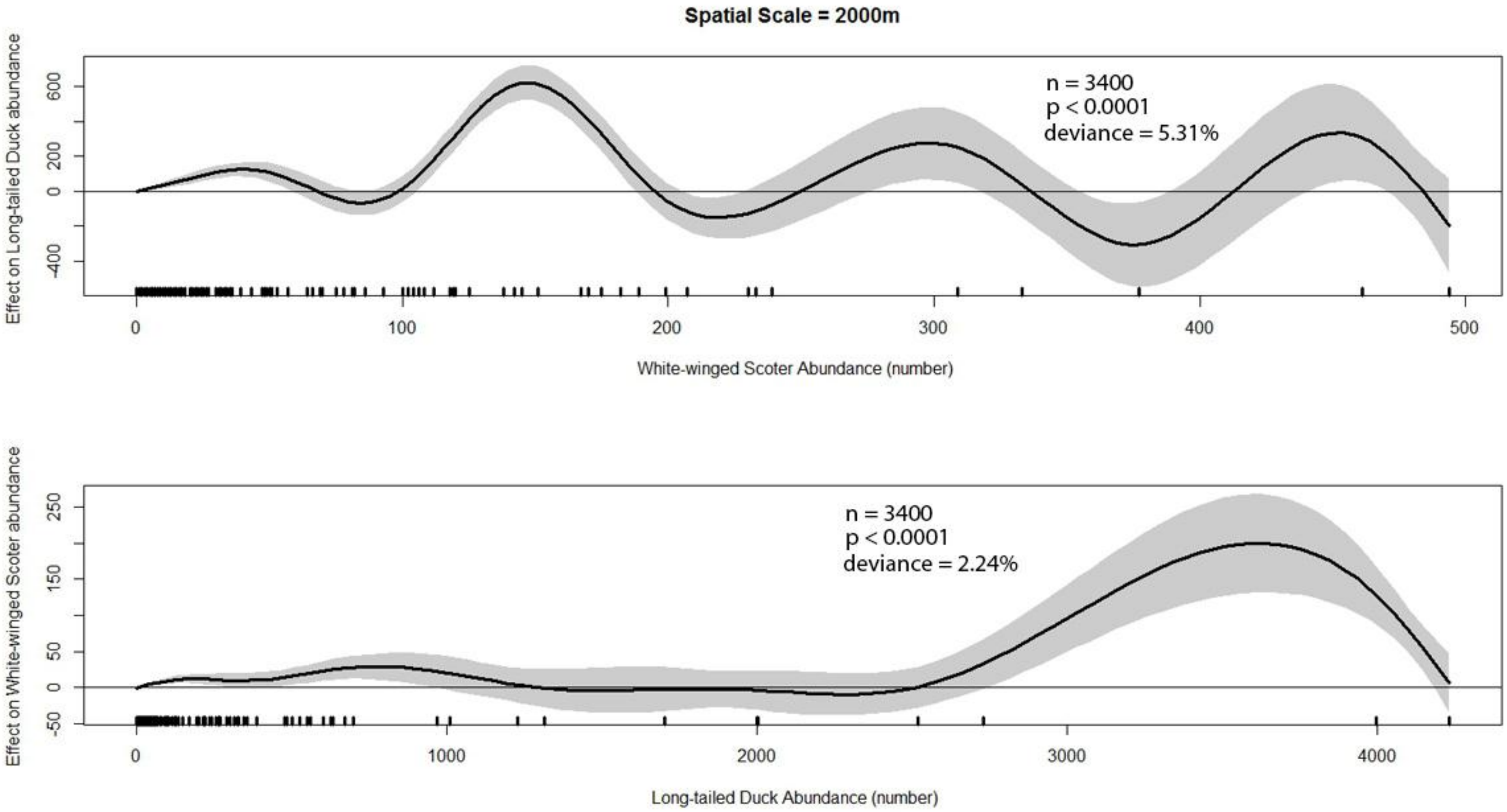


Figure 4.12 – GAM models of interspecific association between Long-tailed Ducks and White-winged Scoters at a spatial scale of 3000m.

