PHYSIOLOGICAL AND BEHAVIORAL THERMOREGULATION IN BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN SARASOTA, FLORIDA

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A Thesis Submitted to the
University of North Carolina Wilmington in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Department of Biology and Marine Biology

University of North Carolina Wilmington

2005

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consistent with the

Journal of Comparative Physiology B

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ABSTRACT

The temperature differential (ΔT) between a body surface and the ambient

environment is one factor that influences heat loss. Organisms can affect ΔT

physiologically, by controlling body surface temperature, and behaviorally, by choosing

the ambient temperature to which they are exposed. These physiological and behavioral

mechanisms of thermoregulation were investigated across seasons in a resident

community of bottlenose dolphins (*Tursiops truncatus*) in the Sarasota Bay, Florida

region, where water temperatures range annually from 11 to 33°C. Because the dorsal fin

is a highly dynamic thermal window, temperatures of this surface were measured on

wild, free-swimming dolphins using infrared thermography. Distribution of these year-

round resident dolphins was compared across seasons to assess whether or not local

changes in distribution reflect seasonal use of microclimates. Independent, continuous

measurements of water temperature at eight locations throughout the region were used to

describe the annual thermal profile of Sarasota Bay.

To calculate ΔT, water temperatures measured during thermal imaging were

subtracted from dorsal fin surface temperatures. There was a positive, linear relationship

between dorsal fin surface temperature and water temperature, as mean ΔT across all

seasons was similar. Dorsal fin surface temperatures appear to be modulated in response

to environmental temperature to maintain a steady ΔT at the dorsal fin skin surface across

seasons. In winter, increases in insulation, both integumentary (*i.e.* blubber) and vascular

(*via* reduced perfusion and utilization of countercurrent heat exchangers) must account

for the protection of core temperature and stability of ΔT.

Water temperature throughout the Sarasota Bay region changed dramatically across seasons and, overall, these patterns were similar throughout the study area. Temperatures tended to plateau in both winter and summer, and change continuously in spring and fall. Overlaid on this annual pattern of temperature change were short-term, cyclical variations in water temperature, with peak frequencies at 11 and 19 days. The amplitudes of these cyclical changes could vary between sites, creating regional heterogeneity in water temperatures across the study area. The amplitudes of these cyclical changes were more pronounced in winter than in summer at all sites; thus, temperatures within the summer were the most stable of any season.

To assess dolphin distribution, individuals were classified based on age, sex and reproductive status. Within a season, distribution patterns appeared to be specific to particular dolphin classes. Though not always significant, differences between these distribution patterns were more apparent in summer, spring, and fall, and less so in winter. Water temperatures during summer were, overall, the least variable, and in the transitional spring and fall seasons, water temperatures across the seven measurement sites were most similar to each other. In contrast, during winter, when water temperature oscillations could vary by up to 6°C over a period of 10-11 days, dolphin classes were more similar in their distributions.

The relationship between dolphin distribution and water temperature was investigated to assess whether or not a particular dolphin class was consistently observed in warmer or cooler water temperatures, relative to any other dolphin class. In only one dolphin class, and in only one season, was there a significant statistical relationship. Adult males in summer were found to be distributed in significantly cooler water

temperatures than all other classes. This result is interesting, as adult males have the

smallest surface area to volume ratios across which heat dissipation may occur, in

comparison to other dolphins, and it was found in summer, when water temperatures are

warmest and most stable. Thus, water temperature may be an important factor

influencing the distribution of adult male dolphins, but other biotic and abiotic factors

likely play an important role in dolphin distribution throughout the Sarasota Bay region.

ACKNOWLEDGEMENTS

wide-eyed sophomore undergraduate on a research trip Florida, where this all began!

Thank you for your love and encouragement over the years and for all of the experiences

we have shared. You mean more to me than you will ever know.

DEDICATION

I dedicate this thesis to my mother, Jackie, for the unconditional support and encouragement she has given me as I pursue my dreams. This thesis is also dedicated to my father, Dominic, who introduced me to the Chesapeake Bay as a child and with whom I share my fondness for the water. Thank you for all of the love and support you have given me over the years!

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INTRODUCTION

A community of approximately 150 bottlenose dolphins (*Tursiops truncatus*) resides year-round throughout the inshore waters of Sarasota Bay, Florida, U.S.A. and up to several kilometers offshore in the adjacent Gulf of Mexico (Scott *et al*. 1990, Wells 2003) (Figure 1). The inshore waters are predominantly characterized by shallow bays and seagrass flats but also contain deeper channels and passes that lead to the Gulf of Mexico. Dolphins often utilize shallow bays for protective nursery areas, seagrass beds for feeding, and channels and passes for traveling (reviewed in Scott *et al.* 1990). Thus, this area provides apparently adequate, year-round habitat for bottlenose dolphins (Wells 1993a). However, these non-migratory dolphins experience considerable seasonal variation in water temperature, which ranges from 11 to 33°C annually (Barbieri *et al.* 2005, Irvine *et al.* 1981, Wells *et al.* 1987).

Dolphins that remain in the Sarasota Bay region year-round experience larger changes in environmental temperature than do some bottlenose dolphins along the mid-Atlantic coast that migrate in direct or indirect response to water temperature (Scott *et al*. 1988, Barco *et al*. 1999, McLellan *et al*. 2002). For example, Barco *et al*. (1999) correlated the presence of bottlenose dolphins in the nearshore waters of Virginia, U.S.A. with seasonal changes in water temperature but not with changes in photoperiod or prey availability. Dolphins were not sighted in this area between late November and early April when water temperatures were below 16.0°C (Barco *et al*. 1999). Aerial surveys off the northeast coast of the United States demonstrated that inshore groups of bottlenose dolphins were seldom found in water temperatures below 17.5°C (Kenney 1990). Because water temperatures in Sarasota Bay can be as low as 11°C, these
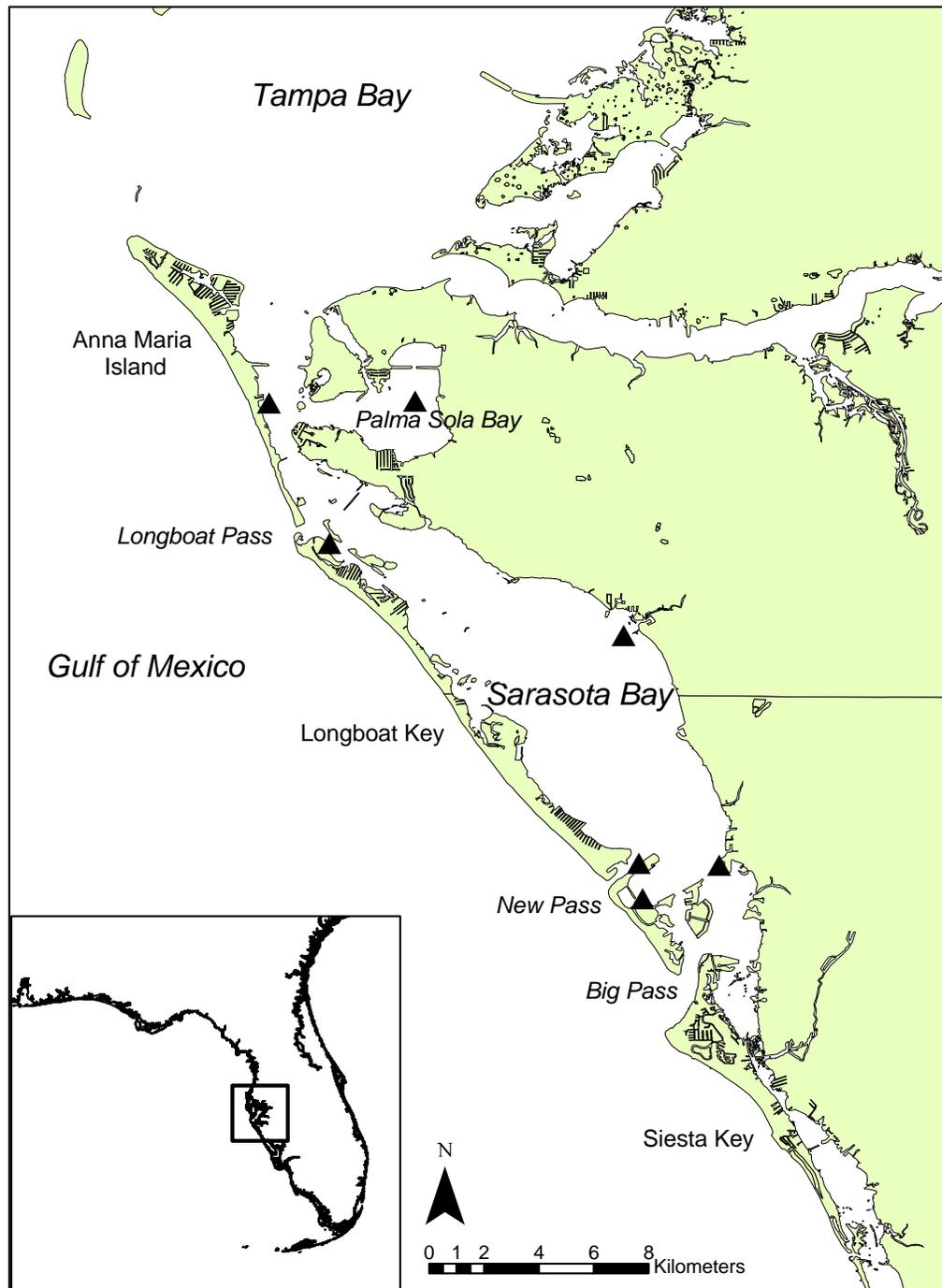
Figure 1. Map of the Sarasota Bay, Florida region (Florida Department of Environmental Protection, Tallahassee, FL). The study area encompasses a 40km stretch of water between barrier islands and the mainland, and is bound by Tampa Bay to the north and Big Pass to the south (Wells 1993a). Triangles represent the seven data logger locations where continuous, independent water temperature measurements were recorded. For all map figures, the NAD 1983 Projection was used.

resident dolphins may be exposed to lower winter temperatures than some conspecifics along the east coast of the U.S.A.

Zolman (2002) determined that bottlenose dolphin density in the Stono River estuary, South Carolina, U.S.A. was positively correlated with water temperature and photoperiod and was highest during the summer and fall (Zolman 2002). Wells *et al.* (1990) attributed a northward expansion in the distribution of bottlenose dolphins along the California coast to a rise in water temperature due to the El Niño of 1982-1983. This event caused a 3.5°C to 5.0°C increase in regional sea surface temperature, which apparently promoted the northward movement of some dolphin prey species (Wells *et al.* 1990). Thus, seasonal changes in dolphin distribution are influenced by multiple interrelated environmental parameters, including water temperature.

Water temperature is an important environmental feature to which marine mammals, as homeotherms, must respond, as this aquatic habitat is highly conductive and capable of removing body heat 25 times faster than air at the same temperature (Schmidt-Neilsen 1998). Conductive heat loss to the environment (H', Watts) is described by Equation 1:

$$H' = (SA)\ C\ (T_b - T_a),$$

where SA (m^2) is the surface area of the body, C is thermal conductance ($W/m^2\ °C$), and T_b-T_a (°C) is the temperature differential between the body and the ambient water (reviewed in Pabst *et al.* 1999). These three variables can be modulated morphologically, physiologically, and behaviorally in marine mammals to control heat conservation and dissipation (Figure 2; reviewed in Wilmer *et al.* 2000, Schmidt-Neilsen 1998).

ENVIRONMENTAL CHANGE:

water temperature

11°C ⟵⟶ 33°C

ORGANISMAL RESPONSE:

control of heat loss from body to water

physiology: control of body surface temperature

morphology: conductance of the integument

behavior: spatial and temporal* avoidance
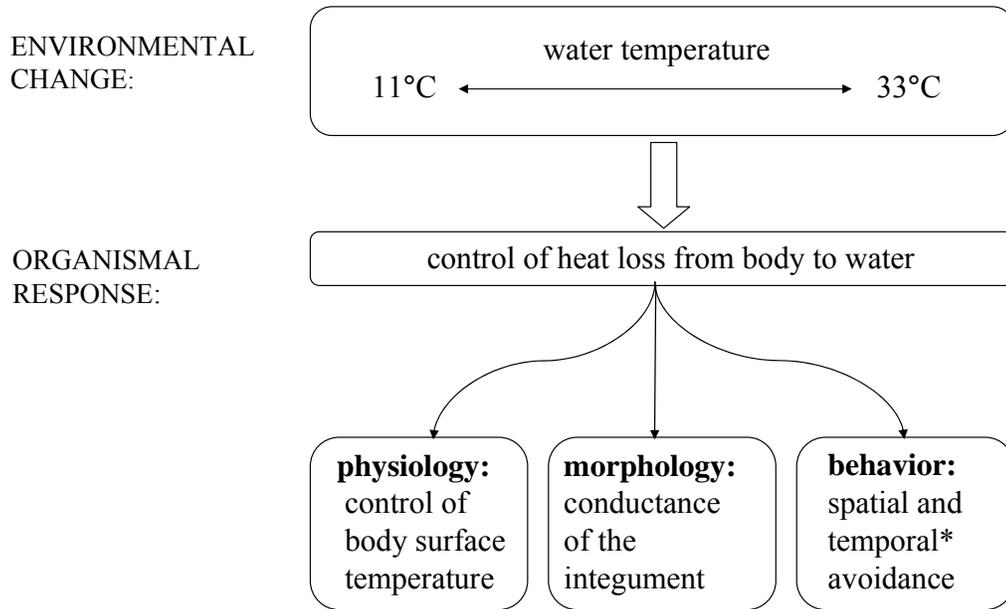
Figure 2. Potential responses of bottlenose dolphins to environmental fluctuation in water temperature, which ranges from 11-33°C in the Sarasota Bay study area (based on Willmer *et al.* 2000).

*NOTE: Temporal avoidance (*i.e.*, migrating away from the region) is not an apparent mechanism of regulation in resident dolphins in Sarasota Bay, FL.

Previous studies suggest that dolphins in the Sarasota Bay region do exhibit seasonal physiological and morphological plasticity. Field metabolic rates were found to be higher in the summer than in winter, implying that the energetic needs of dolphins in this community differ seasonally (Costa *et al.* 1993). Furthermore, blubber lipid content and blubber thickness were shown to increase in winter (Worthy *et al.* 1990, Worthy 1991, Wells 1993b). In comparison, blubber thickness of captive dolphins remained constant throughout the year when diet and water temperature were unchanged (Wells 1993b).

Dolphins may also control heat loss *via* their poorly insulated dorsal fin, pectoral flippers, and flukes, which are dynamic thermoregulatory control surfaces called thermal windows (*e.g.,* Meagher *et al.* 2002, Williams *et al.* 1999, Noren *et al.* 1999). In the dorsal fin, vascular countercurrent heat exchangers permit the transfer of heat from arterial blood at core body temperature to the cooler venous blood, minimizing heat loss to the water (Scholander and Schevill 1955). Alternatively, shunting of blood to superficial veins bypasses the countercurrent heat exchanger, which facilitates heat loss at the skin/water interface and transports cooled blood directly to the body core (Scholander and Schevill 1955, Kvadsheim *et al.* 1997).

Previous studies have shown that mean surface temperatures across the dorsal fin depend, in part, upon water temperature. Noren *et al.* (1999) demonstrated that dorsal fin surface temperatures of captive bottlenose dolphins at rest remained within 1°C of water temperature, which ranged from 28.5-31.5°C. Meagher *et al.* (2002) measured dorsal fin skin surface temperatures of wild, temporarily restrained bottlenose dolphins in the Sarasota Bay region in summer. Mean temperature differentials between the submerged

dorsal fin surface and the water tended to remain within 0.6-0.9°C of water temperature

(27.8-31.9°C) and were highest when measured directly over a superficial vein. No study

has yet, though, investigated the relationship between dorsal fin surface temperature and

environmental temperature in bottlenose dolphins exposed to a wide range of water

temperatures.

Evidence from other well-studied, resident groups of bottlenose dolphins suggests

that dolphins in the Sarasota Bay region may also respond behaviorally to seasonal

changes in water temperature with finer-scale changes in distribution. For example,

Wilson *et al.* (1997) demonstrated that dolphin distribution changed seasonally in the

Moray Firth, Scotland (annual water temperature range 5.5 – 12.5°C). The authors

hypothesized that: (1) seasonal differences in prey distribution related to bathymetry may

influence prey catchability and, thus, dolphin distribution, and (2) inshore waters in the

summer were relatively warmer than other areas and provided habitats that were more

favorable for adult females and newly born calves.

Distribution of resident dolphins in Shark Bay, Australia (annual water

temperature range 14-20°C) was also found to change seasonally (Heithaus and Dill

2002). In cold months, dolphins were predominantly distributed throughout the shallow

seagrass beds, presumably in accordance with the distribution of their prey. In contrast,

dolphin density in these shallow areas decreased during warm months, despite the

consistently high biomass of dolphin prey. This seasonal shift in dolphin distribution was

attributed to an increase in tiger shark density and, thus, predation risk in shallow regions.

The authors concluded that dolphins moved toward deeper, more protected waters for

non-feeding activities when shark presence was high. In both the Moray Firth and Shark

Bay studies, seasonal changes in dolphin distribution occurred, despite the relatively small annual range of water temperatures (6-7°C). Thus, even in areas with relatively low seasonal variability, water temperature can directly and/or indirectly influence seasonal movement patterns of dolphins.

Irvine *et al*. (1981) suggested that there did exist seasonal differences in dolphin distribution in the Sarasota Bay region. In winter, dolphins tended to be concentrated in the nearshore Gulf of Mexico and associated passes, but in summer, dolphins were more concentrated in the shallow inshore channels and bays. These authors proposed that prey availability, rather than abiotic factors, influenced dolphin movement patterns. Waples (1995) demonstrated seasonal differences in distribution and activity between male and female bottlenose dolphins in the Sarasota Bay region, and hypothesized that these changes were influenced by prey distribution. Data on prey distribution were not collected, but seasonal differences in the locations of feeding occurrences by focal dolphins were attributed to movements of pinfish and mullet. Water temperature is one factor that may influence these observed changes in the distribution of both dolphins and prey. To date, no study has described how water temperature varies seasonally throughout the Sarasota Bay region or has tested for a correlation between dolphin distribution and the temperature of their surroundings. The large seasonal difference in water temperature in the Sarasota Bay region and the presence of a resident dolphin community permits a unique investigation into potential mechanisms of dolphin thermoregulation.

The goal of this study was to investigate physiological and behavioral responses of resident bottlenose dolphins in the Sarasota Bay region to seasonal changes in water

temperatures. The dorsal fin surface temperature, an indicator of the animal's physiological response, was measured in free-swimming dolphins using infrared thermography. Comparison of temperature differentials between the dorsal fin and the water were made across seasons to determine whether dolphins differentially utilize this thermal window to control heat loss in response to changing environmental temperature.

The behavioral responses of bottlenose dolphins to seasonal changes in environmental temperature were investigated by examining the seasonal distributions of resident dolphins within the Sarasota Bay region. Because this dolphin community has been so well-studied, distribution patterns could be investigated within each season, between classes of individuals based upon age, sex, and reproductive status. Independent, continuous measurements of water temperature were collected to investigate the annual thermal profile of the Sarasota Bay region. Water temperatures measured at dolphin sightings were compared across dolphin classes within each season to investigate whether dolphins utilize microclimates to control heat loss to the environment.

METHODS

Infrared Thermal Imaging

Dorsal fin surface temperatures of free-swimming dolphins in the Sarasota Bay region were assessed using infrared thermography. The amount of infrared radiation that is emitted from a surface is proportional to its temperature (Clark 1976, Cena and Clark 1973, Watmough *et al*. 1970). This non-invasive technology provided an instantaneous visualization of temperature distribution across the entire surface of the dolphin dorsal fin and the associated boundary layer of water.

Infrared thermal images were collected during surveys of the Sarasota Bay region for 5 to 10 days each in November, February and June in 2002-2004 (Table 1). Surveys were conducted from approximately 0900 to 1700 aboard a 6m long powerboat with at least three observers. Weather-permitting, the survey route was extended to include the coastal Gulf of Mexico up to 1 km offshore. A sighting event began when one or more dolphins were located and approached. Throughout a sighting, the behavior, identity, and number of adult dolphins and calves were recorded. Dolphins were followed until all individuals in a group were photographed and identified or until the dolphins could no longer be located. Sightings ranged from 5-75 minutes in duration, but generally lasted approximately 20 minutes.

