MS. ELIZABETH MURDOCH TITCOMB (Orcid ID : 0000-0003-4682-6708)

Received Date : 15-Jun-2016
Revised Date : 16-Dec-2016
Accepted Date : 17-Dec-2016
Article type : Article

LRH: MARINE MAMMAL SCIENCE, VOL. **, NO. *, ****
RRH: TITCOMB *ET AL*.: MERCURY EXPOSURE AND SOCIAL NETWORKS IN DOLPHINS

Blood mercury concentrations in common bottlenose dolphins from the Indian River Lagoon, Florida: Patterns of social distribution

ELIZABETH MURDOCH TITCOMB,[1] Harbor Branch Oceanographic Institute at Florida Atlantic University, 5600 U.S. 1 North, Fort Pierce, Florida 34946, U.S.A.; **JOHN S. REIF**, Department of Environmental and Radiological Health Sciences, Colorado State University, Fort Collins, Colorado 80523, U.S.A.; **PATRICIA A. FAIR**, Center for Coastal Environmental Health and Biomolecular Research, NOS, NOAA, 219 Fort Johnson Road, Charleston, South Carolina 29142, U.S.A.; **HUI-CHEN W. STAVROS**, o2si Smart Solutions, 2030 Savage Road, Charleston, South Carolina 29407, U.S.A.; **MARILYN MAZZOIL**, Harbor Branch Oceanographic Institute at Florida Atlantic

University, 5600 U.S. 1 North, Fort Pierce, Florida 34946, U.S.A.; **Gregory D. Bossart**, Georgia Aquarium, 225 Baker Street, Atlanta, Georgia 30313, U.S.A. and Miller School of Medicine, University of Miami, 1600 10th Avenue, Miami, Florida 33136, U.S.A.; **Adam M. Schaefer**, Harbor Branch Oceanographic Institute at Florida Atlantic University, 5600 U.S. 1 North, Fort Pierce, Florida 34946, U.S.A.

Abstract

Social network analysis has been shown to be effective in studying the social structure of cetacean populations. Common bottlenose dolphins (*Tursiops truncatus*) inhabiting the Indian River Lagoon (IRL), Florida, have among the highest concentrations of total mercury (THg) in blood reported worldwide. The purpose of this study was to examine the relationship between THg concentrations in IRL dolphins and their social affiliations. Whole blood samples from 98 dolphins with photo-identification sighting histories were collected between 2003–2007 and 2010–2012. Dolphins were categorized into approximate tertiles of low (mean 199.7 µg/L), medium (mean 366.8 µg/L), and high (mean 990.5 µg/L) THg exposure. Social associations between individual dolphins were defined by the proportion of sightings documented with another known individual. Social network measures of individuals and associations between dyads were examined to determine differences among THg categories. Strong social affiliations of individuals within the highest category of THg were found (P = 0.04), suggesting shared exposures among dolphins foraging in specific areas of the estuary. Network measures of strength and affinity were significantly higher in the highest exposure category. This report used social network analysis as a novel

way to examine patterns of exposure to an environmental contaminant in a cetacean population.

Key words: mercury, bottlenose dolphin, *Tursiops truncatus*, social structure, social network analysis.

Social network analysis, *i.e*., the investigation of social structure using network theory, has been shown to be an effective tool for the study of cetacean social structure (Lusseau and Newman 2004, Cantor *et al*. 2012, Mann *et al*. 2012, Titcomb *et al*. 2015) and can enhance our understanding of the structure and function of complex societies (Pinter-Wollman *et al*. 2014). Network theory provides particularly powerful insight when combined with assessments of ranging behavior and habitat use. Interactions between individuals establish the social structure of a population, which in turn can affect individual fitness, information flow, disease transmission, and the genetic structure and viability of populations (Trivers 1985, Lee 1994, Lusseau *et al*. 2006).