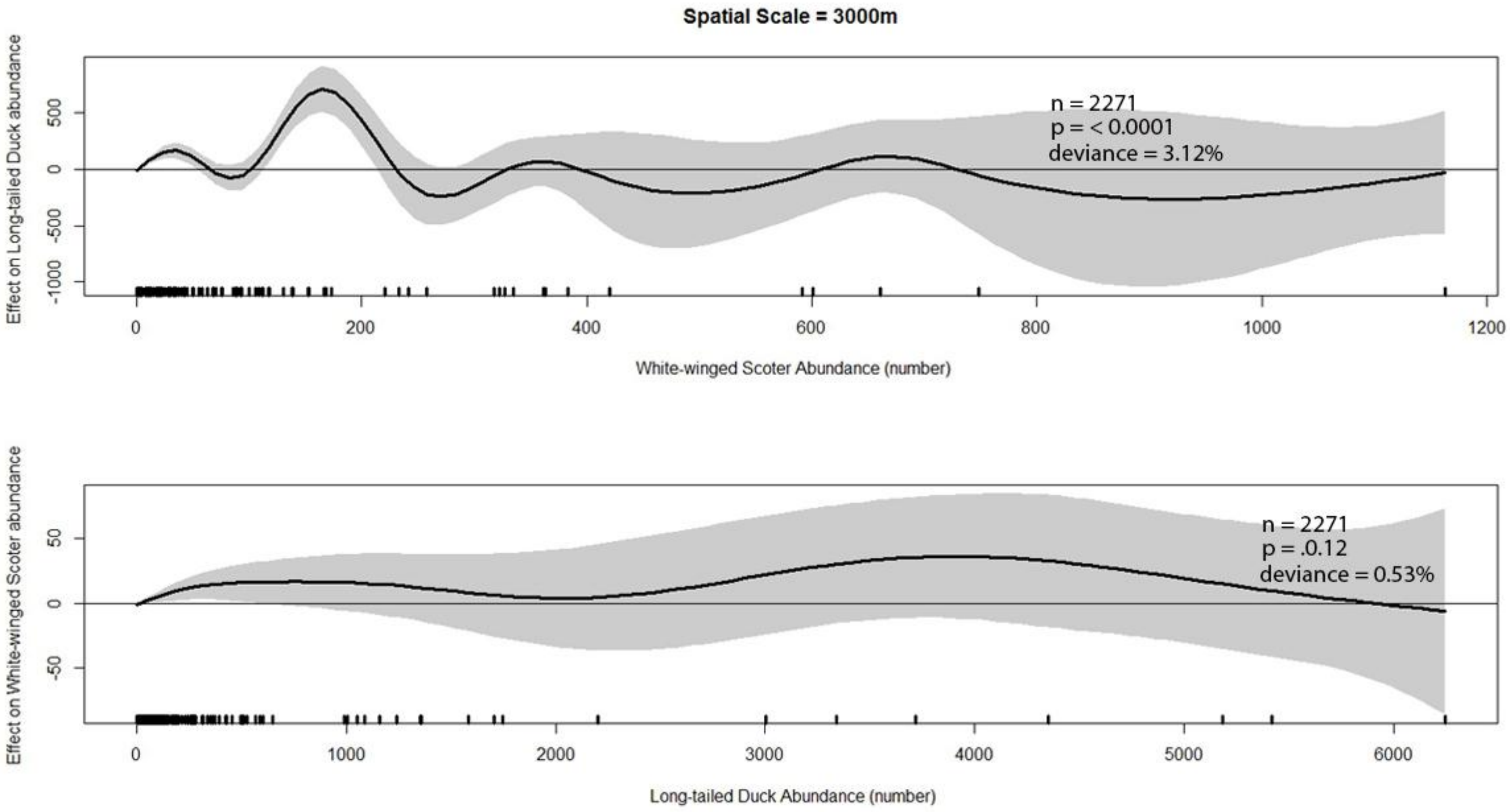


Figure 4.13 – GAMs showing spatial relationship of ducks with proximity to SST fronts classified by CCA