Environmental data collected at the initial sighting location included water temperature, air temperature, relative humidity (Fisherbrand certified traceable hygrometer/ thermometer, Fisher Scientific International, Pittsburgh, PA), depth, clarity, salinity, and latitude/longitude coordinates. Weather and wave conditions including wind speed and direction, sightability, glare, and wave height (Beaufort scale) were also recorded. Surface water temperature was measured with a digital thermometer (AquaCal® ClineFinder™, Catalina Technologies, Tucson, AZ, U.S.A.) or a mercury thermometer. Water temperature measurements through the water column at 0.5m intervals from the bottom to the surface (ClineFinder) were also recorded at multiple locations throughout the study area.

Infrared thermal images were collected from the bow of the boat throughout each sighting event using a FLIR Agema 570 infrared (IR) camera, with an adjacent video camera, mounted on a monopod. The video camera was used to collect real-time video

Table 1. Dates of thermal imaging of free-swimming wild bottlenose dolphins in Sarasota Bay, Florida.

Season	Dates	Number of analyzed thermal images
fall	Nov. 11-21, 2002	61
	Nov. 10-14, 2003	83
winter	Feb. 11-14, 2003	69
	Feb.16-20, 2004	110
summer	Jun. 16-27, 2003	135
	Jun. 15-18, 2004	97

of each sighting (Sony Digital Handycam DCR-TRV 103). Continuous infrared video (Sony Digital Handycam DCR-TRV 340 connected to the infrared thermal camera) was also recorded simultaneously. Video documentation was reviewed at the end of each day to transcribe verbal notes and to confirm the contents of each thermal image.

Infrared thermal images were downloaded to a laptop computer daily and analyzed using ThermaCam Researcher 2001 software (FLIR Systems AB, Sweden). Image quality was rigorously evaluated and only those images that were in sharp focus, where the angle of the dorsal fin was less than $30°$ to the perpendicular plane of the camera, and where the dorsal fin occupied at least 15% of the image were used.   Dorsal fin surface temperatures were measured at three sites in each image: the distal tip and the cranial and caudal regions of the fin base (Figure 3). Care was taken to avoid fin margins, where edge effects can distort infrared temperature measurements (Cena and Clark 1973, Watmough *et al*. 1970). Note that the IR camera specifically measured the temperature of the thin film of water covering the surface of the dorsal fin.

In each image, the difference between the dorsal fin surface temperature measurement and the ambient water temperature was calculated and reported as the temperature differential (ΔT_{dfin-a}). ΔT_{dfin-a} was compared across each of the three measurement sites (Figure 3) using a one-way analysis of variance (ANOVA) (JMPIN Version 5, SAS Institute, Inc., Cary, NC, U.S.A.). There were no significant differences in ΔT_{dfin-a} across measurement sites when data from all field seasons were combined ($p = 0.9803$). The mean difference between the three measurement sites across all seasons was less than $0.1°C$. In addition, when ΔT_{dfin-a} was compared across measurement sites within each field season, differences were not significant ($p = 1.000$). Thus, temperature
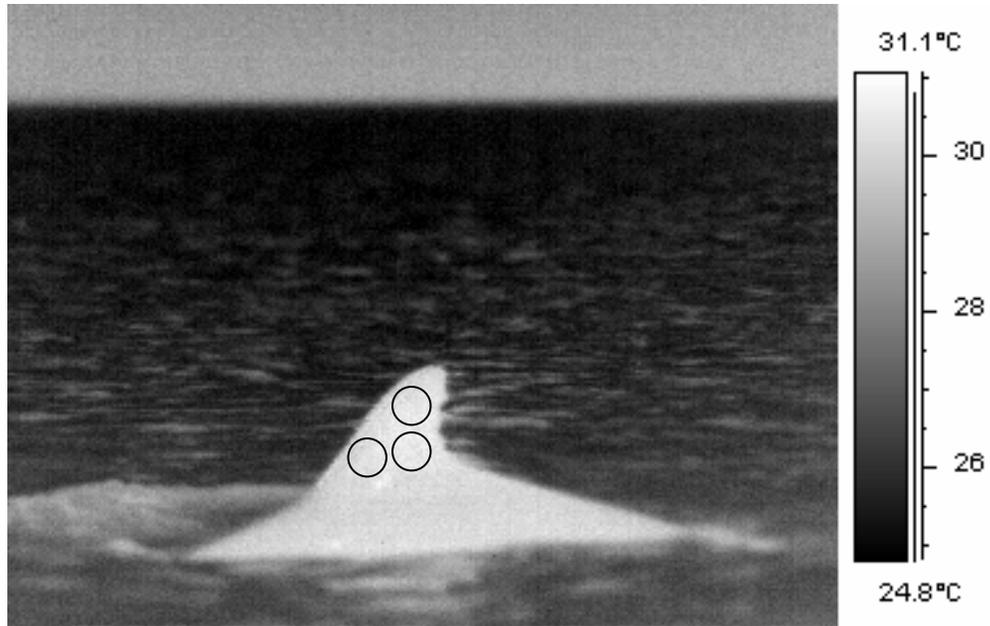
Figure 3. Sites of dorsal fin temperature measurements. Infrared thermal image of bottlenose dolphin dorsal fin and body illustrating sites of dorsal fin temperature measurements. Dorsal fin surface temperatures (T_{dfin}) were measured at the distal tip and the cranial and caudal regions of the fin base (circled) in each infrared thermal image. Circles were drawn to encompass the maximum possible area available in each image, while avoiding the extreme edges of the fin.

differentials were averaged across these three sites for all subsequent analyses.

Mean temperature differentials were compared across seasons using an ANOVA (JMPIN). For all comparisons, an alpha value of 0.05 was used to determine statistical significance. The Tukey Honestly Significant Difference Test (JMPIN) was used to identify significant differences in dorsal fin surface temperatures and temperature differentials across seasons. Linear regression analysis was used to investigate the relationship between water temperature and both dorsal fin surface temperature and ΔT_{dfin-a} across seasons.

Calibration of Infrared Thermal Camera

The use of infrared thermography as both a diagnostic and field-portable investigative tool is well-documented; however, some precautions regarding its quantitative accuracy should be considered (*e.g.*, Clark 1976, Watmough *et al*. 1970). For example, accurately measuring water surface temperature using the infrared thermal camera is difficult given water's high reflectivity. Water surface temperatures, both in the field (ClineFinder) and in a temperature controlled water bath (RE-120 Lauda Ecoline, Brinkmann Instruments, Inc., Westbury, NY, U.S.A.) measured with the infrared thermal camera held parallel to the water's surface were within 0.1-0.2°C (mean 0.15°C) of the water. However, this accuracy decreases rapidly as the angle between the camera and the water surface increases. Because of these errors, independent measurements of ambient water temperature were used in this study (see above).

Calibration experiments were conducted to determine the effect of dorsal fin distance from and angle to the camera. The angle the fin was measured relative to a plane perpendicular to the plane of the camera. To test these variables, a dorsal fin model

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was constructed and secured within a frame. Three copper-constantan, Type T thermocouples (Omega Engineering, Inc., Stamford, CT, U.S.A.) were embedded between two plexiglass sheets that were carved into the size and shape of a bottlenose dolphin dorsal fin and painted with flat gray, epoxy paint. Three holes were drilled through the surface of one plexiglass sheet at the distal tip and cranial and caudal regions of the fin base, sites that matched those measured in free-swimming dolphins. Thermocouple tips were pressed through the holes flush with the outside surface of this sheet and secured using a thin layer of epoxy for waterproofing. To hold a thin layer of water over the fin model, an elastic, matte gray, nylon sock was stretched around the plexiglass. A Fluke Hydra data logger (Fluke Corporation, Everett, WA, U.S.A.) recorded temperature measurements from each thermocouple once per second. To simulate a wet dorsal fin, the fin model was submerged until the thermocouples were within 0.5°C of water temperature (approx. 35°C; water temperature was measured continuously throughout experiment using a fourth thermocouple). Three thermal images were subsequently taken immediately after removal of the model from the water. This process was repeated for each combination of experimental variables listed above.

Dorsal fin surface temperatures were measured, using ThermaCam Researcher software, as described above for field experiments. Surface temperatures reported by the thermocouples were compared to those reported by the infrared thermal camera. The mean difference between temperatures reported by the camera and the thermocouples was -0.56 ± 0.61°C s.d. (range: -1.40 to 0.10°C) for images taken outdoors on a clear, sunny day, where the fin model was positioned from 1 to 20m away and between 0° and 30° angles to the camera. The mean value is negative, indicating that the infrared thermal

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camera tended to report temperatures that were lower than those measured at the thermocouples. This systematic bias may indicate that the underlying thermocouple was more insulated from evaporative cooling than the surface of the nylon sock.

Continuous, Independent Measurement of Water Temperature

Independent and continuous measurements of water temperature were collected from June 28, 2003 to November 11, 2004 to determine patterns of water temperature change and to describe any regional differences across Sarasota Bay. This information was used to elucidate whether or not differences in water temperature across the region could provide a signal to which dolphins may behaviorally respond. Data logging thermometers (HOBO® Water Temp Pro D-6076-A, Onset Computer Corporation, Bourne, MA, U.S.A.) were deployed at a total of 7 sites in the study area from November 2003 to November 2004 (Table 2, Figure 1). Sites were selected to represent the variety of small-scale habitats within the Sarasota Bay region.

Preliminary water temperature data (ClineFinder) collected during synoptic surveys in November 2002 and February 2003 illustrated that temperatures measured through the water column, at positions from 0.5 to 3.5m (bottom) deep, were usually within 1°C of surface water temperature. Therefore, data logging thermometers were secured with plastic cable tie wraps inside hollow cement blocks and sunk to the bottom. Lines attached to the cement blocks were tied to hard structures (dock pilings, channel markers) or buoys. The temperature loggers were covered with antifouling marine bottom paint and programmed to record water temperature every 30 min. Data were downloaded approximately every 2-3 months to a laptop computer (Box Car Pro 4.3 software, Onset Computer Corporation, Bourne, MA,U.S.A.) and graphed in Microsoft

Table 2. Locations of data logging thermometer placement in Sarasota Bay, Florida. Mean annual temperatures were recorded from Nov. 10, 2003 to Nov. 11, 2004.

Site	Location description	Approx. depth (m)	Mean water temperature (ºC)
Mote Marine Lab back dock	shallow, protected bay in southern portion of Bay	2.0	incomplete
New Pass dock	pass between southern portion of Bay and Gulf	4.0	24.29
Moore's Restaurant, Longboat Key	just south of pass between mid-northern portion of Bay and Gulf	3.5	24.15
Palma Sola Bay marker 20	middle of shallow, protected bay, SE corner of study area	2.0	24.33
Hart's Landing dock	shallow, southeast corner of Sarasota Bay	1.5	24.53
Anna Maria Sound	shallow, northwest corner of study area	1.5	24.07
entrance to Bowlee's Creek Marina	east-central portion of Sarasota Bay	2.5	24.46

Excel. Individual thermometers were distributed differently around these seven sites after each downloading session so that no particular thermometer was in the same location for more than 2-3 months at a time. The HOBO thermometers were calibrated in a temperature-controlled water bath and were within ±0.1°C of water bath temperature.

Preliminary analysis of long-term temperature records indicated multiple, short-term, cyclical patterns of temperature variation. Thus, local and seasonal trends in water temperature throughout the study area were described using spectral density analyses (SAS). This process identified the primary cyclic patterns in the water temperature data for all measurement sites. The cyclical patterns that were identified in spectral density analyses were then compared across all data logger sites by comparing the amplitude of temperature change at each site.

Seasons were defined by the following three-month groups: summer (June-August); fall (September-November); winter (December-February); spring (March-May). To permit comparison of trends in independent water temperature measurements to those of dolphin distribution, mean temperatures between 0900 and 1700, corresponding to the hours of dolphin survey activity, were used in this analysis.

Seasonal Dolphin Distribution Patterns

To determine whether there existed seasonal differences in the distribution patterns of bottlenose dolphins in the Sarasota Bay region, a Geographic Information System (GIS) was created. Resident individuals within the Sarasota Bay region are identifiable, and this important information permitted comparisons between males and females, between sexually mature and immature males, and between females with and without dependent calves. Data from sightings of dolphins identified during surveys

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conducted from April 2001 to April 2003 (n=1393 sightings) were stored in a database (Microsoft Access 2002). An analysis grid (cell size, 1 km^2) was created using a visual basic fishnet extension (Nicholas, 2003) in the UTM Zone 17N NAD 1983 projection and stored as a polygon shapefile in ArcGIS 9.0 (ESRI, Inc., Redlands, CA, U.S.A.).

The following steps were taken to correct for survey effort. Tracklines of each survey, which were downloaded from a GPS and stored as shapefiles, were intersected with the grid. The lengths (km) of each trackline within each grid cell were measured using a visual basic command in X Tools Pro (DataEast LLC, 2004). Total distance surveyed per grid cell (km) was subsequently summed over the time period of interest. Starting coordinates of each sighting event were spatially joined to the corresponding grid cell in ArcGIS. To calculate the total number of sightings per kilometer surveyed, the number of sightings within each grid cell within a time period was divided by the total kilometers surveyed within that grid cell within that same time period. The resulting value, sightings per unit effort (SPUE), was used as an indicator of dolphin density within each grid cell. SPUE values were mapped at the centroid of each grid cell, and cells with density values of zero were not represented. The possibility that a dolphin was observed in one grid cell from a trackline located in an adjacent grid cell was not accounted for in this study.

Identified dolphins were classified into seven different categories based on age and reproductive status. Dolphins were divided into (1) adult males, (2) subadult males, and (3) adult females. Adult females were further subdivided into those (4) with and (5) without calves. Because the thermal requirements of newborn and older calves may differ from those of adults (*e.g.*: Dunkin *et al.*, 2005), females with calves were further

subdivided into (6) those with young of the year (yoys) and (7) those with older calves that were between one and three years of age (Table 3). Distribution (in SPUE) was compared across all these classes within a season and within the same class across different seasons. Pairwise comparisons between the spatial distributions of different classes were made according to the methods described by Syrjala (1996), using 1000 permutations in the Quickbasic program GEODISTN. In this program, SPUE values were normalized; thus, absolute differences in abundance between two dolphin classes did not influence statistical comparisons. This program computed a test statistic for the null hypothesis that the normalized distributions of the two classes were the same. This statistic was the sum of the squares of the difference between the cumulative distribution functions for each of the two classes being compared, across all sampling locations that they have in common. Significance was determined within the program using the Cramér-von Mises test and the Kolmogorov-Smirnov test, and the Bonferoni adjustment for multiple pairwise comparisons was made (Tabachnick and Fidell, 1996). It should be noted that the Kolmogorov-Smirnov test is more sensitive to a small number of high density observations than the Cramér-von Mises test. Maps complemented statistical tests and permitted more detailed spatial comparisons between dolphin classes (ArcGIS).

The relationship between dolphin distribution and water temperature was investigated to assess whether or not a particular dolphin class was consistently observed in warmer or cooler water temperatures, relative to any other dolphin class. Water temperature measured at the start of each sighting event was matched to each individual

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Table 3. Classifications of dolphins identified. Dolphins sighted were divided into seven classes based on sex, maturity and reproductive status (R. Wells, pers. comm., Read *et al.* 1993, Wells *et al.* 1987).

Category	Definition
adult males	males at least 10 years of age
subadult males	males between 4 and 7 years of age
adult females	females at least 6 years of age (includes all categories below)
adult females without calves	females at least 6 years of age without dependent calves
adult females with calves	adult females with calves (includes both categories below)
adult females with young of the year (yoys)	adult females with calves less than 1 year old
adult females with calves between 1 and 3 years old	adult females with calves between 1 and 3 years old (*i.e.*, does not include yoys)

dolphin identified in that sighting. Individual dolphins and the associated water temperature values were classified into categories as described above (Table 3). Comparisons of water temperature across each dolphin class in each season were made using a repeated measures ANOVA (SAS).

<div align="center">RESULTS</div>

Infrared Thermal Imaging

Across the two year study period, there was a significant positive relationship between mean dorsal fin surface temperature and water temperature (r^2=0.978, p<0.001) (Figure 4). Thus, the temperature differential (ΔT_{dfin-a}) was relatively constant and the mean dorsal fin surface temperature across all seasons was 0.9°C warmer than water temperature (range: 0.12 to 1.35ºC) (Figure 5).