Social associations and ranging patterns are integral parts of dolphin social structure (Wells 1991, Urian *et al.* 2009). In the Indian River Lagoon (IRL), Florida, common bottlenose dolphins (*Tursiops truncatus*) occupy defined home ranges with a high degree of site fidelity and comingle with known social affiliates as shown by longitudinal photo-identification studies of individuals (Mazzoil *et al*. 2008, Titcomb *et al*. 2015). A previous analysis of IRL dolphin social structure found that the population was well-differentiated and organized into distinct communities along the linear lagoon system. Spatial analyses of the population demonstrated that social structure was shaped by individual ranging patterns as well as habitat preference and avoidance behavior (Titcomb *et al*. 2015).

The Indian River Lagoon is a biodiverse shallow-water ecosystem that comprises 40% of Florida’s central east coast. The estuary contains three major basins: the Indian River, the Banana River, and the Mosquito Lagoon, and can be divided into six segments based on unique hydrodynamic and geographic features (Woodward-Clyde 1994) (Fig. 1). The IRL extends 250 km from Ponce De Leon Inlet in the north to Jupiter Inlet in the south and is connected to the Atlantic Ocean by five small, widely spaced inlets and a single lock. The exchange of water between the lagoon and the ocean is limited by the size of these inlets and the shallow nature of the lagoon. Due to limited tidal exchange, the long narrow shape, and shallow depth, the lagoon is particularly vulnerable to the accumulation of pollutants (U.S. EPA 1996).

As apex predators with a long life span, bottlenose dolphins can serve as indicators of environmental contamination and ecosystem health (Reddy *et al*. 2001, Wells *et al*. 2004, Bossart 2006). IRL dolphins bioaccumulate multiple organic contaminants, including PCBs, pesticides, polyfluorinated compounds, and polybrominated esters (Fair *et al*. 2010). Inorganic contaminants and trace elements have also been measured in blood and skin of IRL dolphins (Stavros *et al*. 2007, 2008). Most notably, the concentrations of total mercury (THg) in blood and skin of IRL dolphins are among the highest reported worldwide in delphinids (Reif *et al*. 2015). Further, THg concentrations in blood and skin are significantly correlated with the concentrations in liver of free-ranging Florida dolphins (Stavros *et al*. 2011). Bioaccumulation of THg in IRL dolphins has been associated with pathophysiological effects in hepatic, renal, endocrine, hematological, and immune parameters

(Schaefer *et al*. 2011; JSR, unpublished data).

Concentrations of THg in liver, muscle, and kidney of deceased, stranded dolphins have been used as indicators of environmental contamination worldwide (Reif *et al*. 2015). In the IRL, incorporation of photo-identification data to assign individuals to specific geographic segments demonstrated a north to south gradient in the concentrations of THg in blood (Schaefer *et al*. 2015*a*). The explanation for this spatial distribution is unclear; the lack of local point sources of industrialization and mercury emissions suggests that global transport and atmospheric deposition is responsible for the bulk of the ecosystem burden in Florida. Estuarine ecosystems, including much of southern Florida, are hydrogeological sinks for Hg due to their biogeochemistry, concentrations of sulfates in sediments, and patterns of rainfall deposition (Guentzel *et al*. 2001).

Differences in THg concentrations related to habitat type and ecological factors within a particular environment have been reported in fish species (Chumchal and Hambright 2009). Therefore, geographic variation in Hg concentrations in the apex predator may be related to differences in the concentrations in prey species (Pouilly *et al*. 2013). These spatial differences may reflect regional differences in environmental conditions that include deposition, biogeochemistry and trophic transfer (Stavros *et al*. 2011).

IRL dolphins are known to prey upon fish species that have been found to have detectable concentrations of THg (Tremain and Schaefer 2015). Six prey species of the IRL dolphin (spotted seatrout, *Cynoscion nebulosus*; Atlantic croaker, *Micropogonias undulates*; red drum, *Scianops ocellatus*; spot, *Leiostomus* *xanthurus*; striped mullet, *Mugil cephalus*; and pinfish, *Lagodon rhomboid*) had THg concentrations 3–12 times higher than those reported for the same species in Charleston, South Carolina (Stavros *et al*. 2007).