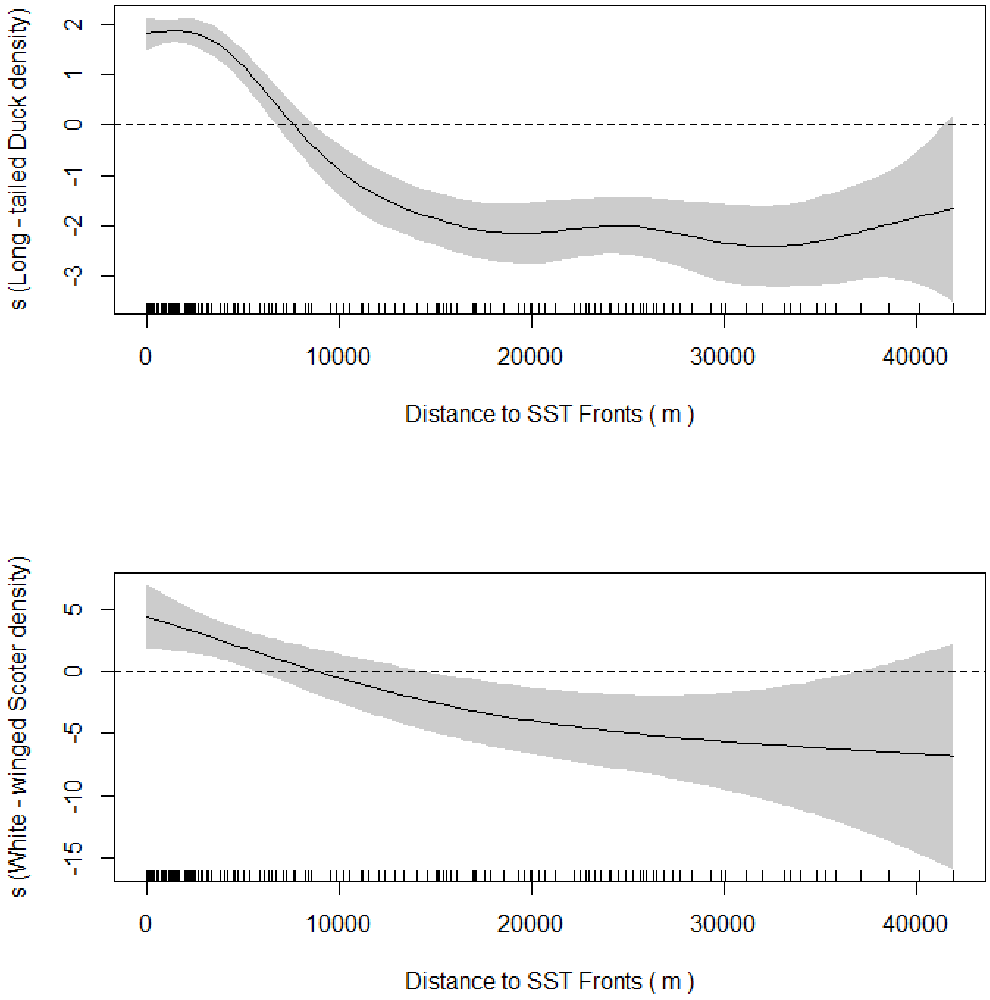


Figure 4.14 – Top - Empirical density of Long-tailed Ducks across Nantucket Shoals from west to east. Bottom – Spatial prediction of Long-tailed Duck density by GAM model with lowest AIC (cf.table 2).