Although dorsal fin temperatures were strongly correlated to water temperature, temperature differentials measured repeatedly on the same individual dolphin did vary. For example, the ΔT_{dfin-a} of FB11 (adult female, born 1984) varied both within a sighting and across seasons (Figure 6). Over a six day period in fall 2002, ΔT_{dfin-a} ranged from 0.3°C to 1.4°C. During a single sighting in winter 2003, ΔT_{dfin-a} ranged from 1.5 to 2.9°C, which was comparable to a 2.8°C measurement recorded for FB11 in summer 2003. On average, most dorsal fin temperatures remained within approximately 1°C of water temperature, but they could reach temperature differentials as high as 4°C. One such occasion was documented in November 2002, when rain and cold air temperatures dramatically reduced water temperature by 10°C in 3 days. The highest temperature
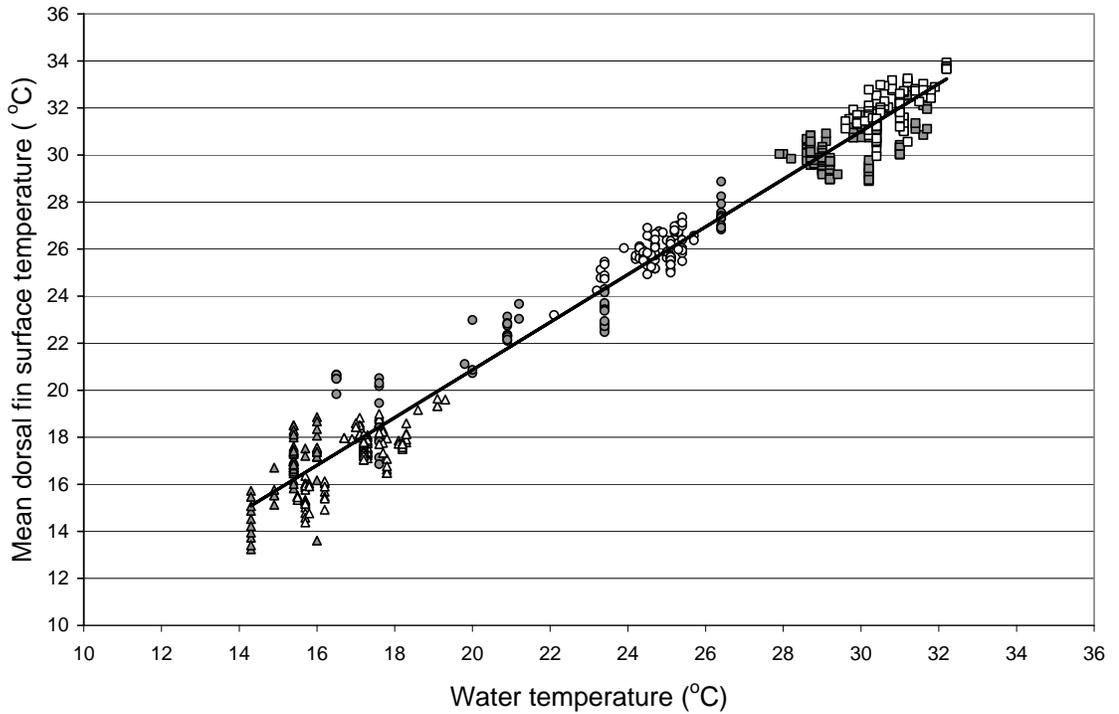
Figure 4. Mean dorsal fin surface temperatures (T_{dfin}) plotted against water temperature (T_a). There was a significant, positive relationship between T_{dfin} and T_a ($r^2=0.978$; $y=0.587+1.01x$; $p<0.0001$). Symbols represent each field season (●Nov. 02; ○ Nov. 03; ▣ Jun. 03; □ Jun. 04; ▲ Feb. 03; △ Feb.04).
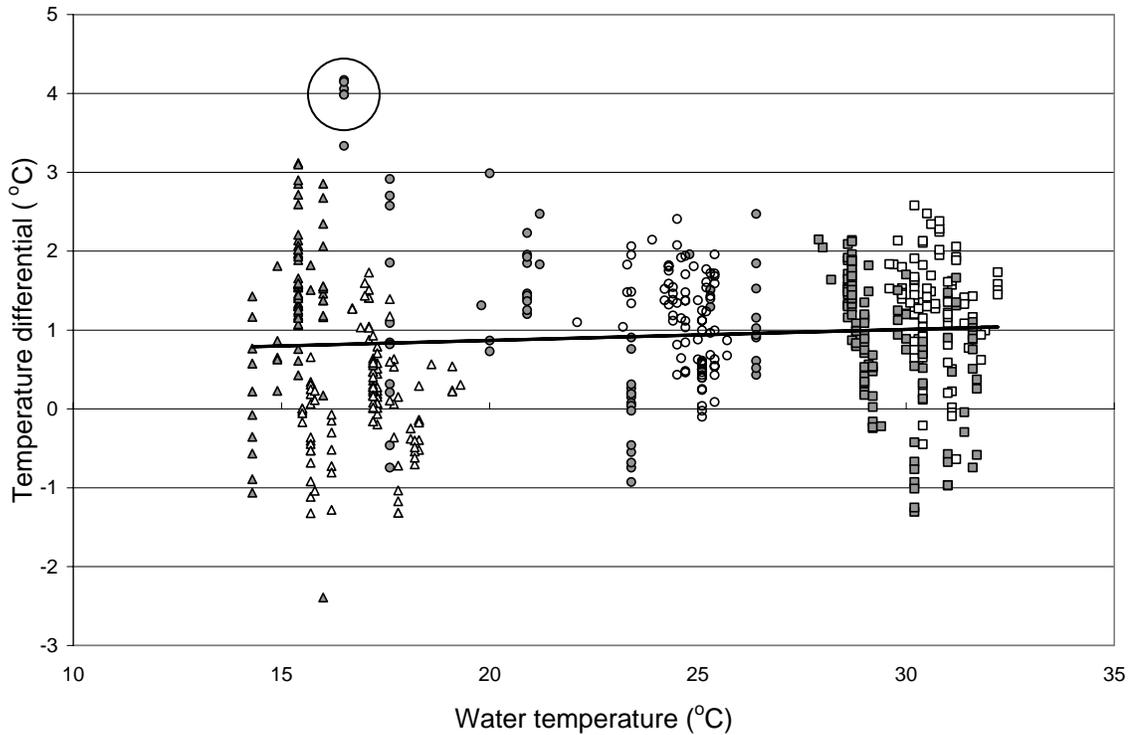
Figure 5. The temperature differential between the dorsal fin and the water (ΔT_{dfin-a}) (°C) plotted against water temperature. ΔT_{dfin-a} values were consistent across winter, fall and summer seasons. Mean temperature differential across all seasons was 0.9°C (r^2=0.008; y=0.589+0.014x; p=0.0333). The highest temperature differentials measured in this study (circled) were observed after a 10°C drop in water temperature in November 2002. Symbols represent each field season (● Nov. 02; ○ Nov. 03; ■ Jun. 03; □ Jun. 04; ▲ Feb. 03; △ Feb.04).
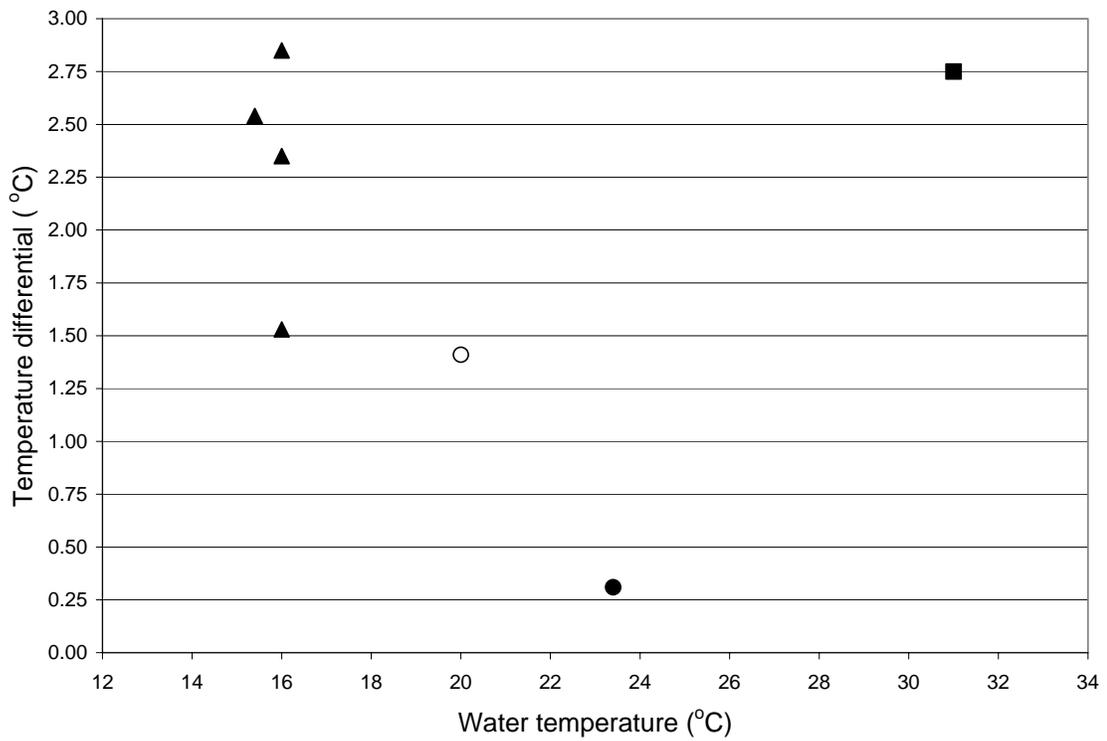
Figure 6. Temperature differentials between the dorsal fin and the water (ΔT_{dfin-a}) (°C) can vary across days and seasons within the same individual. Dorsal fin temperature differentials of FB11 (adult female, born 1984) are shown here, plotted against water temperature. Symbols represent November 2002 (● 14 Nov. 02; ○ 20 Nov. 02), February 2003 (▲ 14 Feb. 03), and June 2003 (■ 17 June 03).

differentials recorded in this study were measured during the two days following this event (Figure 5).

To further investigate ΔT_{dfin-a}, mean values were calculated for each season and year, which ranged from 0.12 to 1.35°C (Figure 7). There was no consistent pattern in mean ΔT_{dfin-a} across seasons; for example, values measured in winter were not always smaller than those measured in summer. Furthermore, values of ΔT_{dfin-a} measured in winter displayed the greatest range: the largest mean ΔT_{dfin-a} was measured in winter 2003 and the smallest mean ΔT_{dfin-a} was measured in winter 2004.

Continuous, Independent Measurement of Water Temperature

Water temperature was continuously recorded at eight sites throughout the Sarasota Bay region to describe the annual thermal profile of this habitat. Because the data logger at Buttonwood Shoal marker was lost on two separate occasions, this incomplete dataset was not included in analyses.

The annual trend in water temperature throughout the Sarasota Bay region was similar across all sites (Figure 8). On average, temperatures measured across all sites were within 0.5°C of each other (Table 2). Mean seasonal water temperatures measured at each of the seven sites are listed in Table 4. Water temperatures in winter were more variable than in summer. Changes in water temperature closely followed those of ambient air temperature; for example, in early Jan. 2004, air temperature rose and fell 2 to 3°C, and water temperature tracked accordingly (Figure 9). Water temperatures at all sites plateaued within the summer and winter seasons, and the fall and spring seasons were characterized by frequent increases and decreases in temperature.

Table 4. Mean seasonal water temperatures measured at seven data logger locations (see Table 2 for site descriptions).

Site	Spring	Summer	Fall	Winter
Mote Marine Lab back dock	23.1	30.3	incomplete	incomplete
New Pass dock	23.2	30.5	26.5	17.2
Moore's Restaurant, Longboat Key	23.0	30.6	26.4	16.9
Palma Sola Bay, marker 20	23.6	30.5	26.3	17.2
Hart's Landing dock	23.6	30.7	26.7	17.6
Anna Maria Sound	23.4	30.4	25.5	16.8
entrance to Bowlee's Creek Marina	23.7	30.7	25.6	17.4
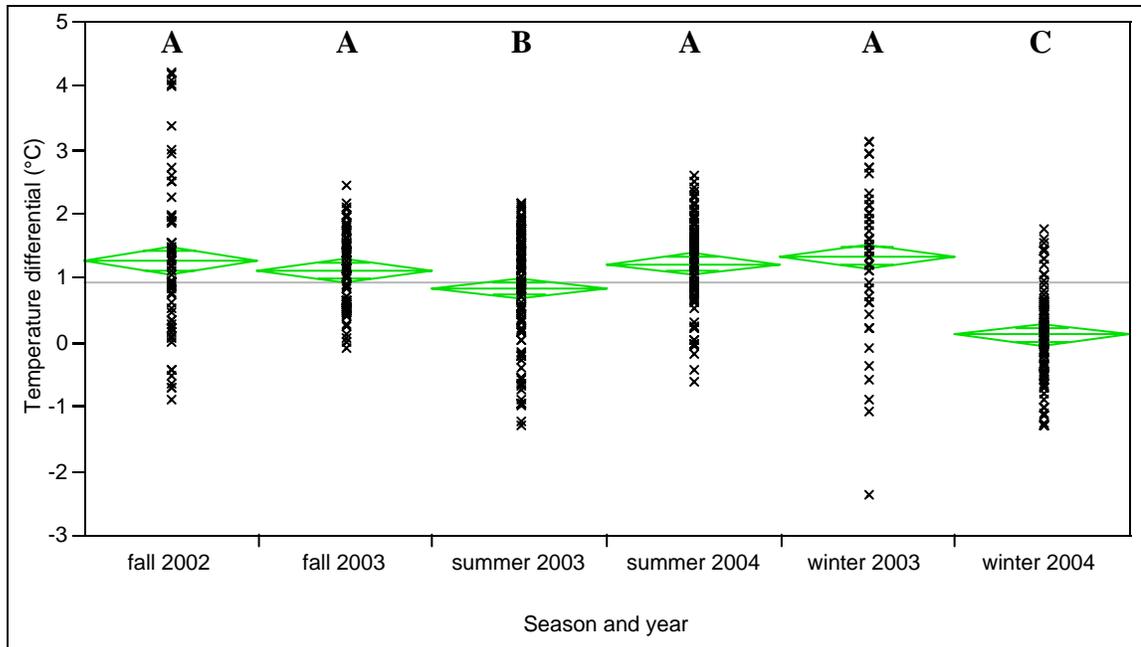
Figure 7. Comparison of temperature differentials (ΔT_{dfin-a}) across field seasons. There was no consistent trend in temperature differentials across seasons. Field seasons labeled with the same letter are not significantly different from each other.
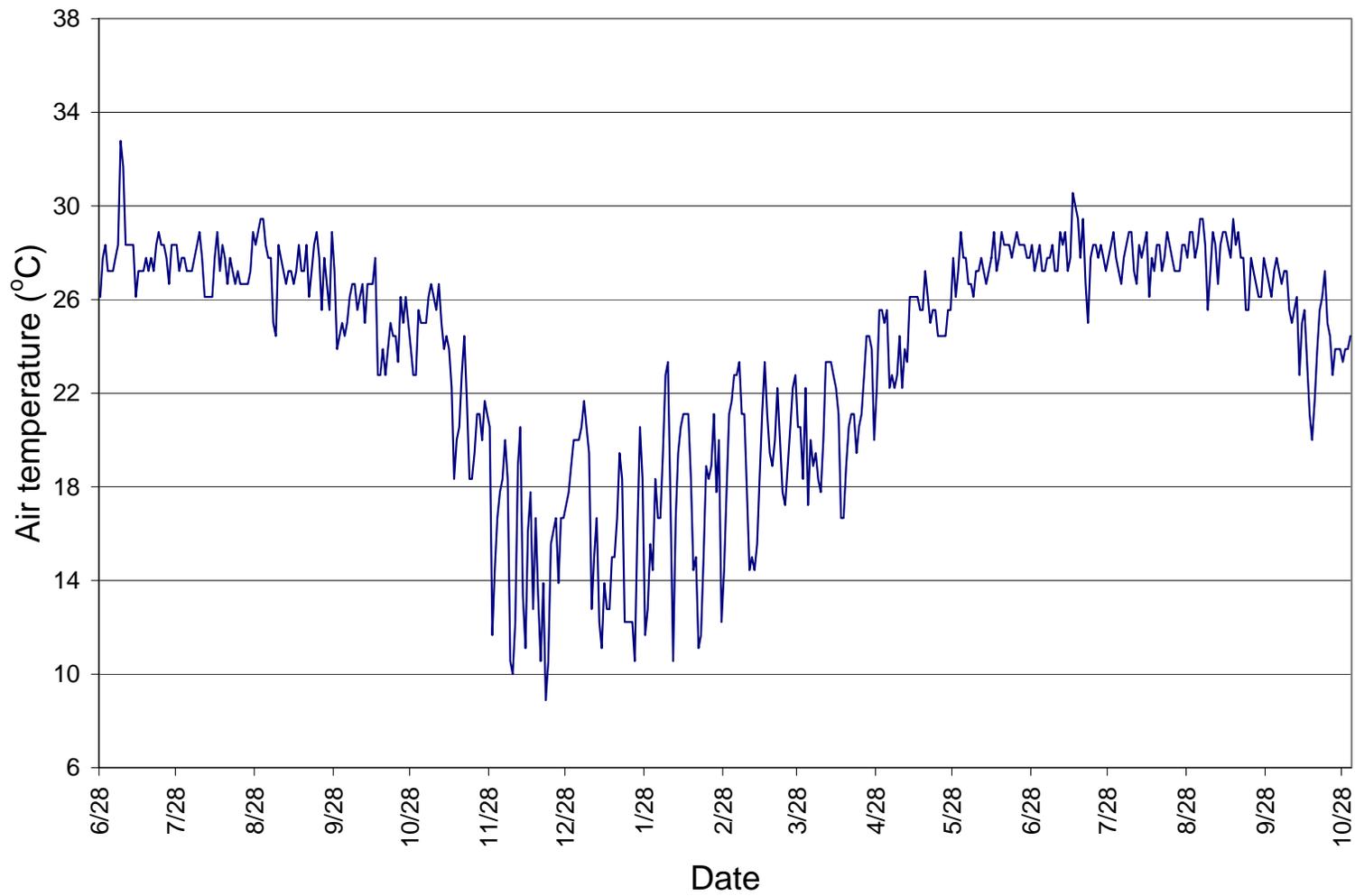
Figure 9. Mean daily (24 hr.) air temperatures from 28 June 2003 to 31 October 2004. Temperatures were measured at the Sarasota Bradenton International Airport.
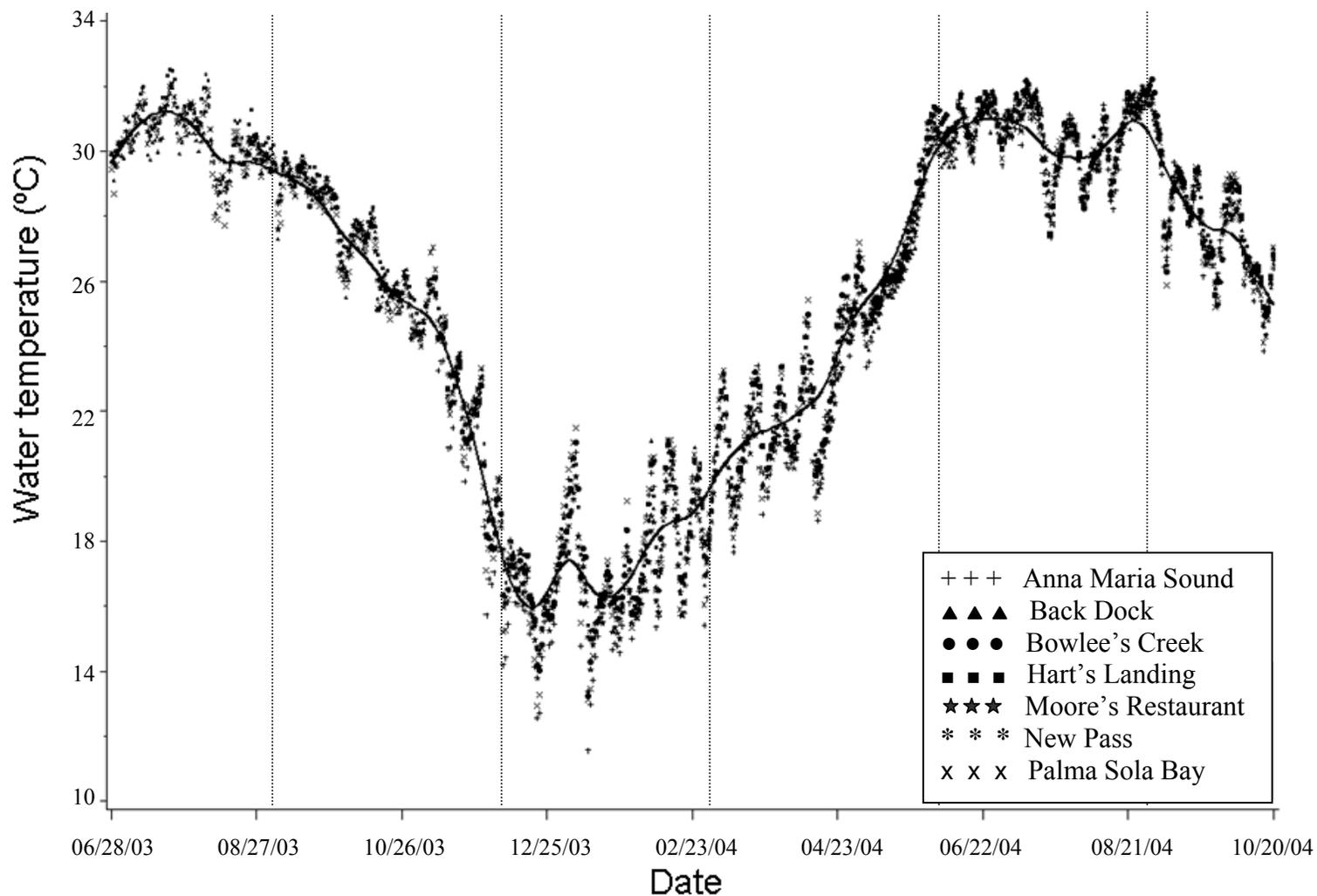
Figure 8. Mean daytime (0900 to 1700) water temperatures measured at seven locations throughout the Sarasota Bay region (see Table 3 for site descriptions). The splined trend line was constructed in SAS to smooth across short-term oscillations in temperatures at all sites. Seasons are delineated by dotted vertical lines.

During late fall and spring, when temperatures undergo relatively rapid changes, water temperatures tended to be most similar across the seven data logger locations and remained within about 0.5°C of each other (Figures 8 and 10A). During summer and winter, when water temperatures plateaued, temperatures varied by 1 to 1.5°C across the seven sites, and shallower locations (Palma Sola Bay, Anna Maria Sound, Hart's Landing, Bowlee's Creek) tended to be warmer than sites located near passes (New Pass, Moore's Restaurant) (Figures 8 and 10B). Figures 8 and 10 illustrate that overall seasonal patterns in temperature change are similar across all sites, but there also exist short-term, cyclical patterns of change.

To investigate short-term, cyclical variation in water temperature across the region, spectral density analyses were run using the overall mean across the six sites with complete data records (Buttonwood Shoal marker and Mote Marine Lab back dock locations were omitted). The largest peak was identified at a period of approximately 360 days, which illustrates the annual periodicity in water temperatures. Short-term cycles were identified as having 11 and 19 day periodicities (Figure 11). To determine if these cycles were related to tidal flow, tide data were gathered from NOAA for the St. Petersburg Tide Station and corrected for Sarasota Bay (www.co-ops.nos.noaa.gov, F. Bingham, pers. comm.). Spectral density analyses were run using the maximum daily change in tidal height (higher high tide – lower low tide). The peak frequency component in the tidal data, 14 days, fell between the two peaks for the water temperature data (Figure 11). Though it is interesting that the water temperature and tidal data cycles are out of phase with each other, it is unclear what influence tide may have on the 11 and 19 day cycles of water temperature change.