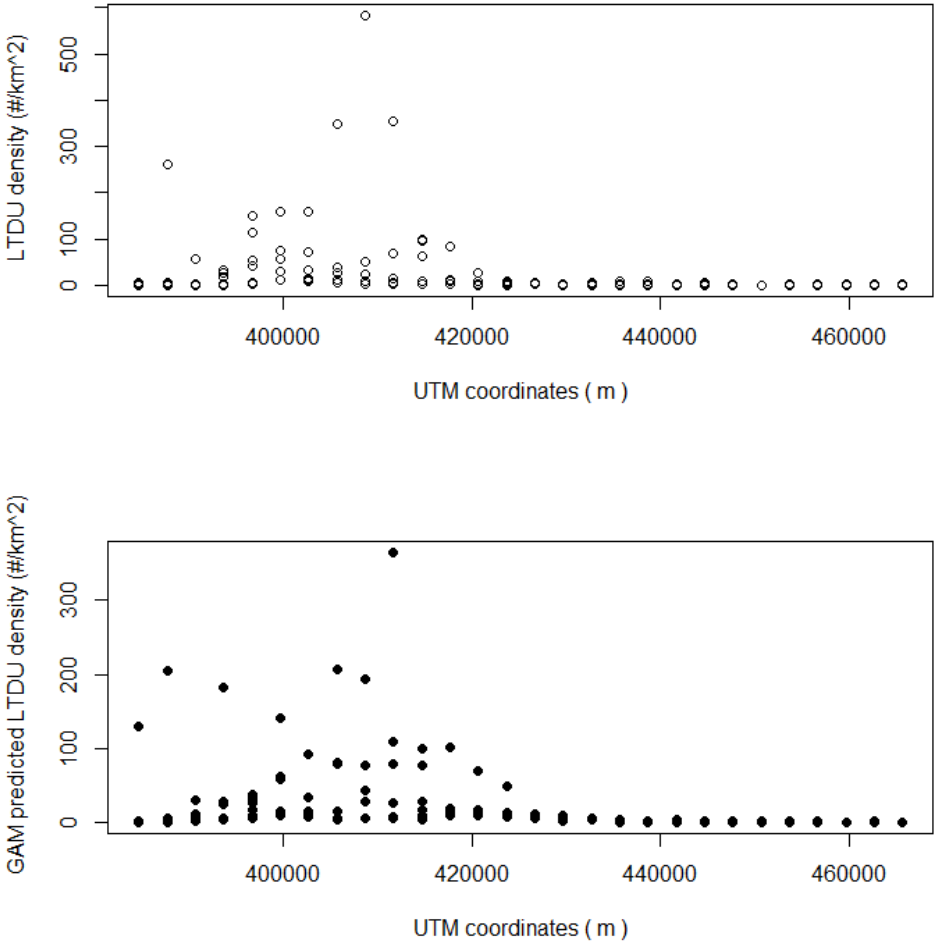


Figure 4.15 – Top - Empirical density of White-winged Scoters across Nantucket Shoals from west to east. Bottom – Spatial prediction of White-winged Scoters by GAM model with lowest AIC (cf.table 2).

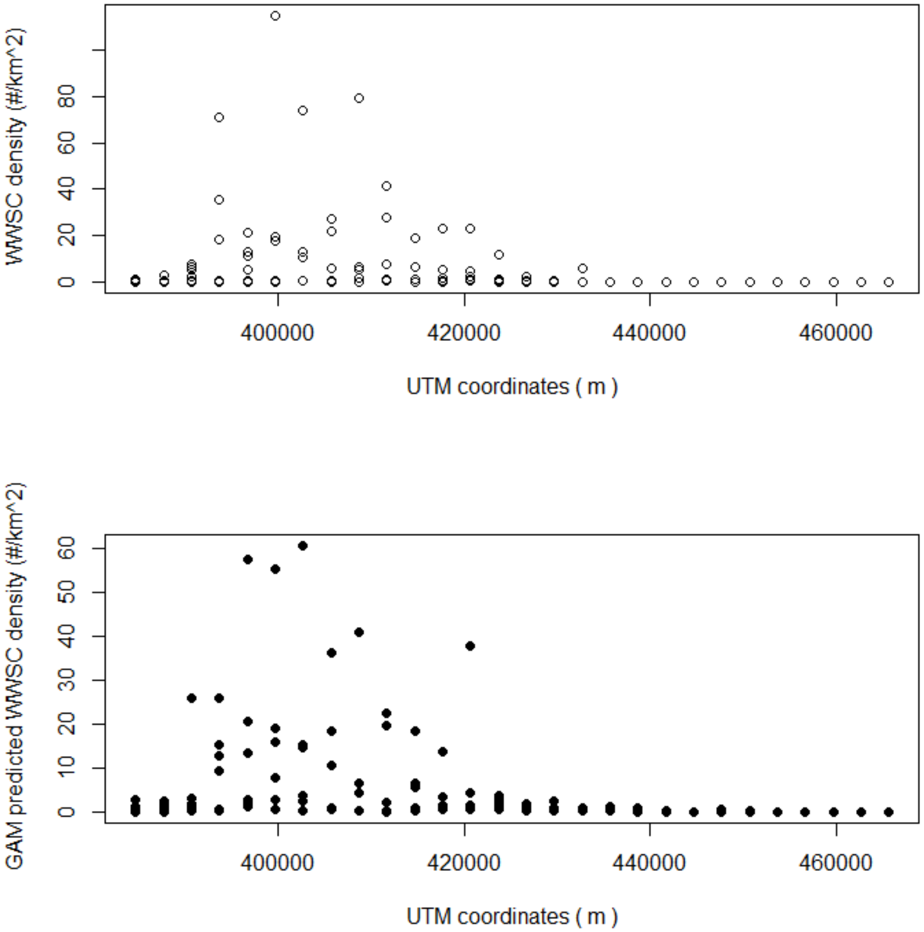


Figure 4.16 – Drifter buoy paths. Drifters released in Gulf of Maine and southeast corner of Nantucket Shoals). Isobaths 30, 40, 50 m symbolized with emboldened shades of grey (darkest 50 m; lightest 30 m).

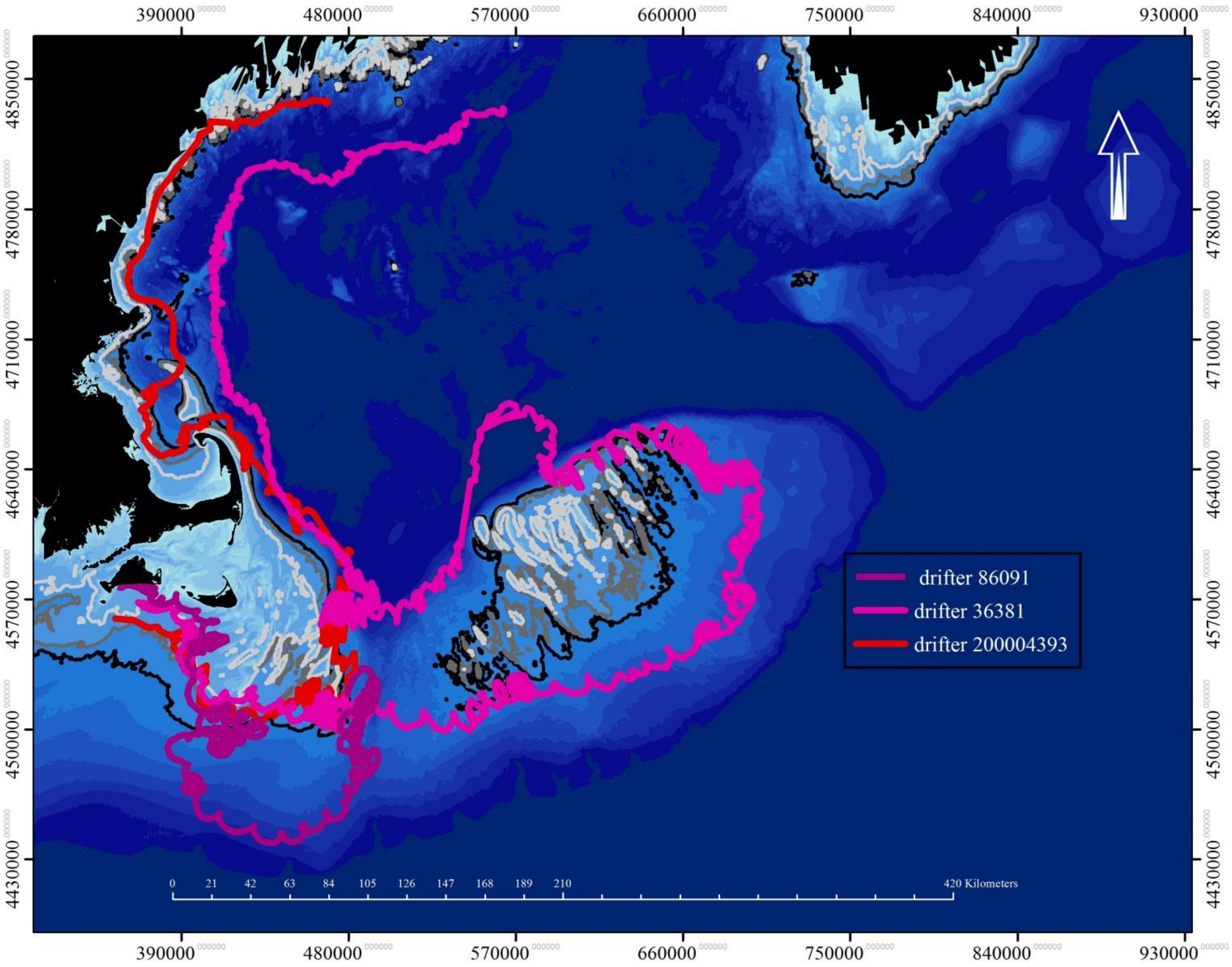


Figure 4.17 – Drifter buoy paths with Long-tailed Duck density (no. / km^2). Isobaths 30, 40, 50 m symbolized with emboldened shades of grey (darkest 50 m; lightest 30 m)