Figure 10. Mean daytime water temperatures (0900 to 1700) from 1 May to 30 Jul. 2004. Temperatures were measured at seven locations throughout the study area (see Table 3 for location descriptions). During periods of rapid temperature change (*i.e.*, late spring), temperatures across sites were most similar (A). During relatively stable periods (*i.e.*, summer), temperature differences across sites were more variable (B). Splines fit to each measurement site were smoothed across short-term oscillations to illustrate the overall trend (SAS).
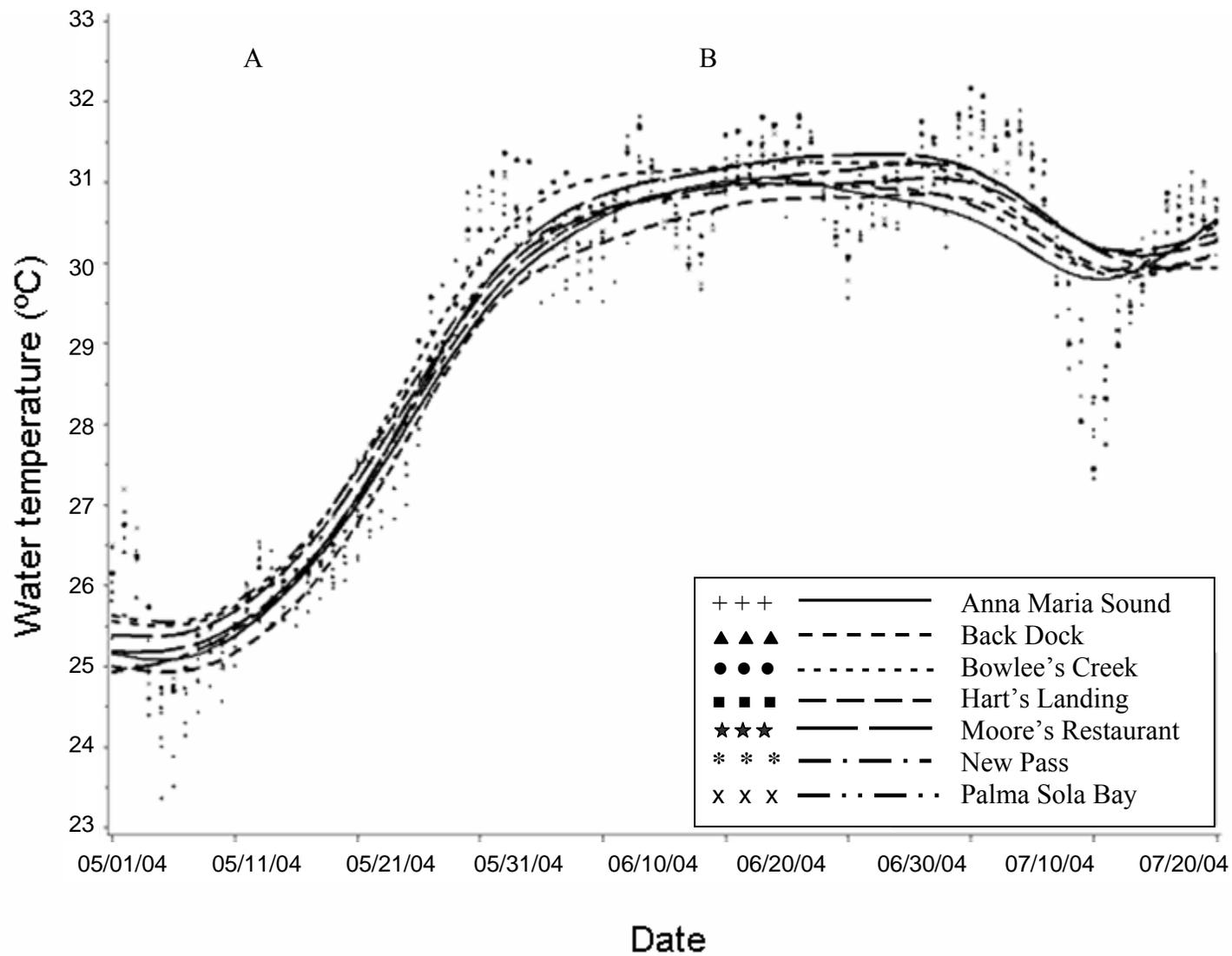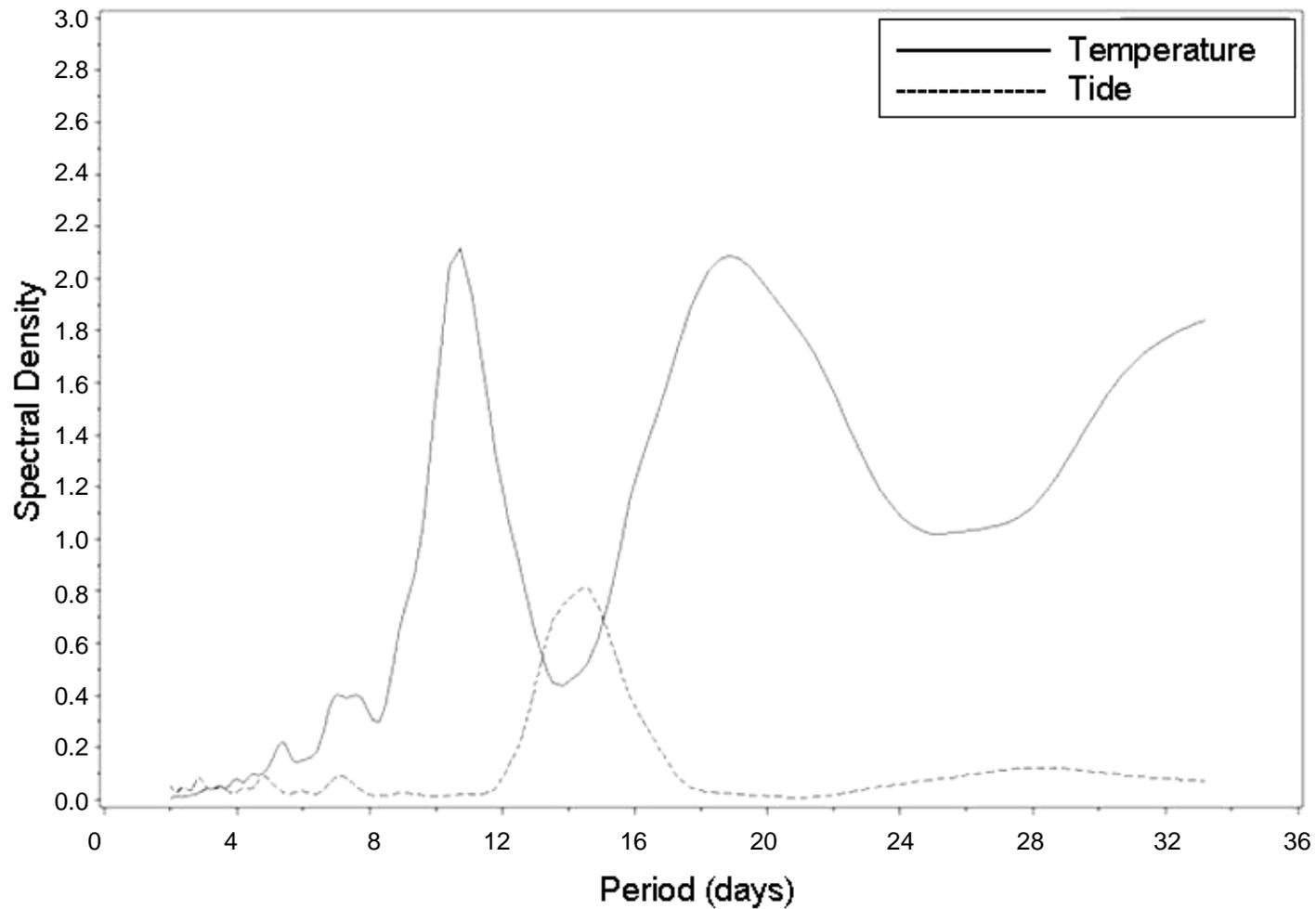
Figure 11. Spectral density analyses of mean daytime water temperatures (0900-1700) (solid line) and the daily change in tidal heights (higher high tide-lower low tide) (dashed line). Peak spectra in water temperatures were observed at 11 days and 19 days. The peak spectrum in the tidal data was 14 days.

To describe how the trends identified in the spectral density analyses were manifested across the six measurement sites, the amplitude of change (°C) at each site, relative to the overall mean temperature at that site (Tables 2 and 4), was investigated (Figure 12). Differences in amplitude illustrate site-to-site variation in the magnitude of the cyclic patterns. These comparisons illustrated that the Palma Sola Bay and Anna Maria Sound sites oscillated more above and below their mean values than other sites. Thus, shallow, inshore sites tended to vary the most over short time periods. In contrast, the New Pass and Moore's Restaurant sites, which are located near inlets, displayed smaller amplitude values, and experienced relatively smaller short-term changes in water temperature.

Seasonal Dolphin Distribution Patterns

Dolphin distribution, in SPUE, was compared across seven classes (Table 3) from 2001-2003. For all seasonal comparisons, data from both years were combined. For some comparisons, the Kolmogorov-Smirnov test reported significant differences, but the Cramér-von Mises test did not. In the following descriptions, these cases are considered significant, but noted with an asterisk (*). Results from both statistical tests are summarized in Table 5.

Within Class-Across Season Comparisons

Within each of the seven dolphin classes, distribution was statistically compared across the spring, summer, fall and winter seasons. No significant differences were found in any of the 42 comparisons that were made. Both the adult male and adult female dolphin classes had similar distributions across all seasons (Figure 13).

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Table 5. Statistical comparisons between dolphin classes within seasons. Alpha values (p) and ranges for each (based on 1000 permutations) are given for each statistical test (CM: Cramér von Mises; KS: Kolmogrov-Smirnov). Significant differences are shown in bold.