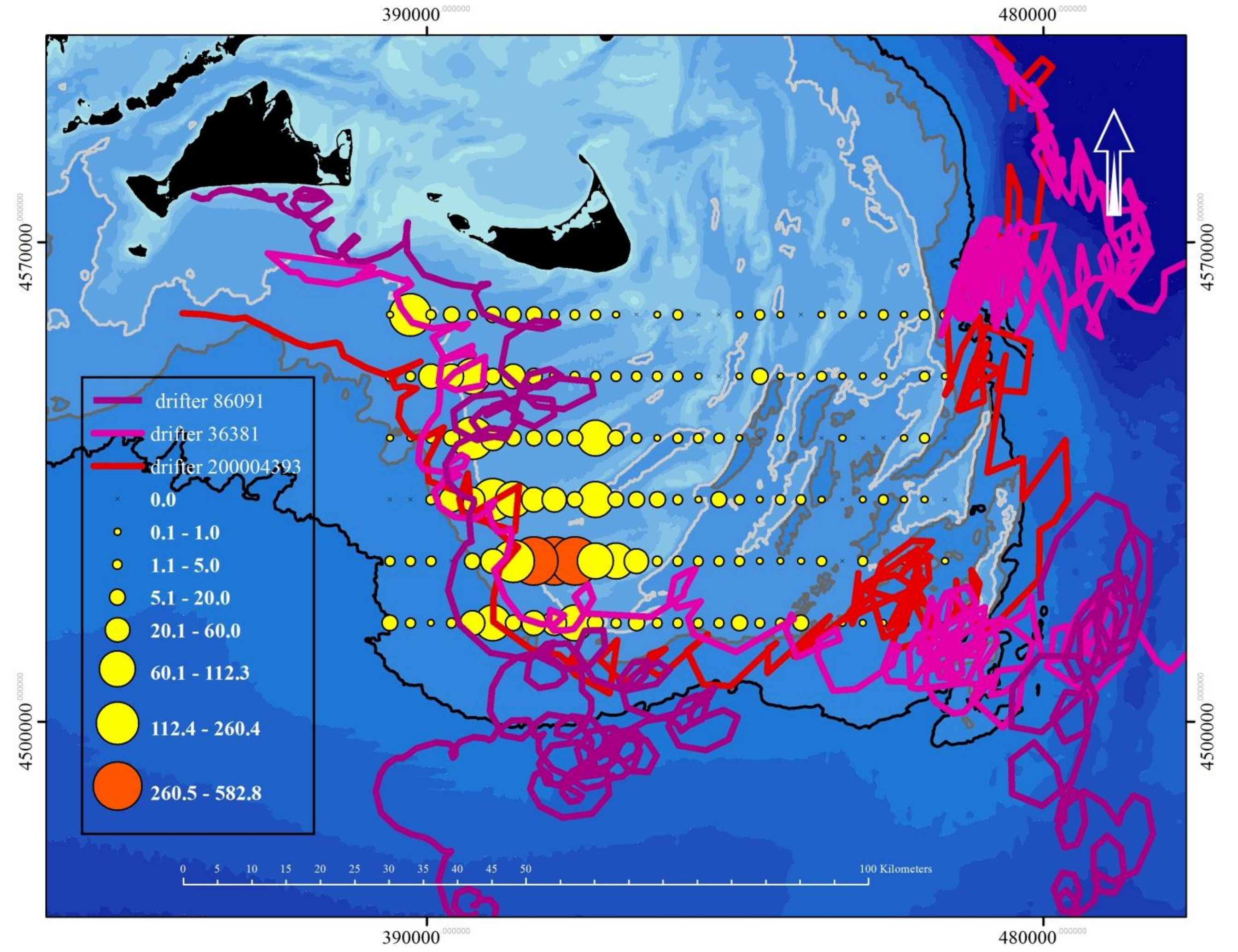
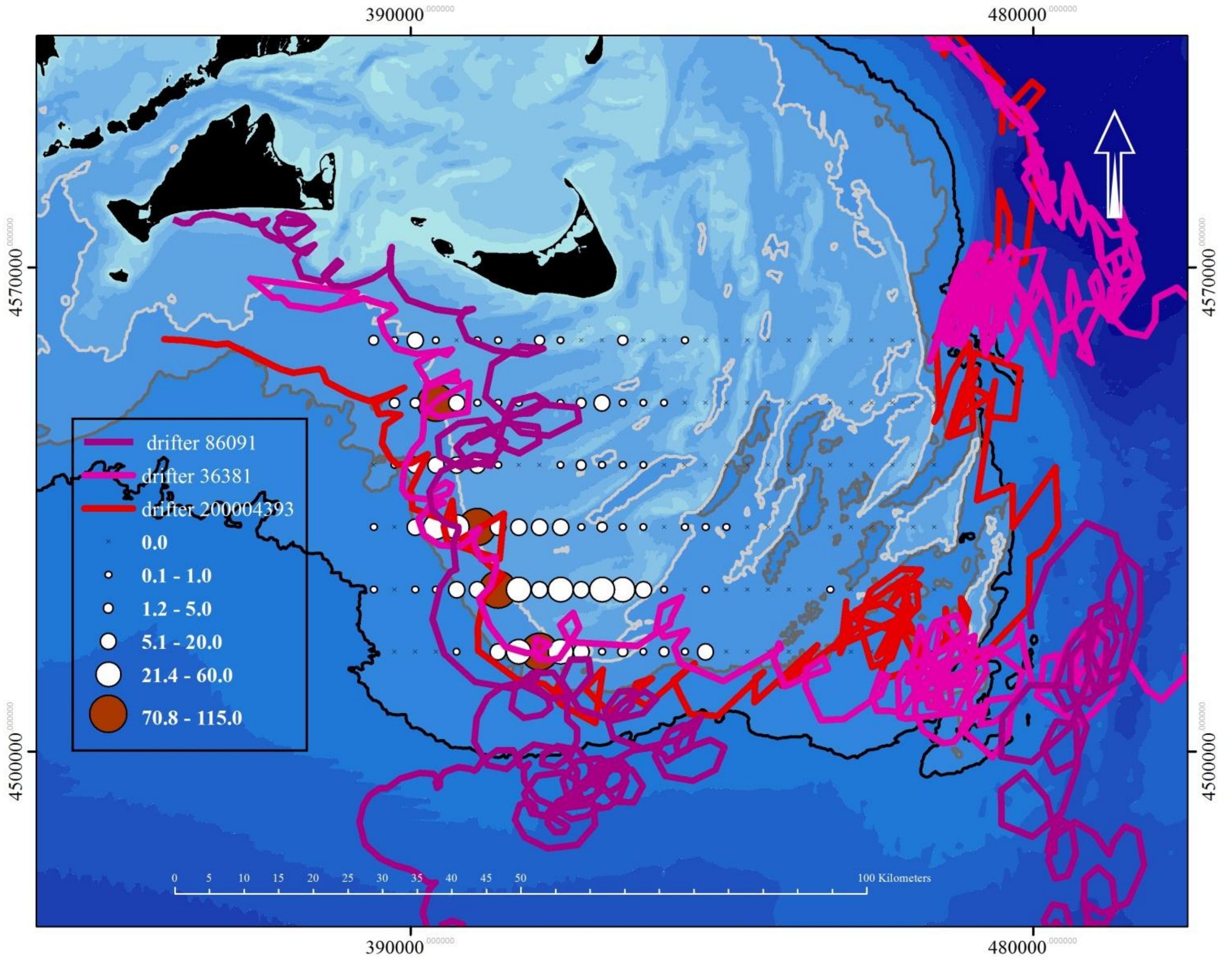


Figure 4.18 – Drifter buoy paths with White-winged Scoter density (no. / km^2). Isobaths 30m, 40m, 50m symbolized with emboldened shades of grey (darkest 50 m; lightest 30 m).



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