| Comparison	p_{CM}	range$_{CM}$	p_{KS}	range$_{KS}$
adult males to adult females; all seasons	0.2040	0.1484-0.2760	**0.0040**	0.0000-0.0120
adult males to adult females; summer	0.4320	0.3536-0.5104	0.1840	0.1312-0.2368
adult males to adult females; fall	0.5720	0.4836-0.6604	0.1880	0.1344-0.2416
adult males to adult females; winter	3.6640	3.5940-3.7340	3.4360	3.3480-3.5240
adult males to adult females; spring	0.9760	0.8672-1.0848	0.1480	0.1004-0.1956
adult females w/ calves to adult females w/o calves; all seasons	**0.0040**	0.0000-0.0012	**0.0040**	0.0000-0.0012
adult females w/ calves to adult females w/o calves; summer	0.2400	0.1800-0.3000	0.0600	0.0292-0.0908
adult females w/ calves to adult females w/o calves; fall	0.2360	0.1764-0.2956	0.1400	0.0936-0.1864
adult females w/ calves to adult females w/o calves; winter	1.9120	1.7856-2.0384	1.6960	1.5708-1.8212
adult females w/ calves to adult females w/o calves; spring	0.1200	0.0768-0.1632	**0.0160**	0.0000-0.0320
adult females with yoys to adult females with calves > 1 year old; all seasons	0.4680	0.3868-0.5492	**0.0040**	0.0000-0.0120
adult females with yoys to adult females with calves >1 year old; summer	0.4400	0.3608-0.5192	0.3480	0.2768-0.4192
adult females with yoys to adult females with calves > 1 year old; fall	1.3240	1.2048-1.4432	1.1560	1.0412-1.2708
adult females with yoys to females with calves > 1 year old; winter	0.1840	0.1312-0.2368	**0.0280**	0.0068-0.0492
adult females with yoys to adult females with calves > 1 year old; spring	0.9560	0.8480-1.0640	1.1440	1.0296-1.2584
adult males to subadult males; all seasons	**0.0040**	0.0000-0.0120	**0.0040**	0.0000-0.0120
adult males to subadult males; summer	**0.0160**	0.0000-0.0320	**0.0320**	0.0096-0.0544
adult males to subadult males; fall	**0.0360**	0.0120-0.0600	**0.0480**	0.0264-0.0856
adult males to subadult males; winter	2.4080	2.2840-2.5320	1.1280	1.0140-1.2420
adult males to subadult males; spring	**0.0200**	0.0020-0.0380	**0.0040**	0.0000-0.0120
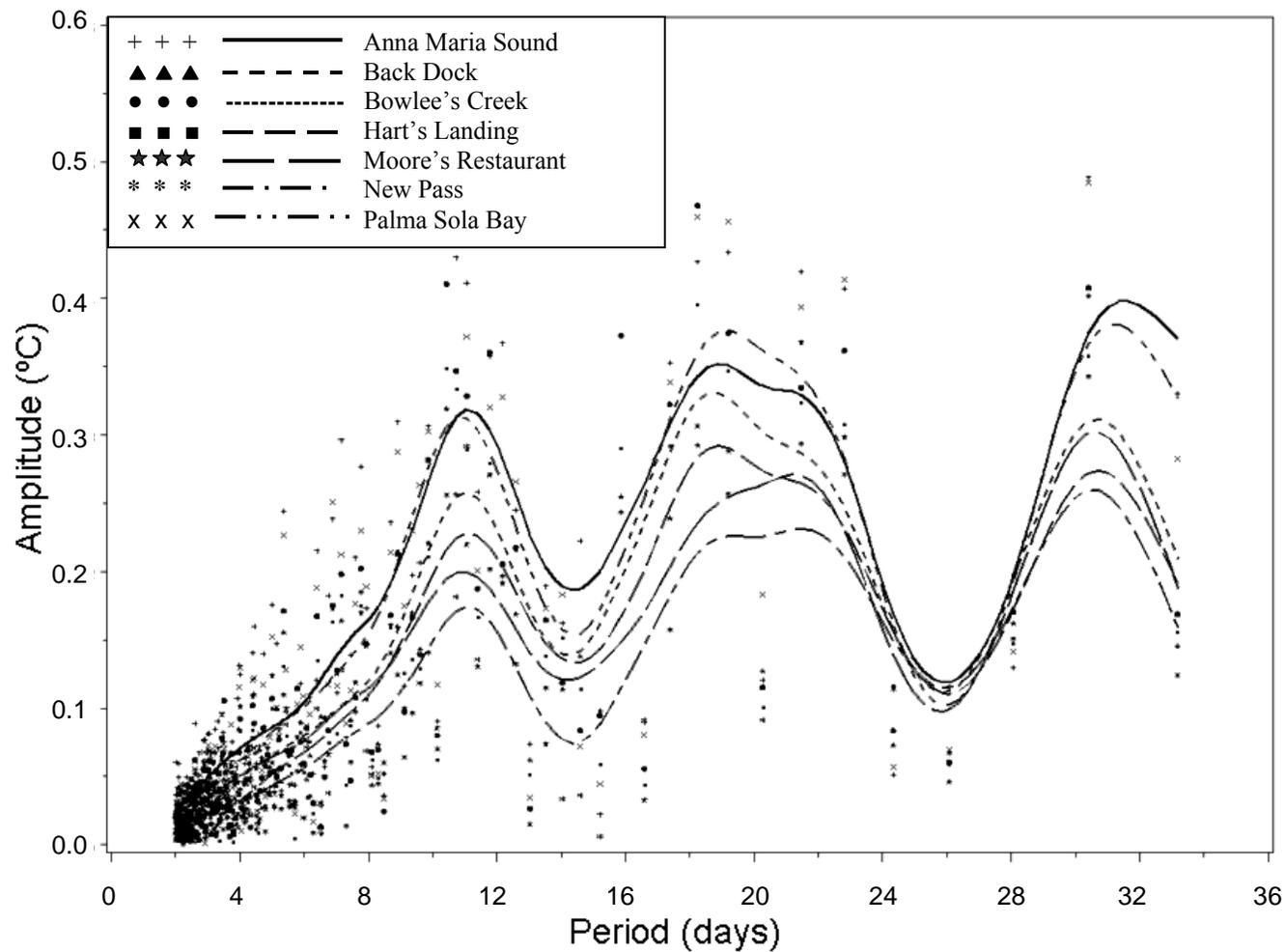
Figure 12. Amplitudes of short-term peak frequency components of mean daytime (0900-1700) water temperatures (°C) at seven measurement sites.
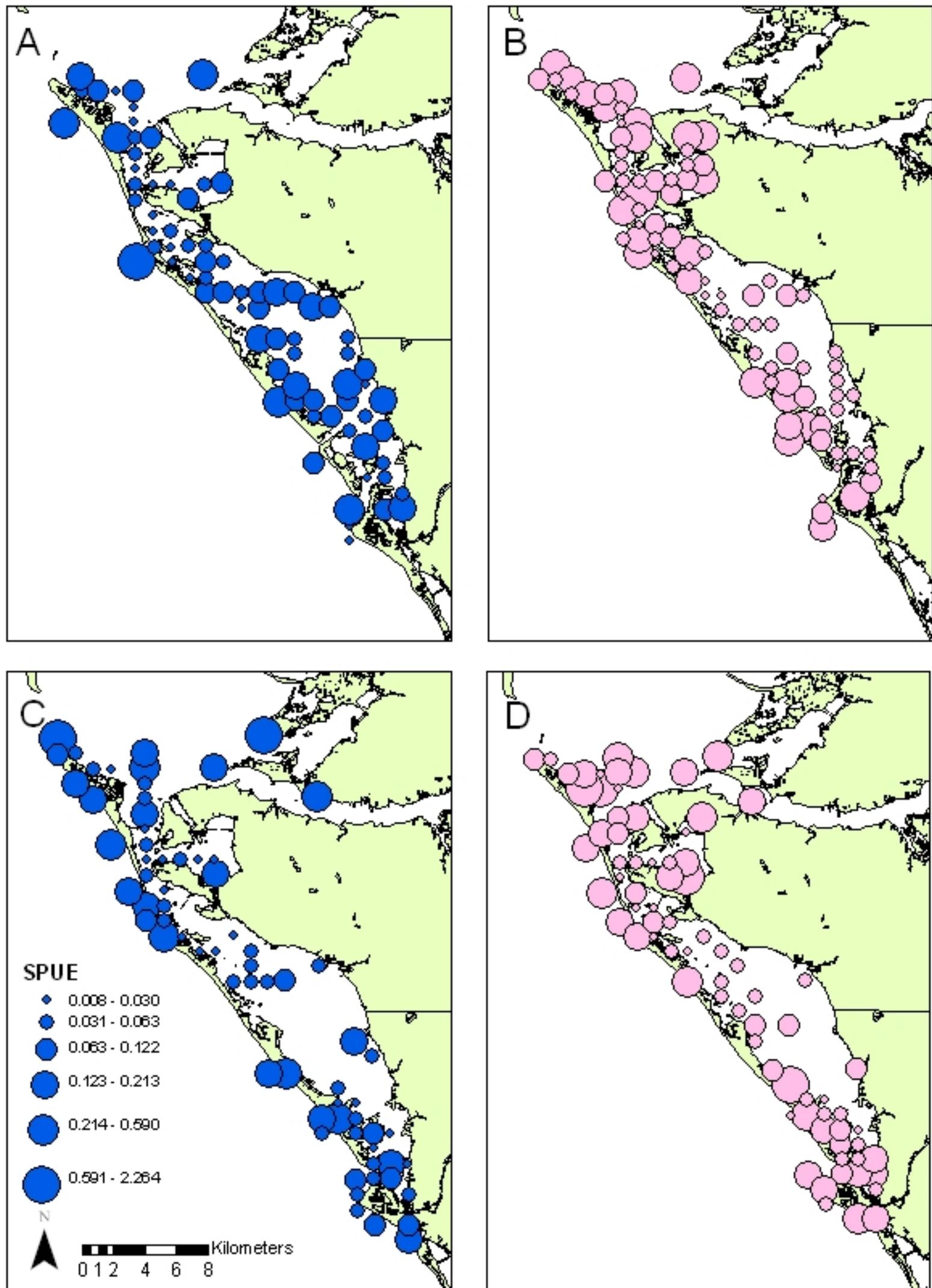
Figure 13. Distributions (sightings per unit effort, SPUE) of adult males and adult females in summers (A, males; B, females) and in winters (C, males; D, females). Scale and legend in C apply to all maps; larger circles represent higher densities.
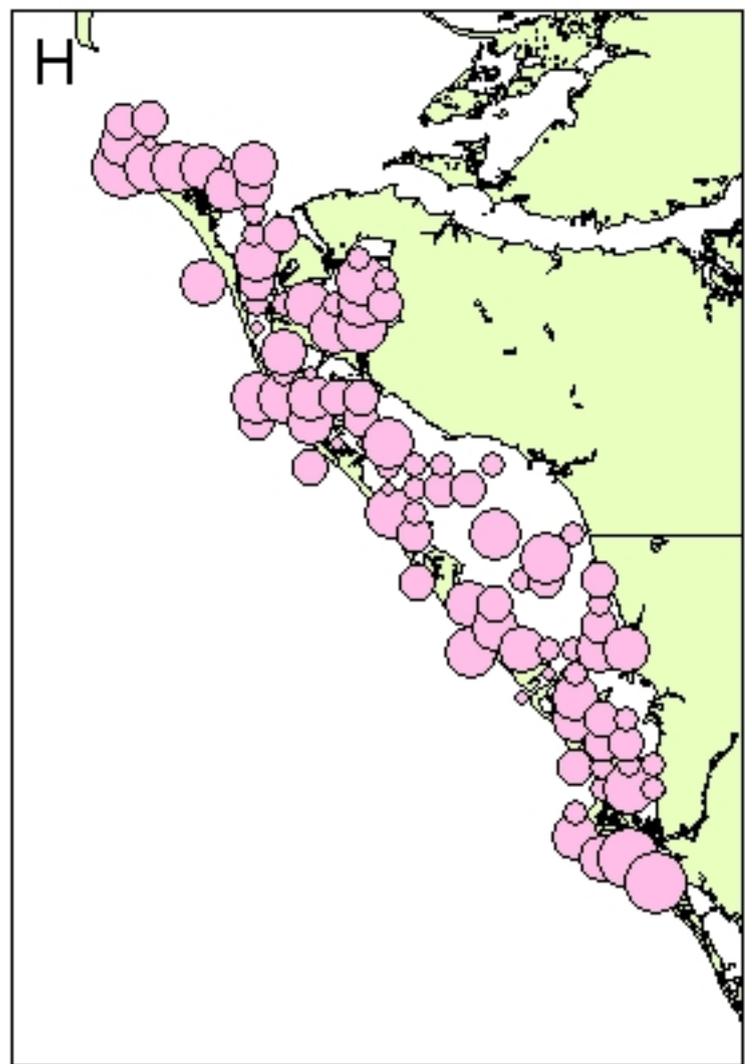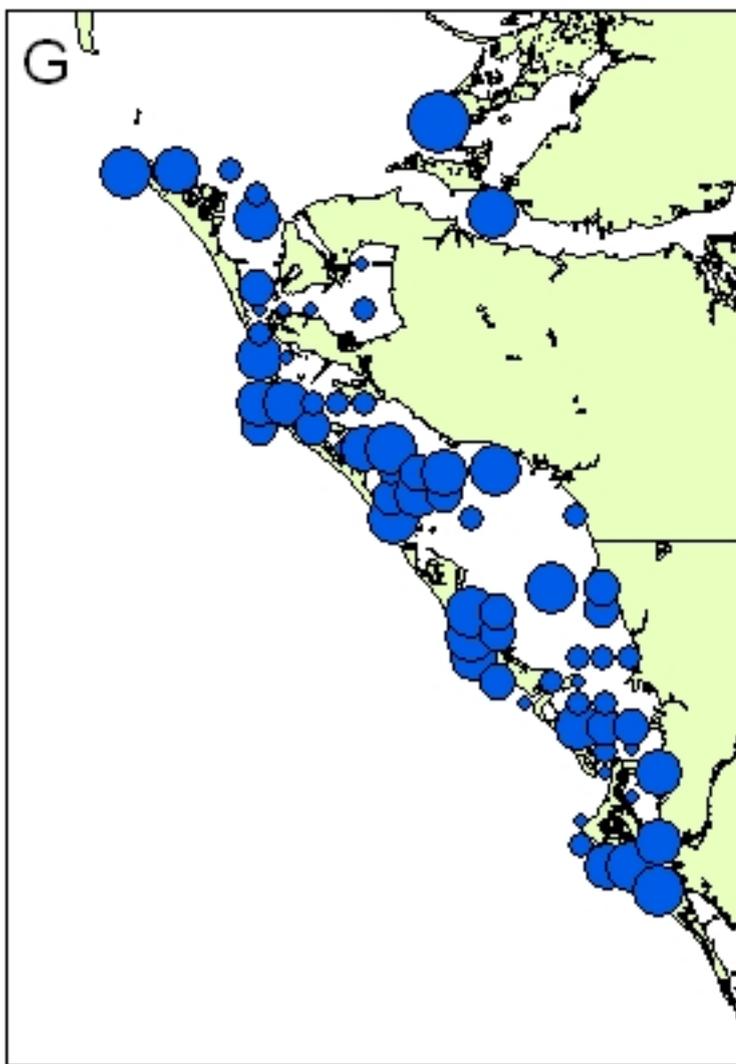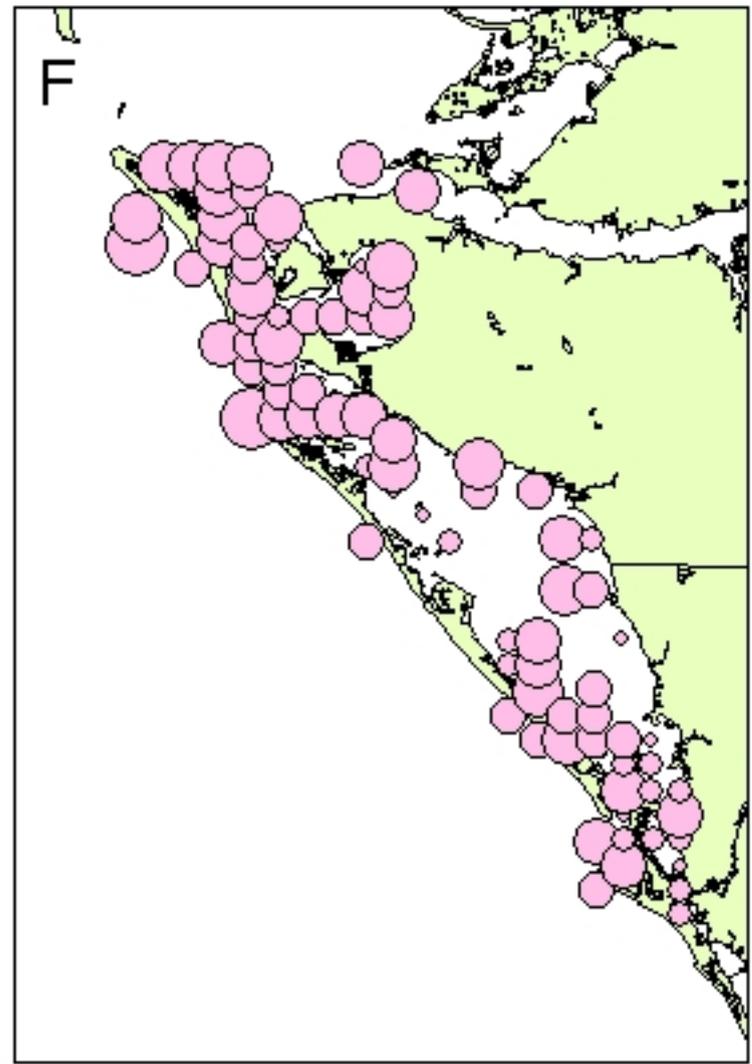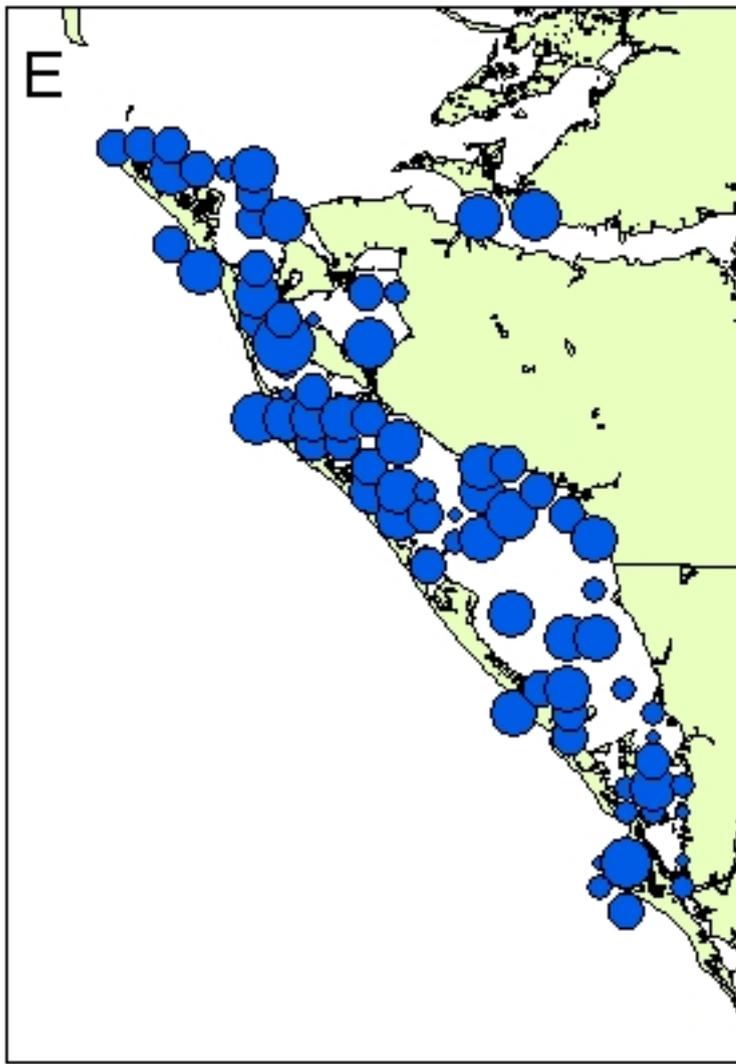
Figure 13, Con't. Distributions (sightings per unit effort, SPUE) of adult males and adult females in falls (E, males; F, females) and in springs (G, males; H, females). Scale and legend in C apply to all maps; larger circles represent higher densities.

Across Class-Within Season Comparisons

Overall, when sightings of adult males and adult females in all seasons were compared, there was a significant difference* between their distributions. While their distributions did not differ significantly within any season, distribution patterns were most similar in winter, and more different in spring and summer (Figure 13). Adult females appeared to be clustered at the northern and southern regions of the study area. Adult males tended to range throughout the region in all seasons, though their distribution within the center of Sarasota Bay was less dense in the winter than in all other seasons (compare Figure 13 C to A, E, and G).

Adult females were divided into four categories for comparisons (Table 3). When sightings in all seasons were combined, the distribution of female dolphins with calves differed significantly from those without calves. Seasonal comparisons revealed that these differences were significant in spring*. Though the distributions of these two classes did not differ significantly in any other season, they were less similar in summer and fall, and most similar in winter (Table 5, Figure 14). When adult females with calves were divided into those with yoys and those with calves between one and three years of age, there was a significant difference between their distributions in winter*, but not in summer, fall, or spring (Table 5, Figure 15). This pattern is different from that observed in within-season comparisons across all other dolphin classes, as their distributions differed significantly in winter, and were similar in all other seasons. Distribution patterns of female dolphins with calves between one and three years of age in summer and winter were similar to those of all adult female dolphins. Densities of females with
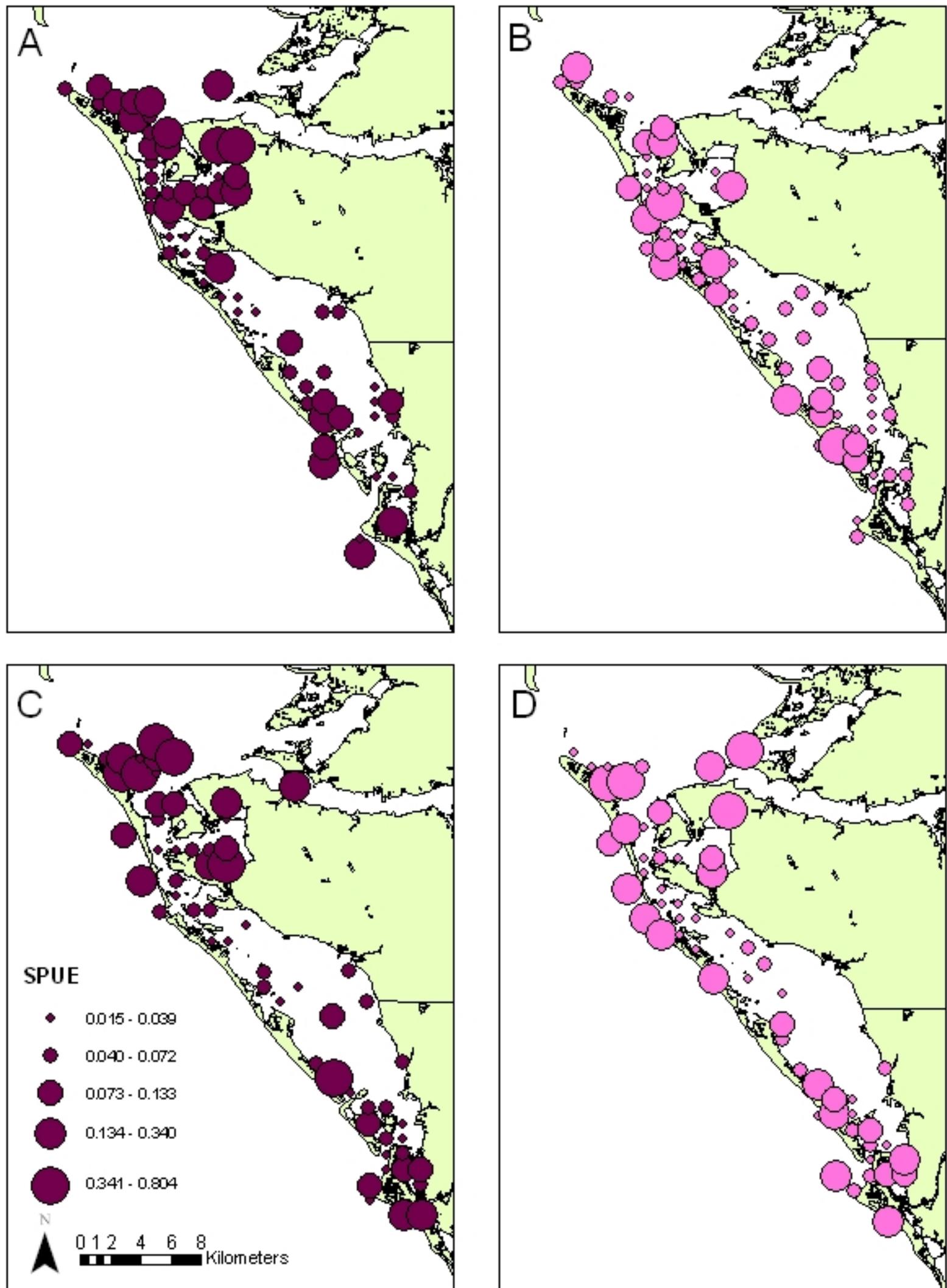
Figure 14. Distributions (sightings per unit effort, SPUE) of adult females with calves (A, summers; C, winters) and those without calves (B, summers; D, winters). Scale and legend in C apply to all maps; larger circles represent higher densities.
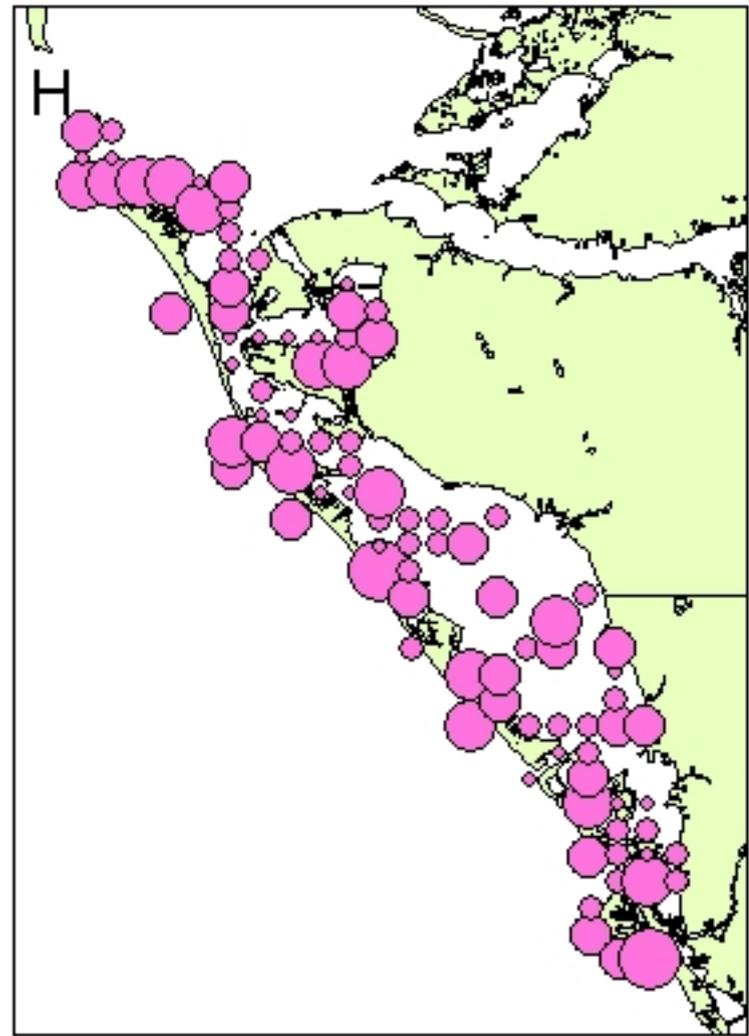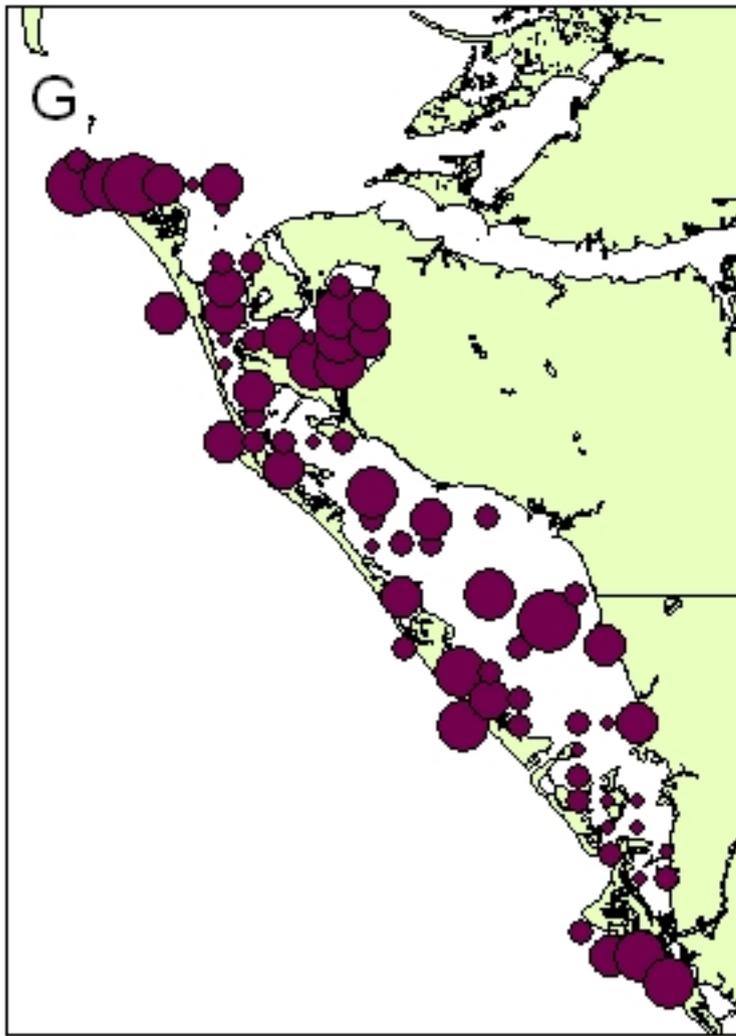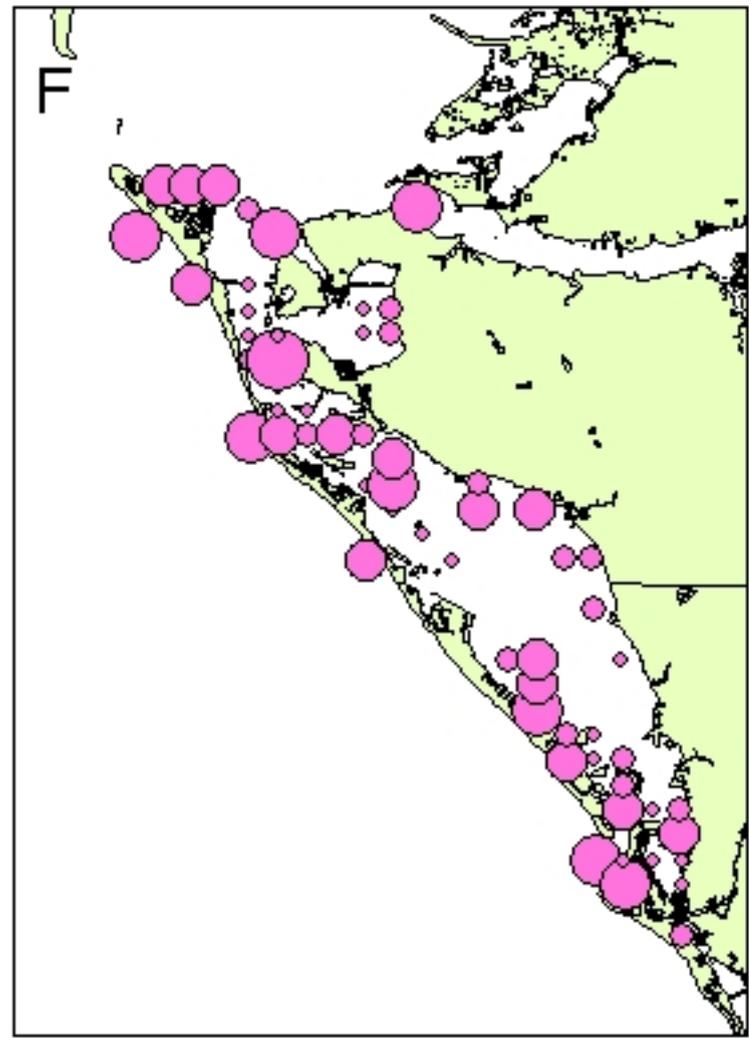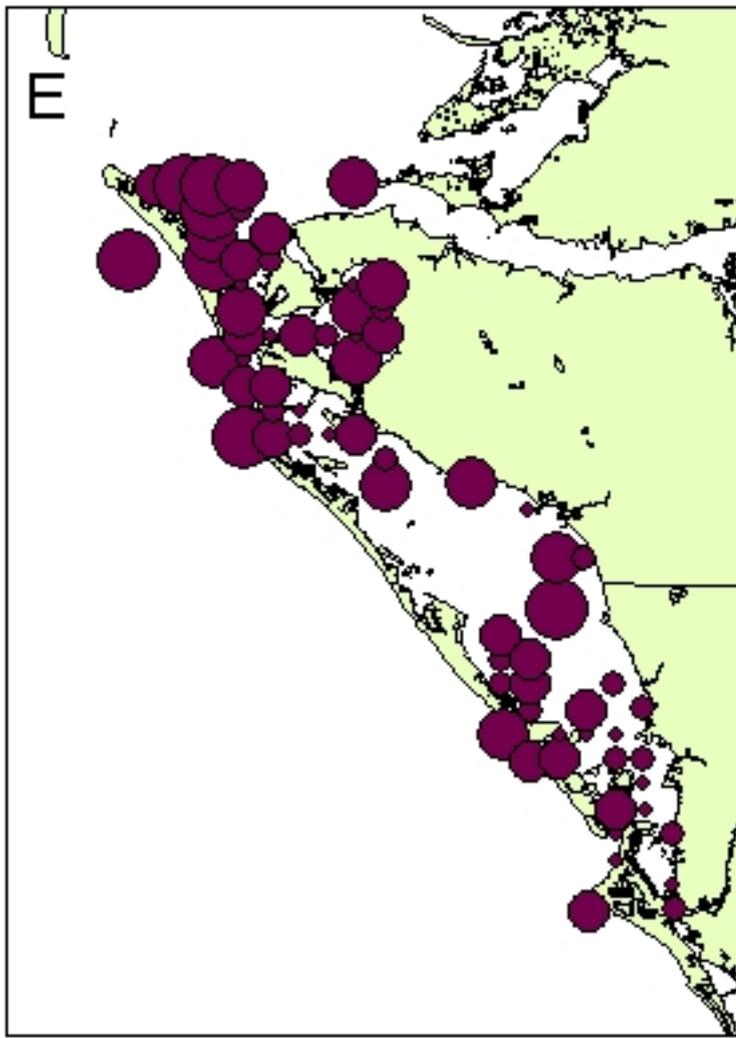
Figure 14, Con't. Distributions (sightings per unit effort, SPUE) of adult females with calves (E, fall; G, spring) and adult females without calves (F, fall; H, spring). Scale and legend in C apply to all maps; larger circles represent higher dolphin densities.
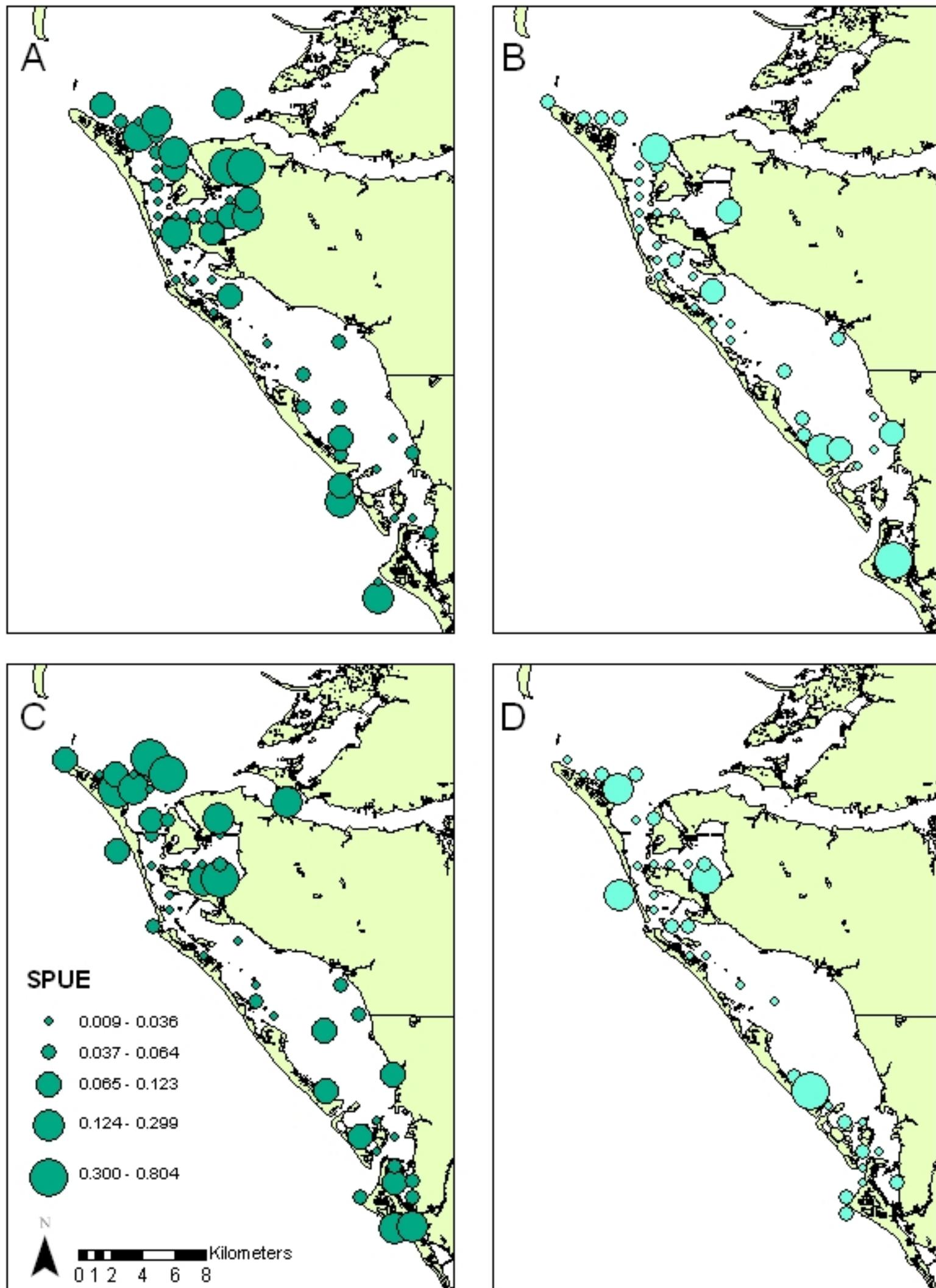
Figure 15. Distributions (sightings per unit effort, SPUE) of adult females with calves that are between one and three years of age (A, summer; C, winter) and adult females with young of the year (B, summer; D, winter). Scale and legend in C apply to all maps; larger circles represent higher densities.
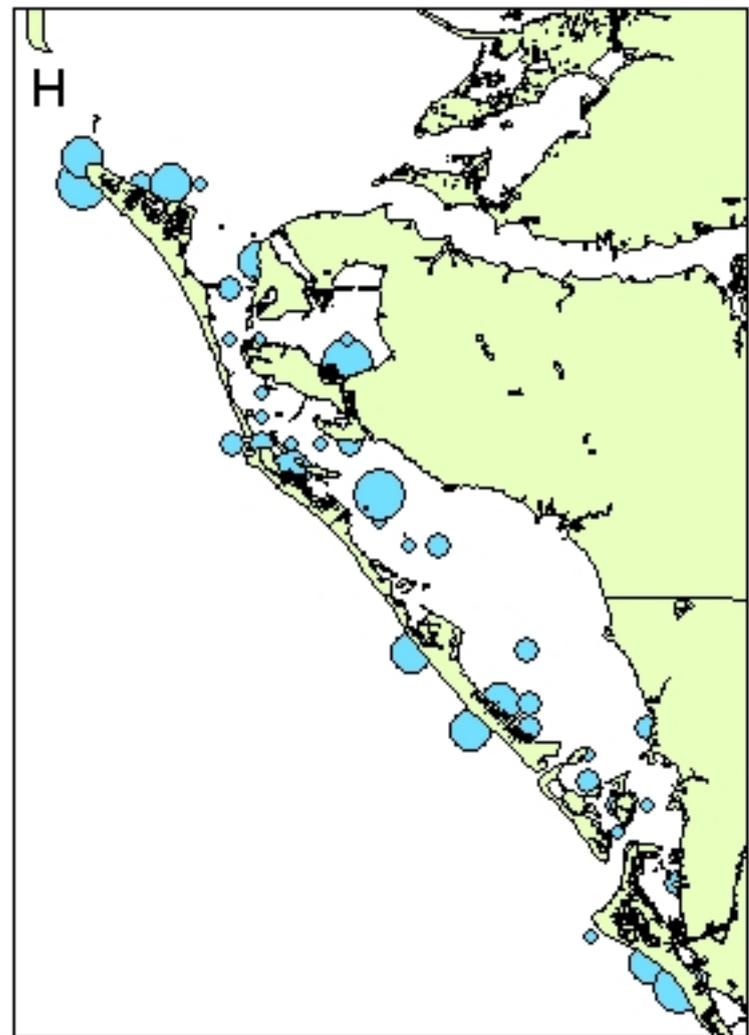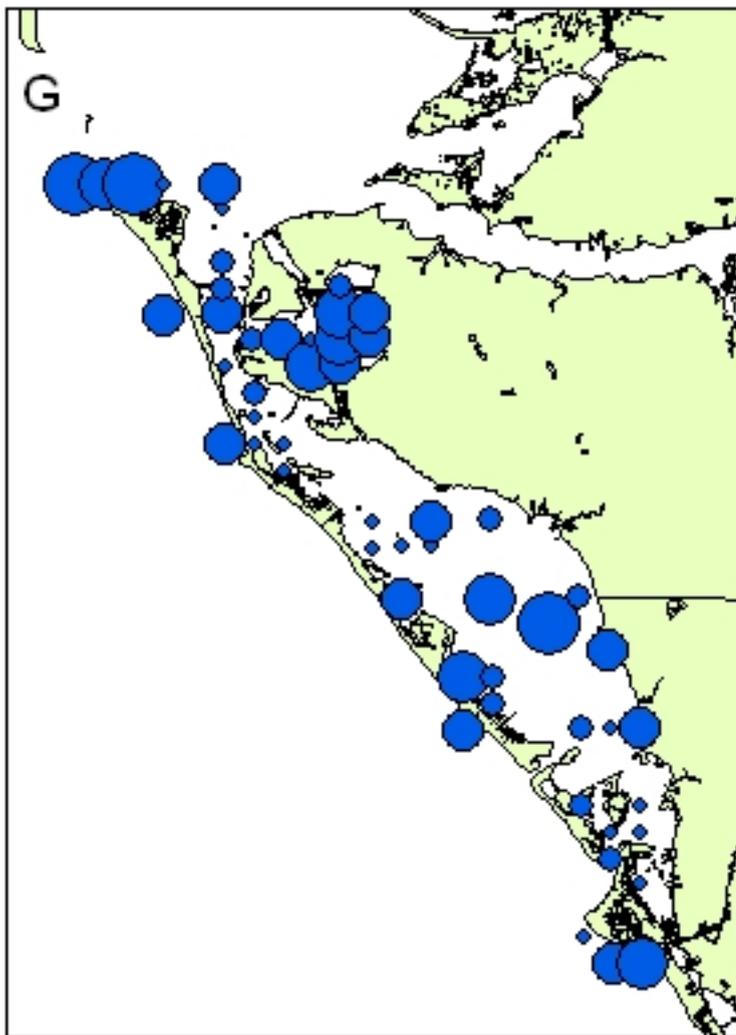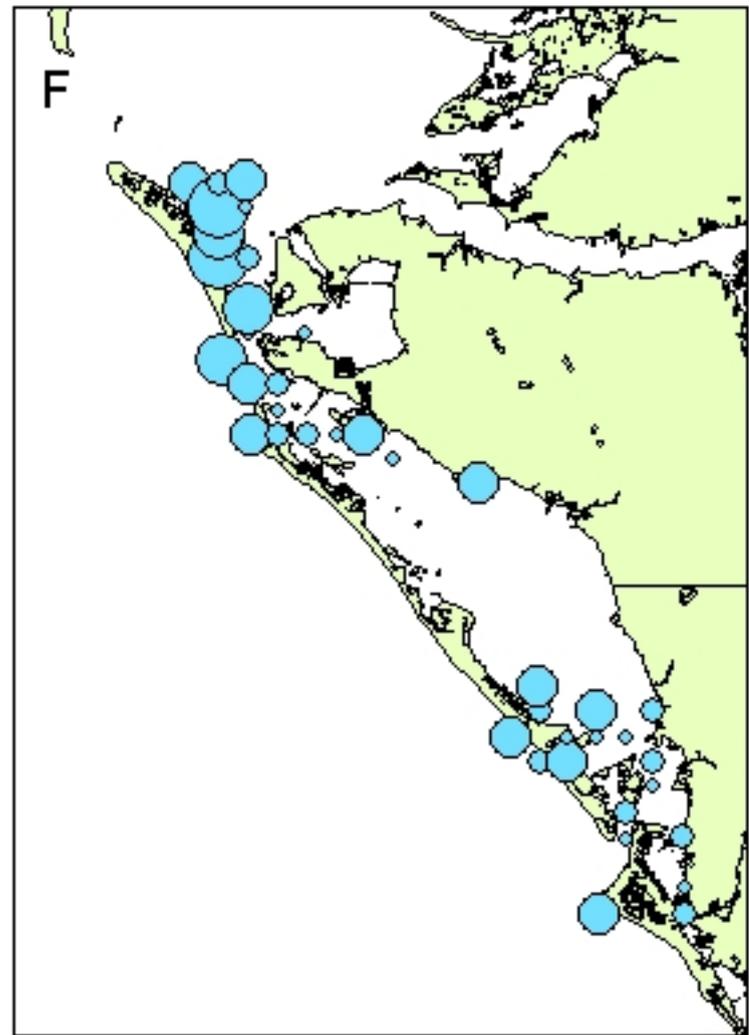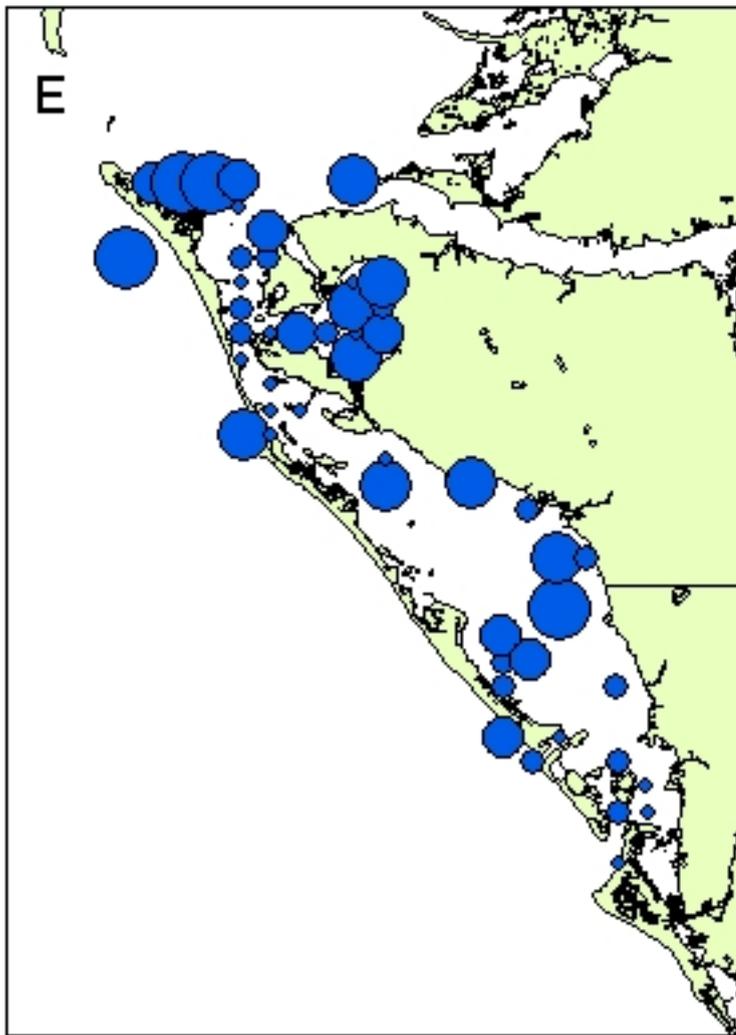
Figure 15, Con't. Distributions (sightings per unit effort, SPUE) of adult females with calves that are not yearlings (E, fall; G, spring) and adult females with yoys (F, fall; H, spring). Scale and legend in C apply to all maps; larger circles represent higher densities.

yoys were lower in both seasons, and their distribution appeared more homogeneous across the study area.

The distributions of adult males and subadult males were most disparate of all dolphin classes. When data from all seasons were combined, the distributions of adult males were significantly different from those of subadult males. Seasonal comparisons revealed that significant differences were manifested in summer, fall, and spring, but not in winter. Adult males were broadly distributed throughout the study area across all seasons; however, the distributions of subadult males in the summer, fall, and spring were biased towards the northern section of the study area and tended to be similar to that of adult females (Figure 16).

To investigate whether or not particular dolphin classes were consistently located in relatively warmer water in winter or cooler water in summer, dolphins were classified into the categories described above, and the water temperatures in which these classes were observed were compared in each season. Summer was the only season within which there were significant differences among dolphin classes. In summer, adult males were found in water temperatures that were, on average, 0.2°C cooler than subadult males (p=0.0079), adult females without calves (p=0.0219), adult females with calves between one and three years of age (p=0.0006), and adult females with yoys (p=0.0017). No other significant differences were found among any other dolphin classes in any season.

DISCUSSION

The goal of this study was to investigate physiological and behavioral mechanisms by which resident dolphins in the Sarasota Bay region, as homeotherms, may control the temperature differential between their body and the environment. The
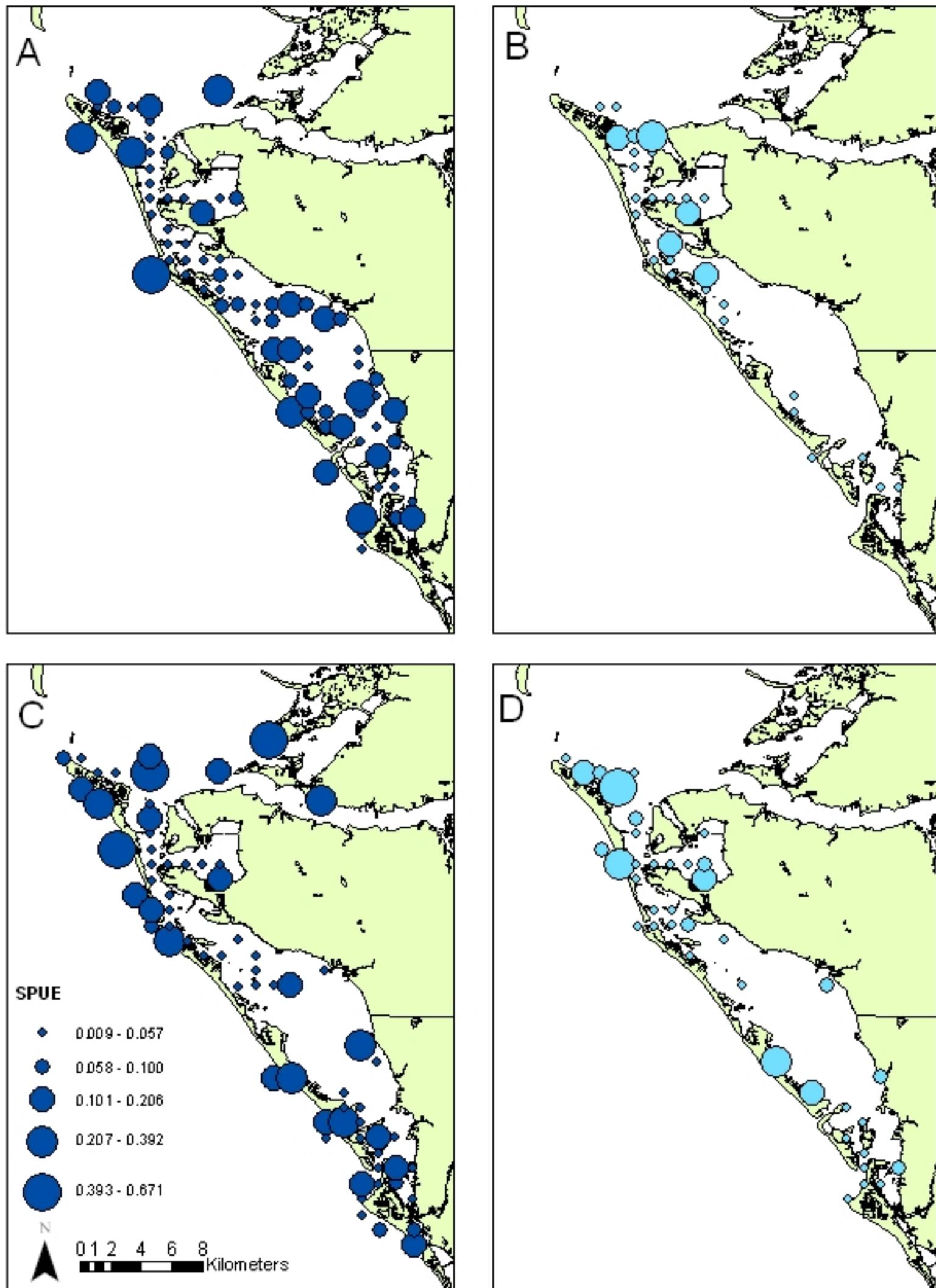
Figure 16. Distributions (sightings per unit effort, SPUE) of adult males (A, summer; C, winter) and subadult males (B, summer; D, winter). Scale and legend in C apply to all maps; larger circles represent higher densities.
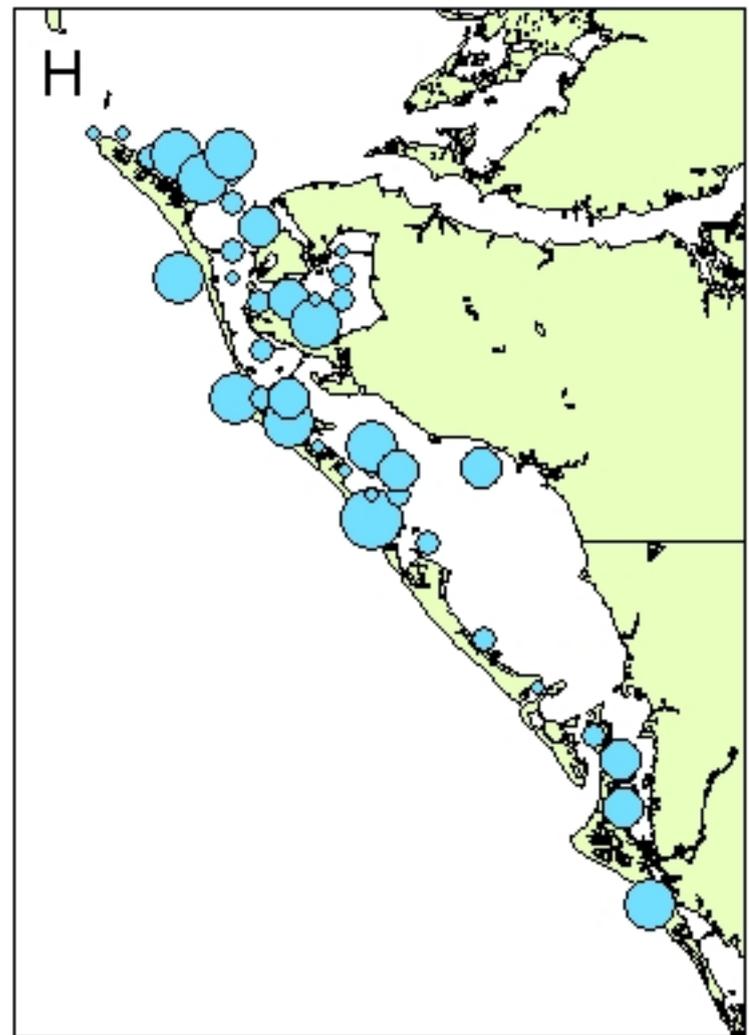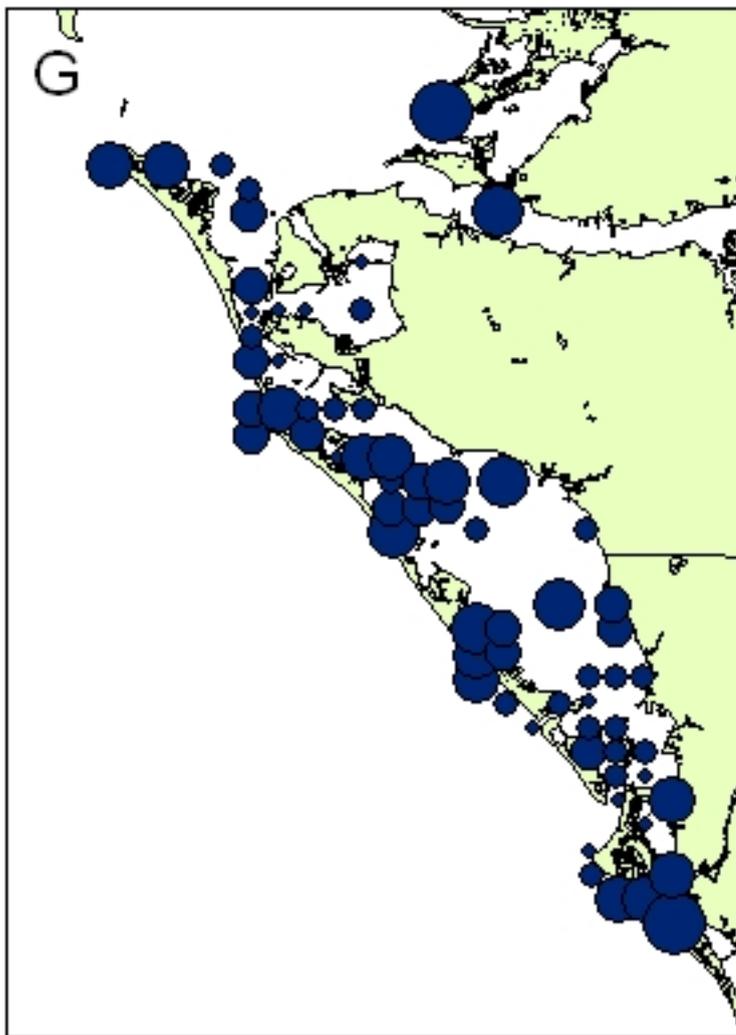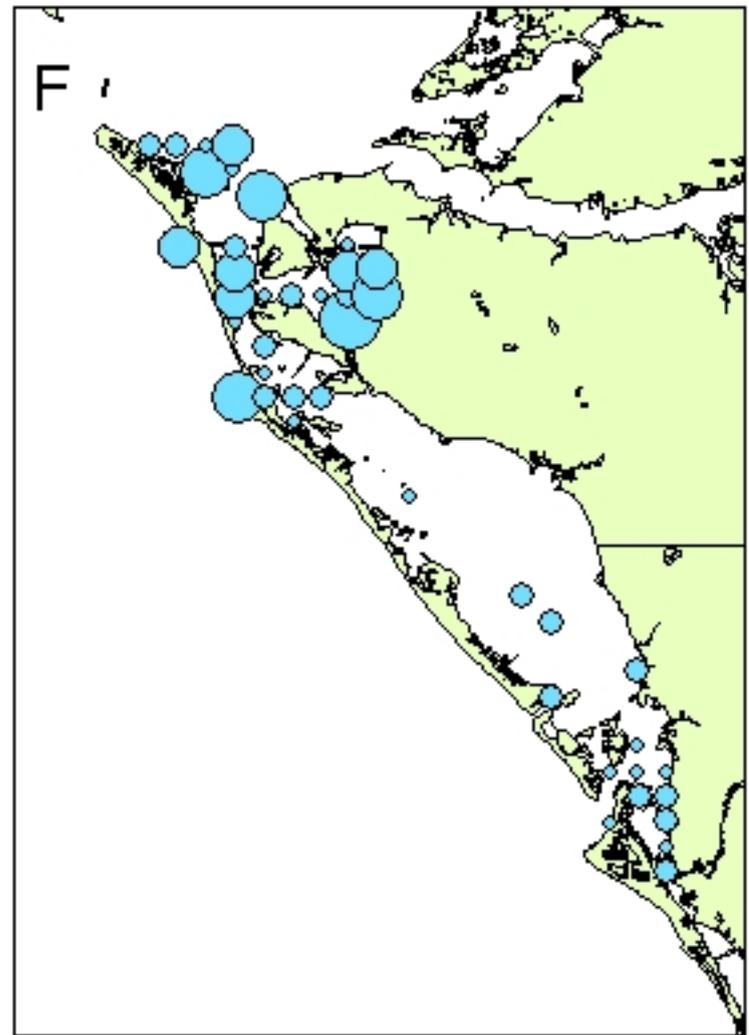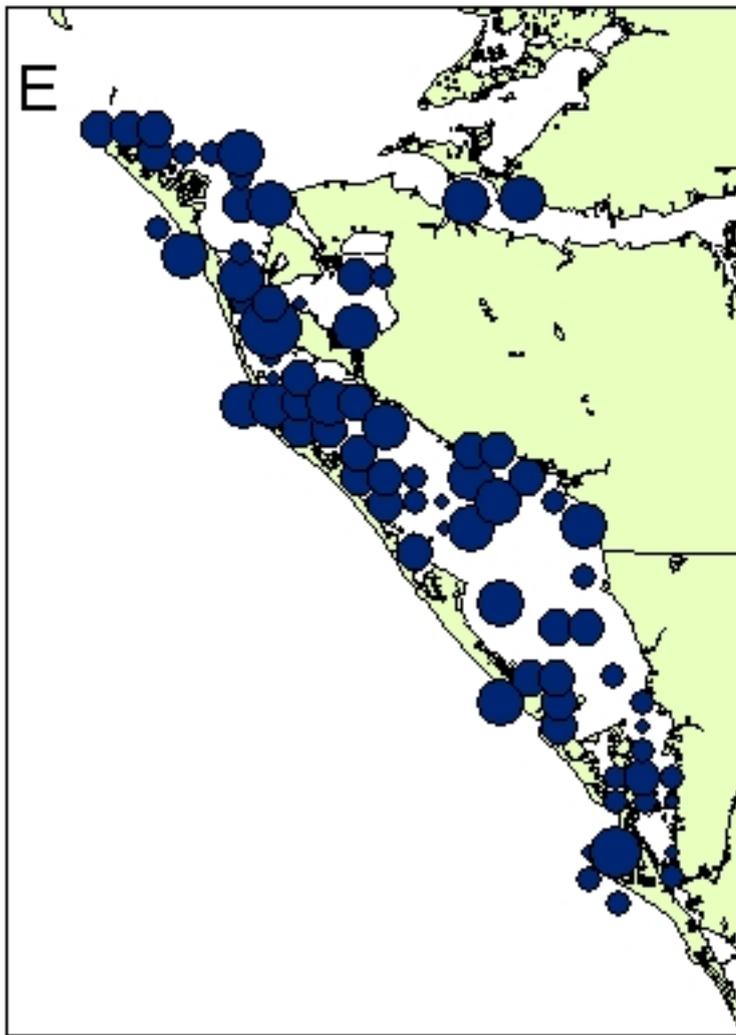
Figure 16, Con't. Distributions (sighting per unit effort, SPUE) of adult males (E, spring; G, fall) and subadult males (F, spring; H, fall). Scale and legend in C apply to all maps; larger circles represent higher densities.

results of this study indicate that dorsal fin surface temperature, a physiological measure, was maintained within approximately one degree of water temperature, across the annual range of 22°C. Independent measurements of water temperature showed that, although all sites varied similarly across seasons, differences in the amplitude of short-term cyclical changes across sites could create regional heterogeneity (*i.e*. microclimates).

Spatial distribution patterns of dolphins, a behavioral measure, tended to differ among dolphin classes, which were classified by age, sex and reproductive status. Within a season, comparisons demonstrated that adult males were the only class found in significantly cooler water temperatures, and this was only observed in summer. In all seasons except winter, dolphin distribution patterns tended to be class-specific. In winter, apparent differences in the distributions of different dolphin classes were less evident. These results are discussed in more detail below.

Physiological Response to Seasonal Changes in Water Temperature

The use of infrared thermography permitted the measurement of dorsal fin surface temperatures of a resident community of wild, free-swimming dolphins across the broad, annual range of water temperatures they experience. The temperature differential values (ΔT_{dfin-a}) measured in this study were small (mean=0.9°C) and relatively consistent across seasons. Although there existed significant differences in mean ΔT_{dfin-a} across some field seasons, there was no clear seasonal pattern. Rather, interannual variation in ΔT_{dfin-a} was as great as interseasonal variation (Figure 7).

Thus, the temperature of the dorsal fin surface is seasonally dynamic and is positively correlated with water temperature. This result suggests that the gradient through the dolphin body from the core to the body-water interface must change

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dramatically across seasons. Figure 17 illustrates this gradient by comparing ΔT_{dfin-a} (described above) to the calculated ΔT between the body core, which remains at approximately 37°C across all seasons (Pabst *et al.*, unpublished data), and the dorsal fin surface ($\Delta T_{core-dfin}$). The temperature gradient through the body, between the dorsal fin-water interface and the core, can be as large as 23°C in winter, but is constrained to 4-7°C in summer, as T_a approaches T_{core}.

Maintenance of a large gradient between the body core and the dorsal fin surface in winter suggests that these dolphins rely on changes in insulation to regulate body surface temperature across seasons. There are two forms of insulation in these marine homeotherms: integumentary and vascular. In winter, enhanced integumentary insulation for dolphins in the Sarasota Bay region is manifested as increases in blubber lipid content and thickness (Wells 1993b, Worthy *et al.* 1990, Worthy 1991). Increases in vascular insulation are effected through heat-conserving, countercurrent heat exchangers in the dorsal fin, flukes and flippers (Scholander and Schevill 1955).

These insulative adjustments, which may permit dolphins to maintain the observed constant temperature differential across seasons, influence overall heat loss by altering the other two variables in the heat loss equation, conductance (C) and surface area (SA) (Equation 1). In the winter, increases in the quality and quantity of blubber will reduce the conductance of the integument and, thus, may reduce heat loss. This insulative adjustment likely permits dolphins to maintain the relatively large gradient between the body core and the body surface. The dorsal fin and other appendages lack this insulative blubber; thus, insulation is effected through changes in the pattern of blood
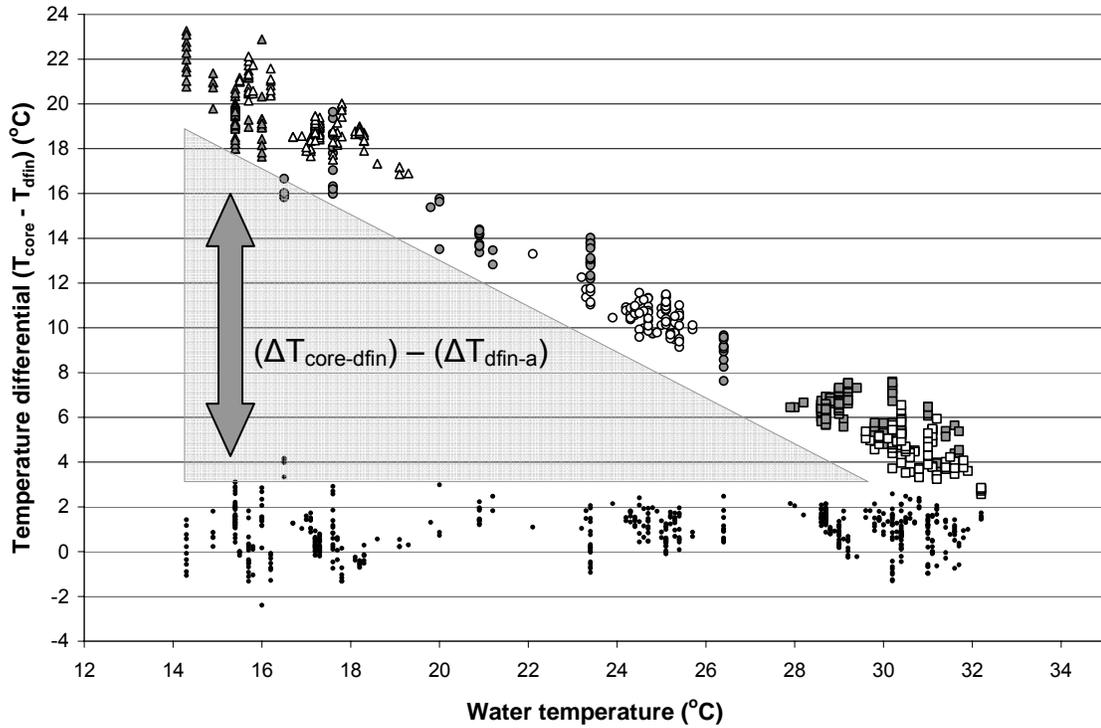
Figure 17. Comparison of temperature differentials between body core temperature and the dorsal fin (T_{core} - T_{dfin}) and the dorsal fin and the water (T_{dfin} - T_a). Core temperatures, which are stable across seasons (Pabst *et al*. unpub. data), were assumed to be 37°C (Pabst *et al*. 1995, Rommel *et al*. 1994). Symbols represent each field season (◉ Nov. 02; ○ Nov. 03; ◼ Jun. 03; ☐ Jun. 04; ▲ Feb. 03; △ Feb.04; • ΔT_{dfin-a} from Figure 5).

flow. Use of the countercurrent heat exchanger in the dorsal fin reduces the effective

surface area, SA, across which heat loss can occur by minimizing the exposure of warm

blood to the skin-water interface. Thus, by seasonally dynamic changes in insulation, the

temperature differential between the dorsal fin surface and the ambient water is

maintained at a small and steady one degree, and heat loss may be subsequently reduced.

Vascular adjustments in insulation, relative to those of the blubber, can occur over

a short time scale. Thus, vascular insulation is a mechanism by which a small

temperature differential across the dorsal fin surface can be maintained during normal

activity. But this dynamic thermal window can rapidly be used to selectively dissipate

body heat when necessary, such as when activity is elevated. Results of previous studies

have demonstrated that this is one circumstance when temperature differentials are often

larger than one degree (Pabst *et al.* 2002).

Thus, this study also demonstrated that the temperature differential between the

dorsal fin and the ambient environment was not invariant. For example, the ΔT_{dfin-a} of

individual dolphins within a short time period (*i.e.,* throughout a day) could vary by more

than one degree. This pattern was observed in FB11 in February 2003, where ΔT_{dfin-a}

ranged from 1.5 to 2.9°C over a period of approximately one hour (Figure 6). The

previous level of activity, feeding occurrences, and reproductive status of the animal

could all influence its thermal status, which is reflected in ΔT. The largest observed

temperature differentials of free-swimming dolphins in the present study were measured

in November 2002, after a precipitous, 10°C decrease in water temperature that occurred

over a period of three to four days. Independent, continuous measurements of water

temperature from 2003-2004 (described above) illustrate that such rapid declines in water

temperature are characteristic of the transitional fall season in this area. The relatively

large ΔT_{dfin-a} values observed after this change suggest that dolphins may increase

metabolic heat production in response to rapidly cooling ambient temperatures. Thus,

there are some circumstances when temperature differentials are elevated in wild, free-

swimming dolphins, but on average, they are approximately one degree.

The relatively consistent temperature differential between the dorsal fin surface

and the ambient water that was found in this study is similar to that measured for

bottlenose dolphin dorsal fins over much narrower ranges of environmental temperature.

Noren *et al.* (1999) and Meagher *et al.* (2002), using heat flux discs, reported that

bottlenose dolphin dorsal fin surface temperatures remained within one degree of the

water, though they were measured across relatively stenothermal conditions (T_a: 28-

32°C) (Figure 18).

Surface temperatures of other delphinid species have also been investigated, and

results of these studies were similar to those found in bottlenose dolphins (Figure 18).

Appendage skin surface temperatures of three captive Hawaiian spinner dolphins

(*Stenella longirostris*) were within approximately 1°C of the water, which was

maintained at a constant 26°C (Hampton and Whittow 1976). Infrared thermography of

spotted dolphins (*Stenella attenuata*) in the Eastern Tropical Pacific (water temperature:

27.6 - 29.8°C) demonstrated that skin surface temperatures were positively correlated

with water temperature (Pabst *et al.* 2002).

The largest temperature range across which dorsal fin surface temperatures have

been previously measured was reported for a restrained, captive Hawaiian spinner

dolphin (McGinnis *et al.* 1972) (Figure 18). In this study, a ten degree decrease in water
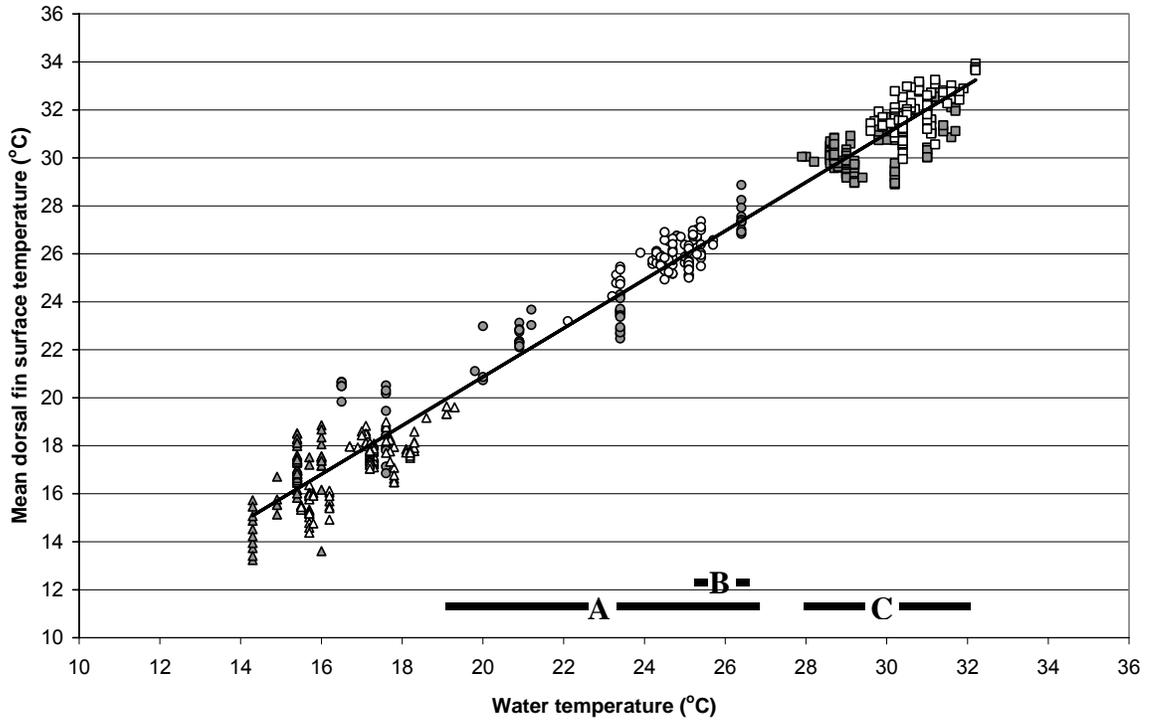
Figure 18. Ranges of water temperatures in which dorsal fin surface temperatures have been previously investigated compared to those in the present study (data from Figure 4) (A: McGinnis *et al.* 1972; B: Hampton and Whittow 1976; C: Meagher *et al.* 2002, Noren *et al.* 1999, Pabst *et al.* 2002). Symbols represent each field season with dolphins in Sarasota Bay (● Nov. 02;○ Nov. 03;■ Jun. 03; □ Jun. 04;▲ Feb. 03; △ Feb.04).

temperature (27.5-17.5°C) was imposed over a brief (90 min.) period of time. The short-term pattern was similar to that observed seasonally in the present study, in that the temperature of the dorsal fin tended to remain within one to two degrees of the water temperature. However, it is unlikely that the conditions investigated by McGinnis *et al.* (1972) are comparable to those experienced by a wild dolphin that were measured across seasons in the present study.

Studies of pinnipeds have demonstrated that temperature differentials between the body surface and the environment are smaller in water than in air (Irving and Hart 1957). For example, Irving and Hart (1957) found that in 0°C water, harbor seals (*Phoca vitulina*) maintained temperature differentials of 1 to 2°C. In contrast, in air, temperature differentials of as high as 24°C in pinnipeds have been reported (T_{air} = 5-12°C) (Mauck *et al.* 2003). Similarly, in muskrat, temperature differentials between most body surfaces and the environment are smaller in water (1°C or less) than in air (approx. 2-7°C) (T_{air} and T_{water} = 10-30°C) (Fish 1979). Thus, the body surfaces of both fully and semi-aquatic mammals tend to maintain small, approximately 1°C, temperature differentials in water.

This constancy in temperature differentials found in fully and semi-aquatic mammals is much more pronounced than in terrestrial homeotherms, which are capable of achieving body surface temperatures much greater than that of their environment.

Previous studies using infrared thermography on woodchucks, barn owls, foxes, and elephants, have determined that these terrestrial homeotherms can achieve temperature differentials in excess of 20°C (Klir and Heath 1992, McCafferty *et al.* 1998, Phillips and Heath 2001, Williams 1990). The body regions of terrestrial mammals that

are highest in surface temperature are often thinly-insulated and/or associated with sensory perception.

In contrast to terrestrial mammals, the consistency of ΔT_{dfin-a} in bottlenose dolphins may be due to the physical properties of the fluid environment in which they live. Water is a much more thermally conductive environment than air; thus, any heat delivered to the dorsal fin surface will be rapidly lost to the surrounding water. Meagher *et al.* (2002) measured higher temperature differentials on the dorsal fins of temporarily-restrained, wild dolphins in warm air than in warm water and attributed this difference to the different conductivities of these two media. The effect of water as a heat sink is more likely to be observed at the thermal windows because these appendages are thin, uninsulated, and are primarily composed of non-heat-generating connective tissue. This is in contrast to the rest of the body, which is larger, insulated, and primarily composed of metabolically active tissues. Thus, it is possible that the conductive properties of the aquatic environment are responsible for the overall conformity of dorsal fin surface temperatures to that of the water.

Behavioral Responses to Seasonal Changes in Water Temperature

Across seasons, dolphin distribution patterns appeared to differ based on age, sex, and reproductive class. Adult females, although seen throughout the study area, were concentrated in the northernmost and southernmost regions of the study area. Results of this and previous studies suggest that adult females prefer these particular regions regardless of season. Wells *et al.* (1980) also determined that most female dolphins were concentrated in the northern region, and this trend was especially apparent for females with calves. Wells *et al.* (1987) identified two distinct clusters of females located in the

Anna Maria Sound and Palma Sola Bay regions. This study also demonstrated that females are concentrated in these regions.

In the present study, subadult males tended to be distributed similarly to adult females. Though only significant for subadult males, distributions of both these classes tended to differ from that of adult males in all seasons but winter. Like adult females, subadult males were more concentrated in the extreme northern section of the region, but adult males tended to range broadly throughout the region. Wells *et al.* (1987) also found that the ranges of subadult males and females overlapped, and in 55% of subadult male sightings, adult females were also observed. Scott *et al.* (1990) reported that adult males traveled across a greater area than adult females, which were more often found in inshore, vegetated habitats.

Thus, across all seasons, distribution patterns were specific to particular dolphin classes. Though these differences were not always significant within a season, distribution patterns across dolphin classes tended to differ more within spring, summer and fall. Dolphin classes were most similar in their distributions during winter. This pattern was particularly evident when the distributions of adult males and subadult males were compared within each season, as they differed significantly in all seasons but winter. Though not significant, the distribution patterns of adult males and adult females were similar to the trend described for adult males and subadult males: they were dissimilar in spring, summer and fall, but not winter. This is consistent with the findings of Waples (1995), who suggested, from focal follows of individual dolphins, differences between the distributions of adult males and adult females within both summer and

winter seasons. The present study found that this pattern was also observed when adult females with calves were compared to those without calves.

Independent measurements of water temperature throughout the Sarasota Bay region showed that overall patterns of temperature change were consistent throughout the study area. Late in the fall and spring seasons, water temperatures were characterized by rapid, precipitous change and varied little between measurement sites. However, in summer and winter, when water temperatures plateaued, short-term, cyclical variation in water temperature was apparent (Figure 10). Water temperatures during summer were least variable, and oscillated within 2°C, but those in winter could vary by up to 6°C over a period of 10-11 days. The amplitudes of these short-term oscillations displayed site-to-site differences, with shallow, inshore sites tending to vary the most. Small differences existed between measurement sites in mean water temperatures and in the variability of short-term oscillations (Tables 2 and 4, Figures 8 and 10).

Thus, if water temperature is an important determinant of dolphin distribution within a season, there exists some heterogeneity within the environment from which dolphins may choose. Interestingly, in only one class of dolphins, and in only one season, was there a statistically significant relationship between spatial distribution and water temperature. This difference was manifested in adult males during the summer, as sightings of these dolphins occurred in significantly cooler waters than all other dolphin classes. Though the difference between mean water temperatures where adult males were observed and those where other dolphin classes were observed was small (0.2°C), it may have important implications for the heat balance of adult males.

Adult males are largest in body size of all bottlenose dolphins in the Sarasota study area (Read *et al.* 1993, Tolley *et al.* 1995) and, thus, have the smallest surface area to volume ratios across which body heat may be dissipated (although the flukes may be proportionally larger in males than females; Tolley *et al*. 1995) (Table 6). Considerable differences in body size and mass between adult male and female dolphins are more likely due to differences in girth than length (Table 6) (Read *et al.* 1993, Wells *et al*. 1999). Heat loss may be particularly challenging for adult males in summer, as water temperature approaches core temperature (Figure 18). Thus, for adult males, exposure to water temperatures that are, on average, 0.2°C cooler than other areas may be effective means of increasing heat dissipation.

The following calculations were made to estimate the additional heat adult males could dissipate with an additional ΔT_{dfin-a} of 0.2°C. Heat flux data collected from the dorsal fins of free-swimming dolphins using a thermal TracPac (Westgate *et al*., 2001) demonstrated that on average, 85W/m^2 of heat is lost per degree Celsius of temperature differential between the body and the water (Westgate, pers. comm.). Meagher *et al*. (2005) reported that heat flux values measured on the body flank and peduncle of temporarily-restrained, wild bottlenose dolphins in Sarasota were similar to those measured at the thermal windows. Thus, if it is assumed that heat flux rates are similar across the body, an adult male dolphin with a 2.5m^2 surface area experiencing a 0.2°C larger temperature differential between the body and the water, will dissipate an additional 42W of heat:

$$\frac{85 \text{ W}}{\text{m}^2 \, °\text{C}} * 2.5 \text{ m}^2 * 0.2°\text{C} = 42 \text{ W}$$

Table 6. Comparison of morphometric measurements of adult male and adult female bottlenose dolphins. Values from Read *et al.* (1993) are the mean of two estimates, based upon cross-sectional and jack-knife Gompertz growth models (see their Table II). Surface area and volume were estimated, excluding the head and appendages, by modeling the body trunk (ear to anus) as a cylinder and the tailstock (anus to fluke insertion) as a truncated cone.

*Calculated using data from Read *et al.* (1993), Tolley *et al.* (1995), UNCW Marine Mammal Stranding Program; methods from Dunkin *et al.* (2005), Gales and Burton (1987).

	Adult males	Adult females	Reference
Mass (kg)	261.9	192.4	Read *et al.* 1993
Standard Length	264.9	249.7	Read *et al.* 1993
(rostrum to fluke notch) (cm)	256.6	249.7	Tolley *et al.* 1995
Girth (maximum) (cm)	154.3	140.2	Read *et al.* 1993
	152.2	141.9	Tolley *et al.* 1995
Surface area (m^2)	2.47	2.04	calculated*
Volume (m^3)	0.25	0.19	calculated*
Surface area / volume	9.9	10.7	calculated*

An adult male bottlenose dolphin could, thus, dissipate an additional 3.6MJ of heat per day, relative to other Sarasota dolphins, by selecting water temperatures that are, on average, 0.2°C cooler:

$$42 \text{ W} = \frac{42 \text{ J}}{\text{s}} * \frac{60 \text{ s}}{\text{min.}} * \frac{60 \text{ min.}}{1 \text{ h}} * \frac{24 \text{ h}}{1 \text{ d}} = \frac{3.6\text{MJ}}{\text{d}}$$

To interpret this 3.6MJ of heat in the context of total energy expenditure, the mass-specific metabolic rate for bottlenose dolphins (in $l\ O_2\ h^{-1}\ kg^{-1}$) was converted into comparable units, MJ per day. A mass-specific resting metabolic rate of $0.392\ l\ O_2\ h^{-1}\ kg^{-1}$ (Williams *et al.* 2001) was converted from $l\ O_2$ to kJ using the conversion factors shown below. This number was multiplied by the body mass of an adult male dolphin, which was estimated at 262kg (Read *et al.* 1993), and by 24h to obtain the amount of energy expended per day. Thus, the total daily energy expenditure can be estimated at 49.5MJ for an adult male bottlenose dolphin:

$$\frac{0.392\ l\ O_2}{h\ kg} * \frac{4.8\text{kcal}}{l\ O_2} * \frac{4.184\text{kJ}}{\text{kcal}} * 262 \text{ kg} * \frac{24h}{d} = \frac{49.5\text{MJ}}{d}$$

The additional 3.6MJ of heat that an adult male dolphin could potentially dissipate per day with a temperature differential increase of 0.2°C represents 7.3% of this total daily energy expenditure.

The result that adult males were observed in relatively cooler water temperatures than other dolphin classes in summer suggests that the stability of water temperatures during this season provides a cue to which these dolphins may respond. The importance of local differences in water temperature may be greatest in summer, because water temperatures approach core temperature and constrain ΔT_{dfin-a} (Figure 18). This

restriction of ΔT_{dfin-a} in summer may have particularly important implications for heat loss by adult males, because of their large body size and disadvantageous surface area to volume ratio. In contrast, in winter, there exists a large gradient between core and water temperatures, and, thus, a greater potential for larger ΔT_{dfin-a} values to be achieved. Thus, local differences in water temperatures may be less likely to influence dolphin distribution, in particular, that of adult males, during winter. In addition, differences in distribution may not have been observed in winter because of the relatively large short-term oscillations in temperatures compared to summer. Adult males were the only class found in significantly different water temperatures within a season, relative to other dolphin classes. These results suggest that factors other than water temperature influence the distribution of most dolphin classes in the Sarasota Bay region.

Previous studies of the Sarasota Bay and other regions have suggested that dolphin distribution is driven by biotic factors, including prey movements, predator abundance, and reproductive requirements (*e.g.*, Barros and Wells 1998, Heithaus and Dill 2002, Irvine *et al.* 1981, Mann *et al.* 2000, Waples 1995, Wells *et al.* 1980, Wells 1990, Wells 1993a). Within the Sarasota Bay region, studies suggest that dolphins are distributed in accordance with seasonal changes in prey distribution (Barros and Wells 1998, Irvine *et al.* 1981, Wells *et al.* 1980, Wells 1990, Wells 1993a). Irvine *et al.* (1981) and Barros and Wells (1998) suggested that dolphins follow their primary prey, including pinfish, pigfish and mullet, from shallow, inshore waters in summer to passes and the nearshore Gulf of Mexico in winter. The results of this study lend support to this suggested pattern, but it was not designed to specifically test this hypothesis. The results

of this study also indicate that dolphins are not found exclusively in either of these habitats in any season.

Thus, the present study may indicate that Sarasota dolphins feed opportunistically across all seasons, and their distribution does not simply follow hypothesized prey movements. Resident dolphins most often forage on individual prey items in relatively small, non-cooperative groups (Barros and Wells 1998, Wells *et al.* 1987). The life histories of primary dolphin prey species seem to differ, and how dolphin foraging may change in response to seasonal prey movements is poorly understood. Pinfish are associated with shallow seagrass beds in the inshore waters of Sarasota Bay for most of their lives, though small-scale changes in distribution have been documented in one study (reviewed in Barros and Wells 1998, Waples 1995). In Sarasota Bay, dolphins most often forage on individual prey items in relatively small, non-cooperative groups (Barros and Wells 1998). In reviewing mullet life history characteristics, these authors noted that mullet form large schools when they migrate to the Gulf of Mexico to spawn, aggregations that would not characteristically be utilized by foraging dolphins. Detailed information on seasonal changes in prey abundance and distribution, as well as up-to-date habitat maps are needed to more fully understand the spatial and temporal relationships between dolphins and their prey.

Presence of sharks is another biotic factor that influences dolphin distribution (*e.g.*, Heithaus and Dill 2002, Wells 1993a, Wells *et al.* 1980). In the Sarasota Bay region, shark abundance is highest in spring and summer (Wells 1993a, Wells *et al.* 1980). Dolphins may seek inshore waters for protection, because large bull sharks are more abundant offshore and because the shallow nature of these areas facilitates shark

detection (Wells 1993a, Wells *et al.* 1980). Newborn calves may be particularly

susceptible to predation, and Wells (1993a) suggested that female dolphins with calves

prefer shallow waters for the protection they offer.

In addition to protection, inshore waters likely provide abundant food resources

and calm conditions in the spring and summer, which make these areas ideal for females

rearing calves (Waples 1995, Wells 1993a). In the Sarasota Bay region, such "nursery

areas," have been shown to support a greater number of female dolphins with calves in

the spring and summer seasons, but not in winter (Wells 1993a). Distribution analyses in

the present study showed that these regions supported higher densities of females with

calves in the spring, summer and fall seasons, in comparison to females without calves.

Waples (1995) found that females spent a greater proportion of time feeding in the

summer than males, which supports the notion that food availability is higher in these

regions.

Temperature may affect the seasonality of reproduction in dolphins; thus, another

characteristic of nursery areas may be that they are relatively warmer than other regions.

Mann *et al.* (2000) found that the greatest number of births corresponded to the warmest

water temperatures in Shark Bay, Australia. These authors suggested that warm

temperatures are advantageous to newborn calves, because they are less capable of

thermoregulation, and to lactating females because prey densities are often higher.

Similarly, Wells *et al.* (1987) found that most calves in the Sarasota Bay region were

born in water temperatures in excess of 27°C. Although this study did not assess the

timing of birth, it is interesting that adult females with calves or yoys were not found in

water temperatures significantly warmer than other dolphin classes in any season.

Shallow, inshore regions commonly classified as nursery areas, such as Palma Sola Bay, exhibited greater fluctuation in water temperature than other sites (Figure 12). Thus, use of shallow inshore areas by females with calves, observed in the present study, is likely driven by factors other than water temperature, such as food availability and protection from predators.

Thus, the physiological response of bottlenose dolphins to water temperature in the Sarasota Bay region is characterized by a small and steady temperature differential between the body surface and the ambient water. This relationship is likely driven by seasonal changes in integumentary insulation that are supplemented by shorter-term adjustments in vascular insulation; however, this relationship is likely to be strongly influenced by the physical properties of the highly conductive medium in which these mammals reside.

Dolphin distribution patterns tended to differ between dolphin classes, based on age, sex and reproductive status. Biotic factors such as prey availability, protection from predation, and reproductive needs are likely the main influences on the distribution of many dolphin classes. A comprehensive investigation of how the interactions between biotic and abiotic factors influence dolphin distribution is necessary to better interpret seasonal distribution patterns of dolphins. In particular, these factors include habitat type, dolphin foraging ecology, and seasonal movements of primary dolphin prey species. Though water temperature, alone, did not appear to directly influence the distribution of most dolphin classes, it is likely that water temperature influences some of these other variables. However, water temperature may be an important factor to which adult male dolphins respond in summer. This class was distributed in relatively cooler water

temperatures than all other classes in summer. Thus, behavioral thermoregulation may be an important mechanism used to dissipate excess body heat in these largest individuals. Future research should be directed at understanding how small differences in temperature can be influential in dolphin thermoregulation.

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