Differences in prey selection and habitat utilization likely have an effect on exposure to mercury and other environmental contaminants. According to de Waal and Luttrell’s (1986) similarity principle, it may be more beneficial for individuals who share similar foraging tactics to forage together, since by coordinating their behavior they may receive by-product benefits. Dolphins have been known to associate preferentially with individuals who share similar foraging tactics and priorities (Gero *et al*. 2005, Díaz López and Shirai 2008), forage cooperatively (Connor *et al*. 2000), and use food-related social signaling between social affiliates (King and Janik 2015). Dolphin social structure can be influenced by feeding associations (Díaz López and Shirai 2008) and communities sharing habitats have been known to be socially segregated based on foraging strategies, such as dolphins who feed without human cooperation *vs*. those who cooperate with local fisherman. (Chilvers and Corkeron 2001; Daura-George *et al*. 2012). In some dolphin populations, foraging techniques may be transmitted from mother to calf *via* social learning processes (Weiss 2006, Sargeant and Mann 2009), suggesting that groups with mother calf pairs likely use the same feeding strategies. Further, stable isotope analysis has detected fine scale differences in fatty acid signatures between IRL dolphins inhabiting the northern and southern areas of the lagoon (Browning *et al*. 2014). Longitudinal studies that document social structure, foraging habits, and habitat use in the IRL dolphin population may provide additional insight into factors that lead to the accumulation of Hg from the local environment. The purpose of this study was to examine the relationship between THg concentrations and measures of social affiliation in IRL dolphins.

METHODS

Free-ranging bottlenose dolphins (*Tursiops truncatus*) inhabiting the IRL were captured, sampled, and released during the Bottlenose Dolphin Health and Environmental Risk Assessment Project (HERA) between 2003–2007 and 2010–2012 using previously described techniques (Fair *et al*. 2006). Age was determined by examination of dentine layers in an extracted tooth (Hohn *et al*. 1989). Whole blood samples were drawn from the periarterial venous rete in the flukes as soon as possible after the animal was restrained with a 19-gauge, 1.9 cm, butterfly catheter (Becton Dickinson, Franklin Lakes, NJ) and collected in S-monovette tubes for trace metal analysis (Sarstedt Inc., Newton, NC). The collection vials were placed on dry ice, transported to the laboratory, and frozen at −40°C until analysis (Stavros *et al*. 2008).

A complete description of the analytic methods for determination of THg concentrations in blood was published previously (Stavros *et al*. 2008, Schaefer *et al*. 2015*a*) and are described briefly here. Total mercury concentration was determined in whole blood samples using combustion atomic absorption spectrometry (CAAS). Laboratory analyses were conducted by the National Oceanic and Atmospheric Administration (NOAA), Center for Coastal Environmental Health and Biomolecular Research from 2003 to 2005 and by the Florida Wildlife Commission, Fish and Wildlife Research Institute from 2006 to

2012. The CAAS analysis was conducted with a calibrated DMA-80 Direct Mercury Analyzer (Milestone Inc., Shelton, CT) in both laboratories using EPA Method 7473 (U.S. EPA 2007). Quality control procedures included analysis of laboratory method blanks, duplicate or triplicate tissue samples, and certified reference material (TORT-2 or DOLT-4 obtained from the National Research Council of Canada) for each group of 10 samples analyzed (U.S. EPA 2007). Duplicate matrix spikes were completed for each group of 40 samples analyzed. THg concentrations were reported as micrograms per liter (µg/L wet weight). Inter-laboratory variability was compared using an independent sample *t*-test. No statistically significant differences were detected in the current analysis or the results previously reported by Schaefer *et al.* (2015*a*).

Boat-based photo-identification surveys were conducted on a quarterly basis in the IRL (Fig. 1) from July 2002 to December 2012 to document behavior, spatial distribution, and social affiliations among individual dolphins. Details of survey design, data collection, and analysis of digital images have been described previously (Mazzoil *et al*. 2008). A sighting group was defined as an aggregation of dolphins within 100 m of each other that were engaging in similar behavior. All of the members of an identified sighting group were considered to be associated. Due to the methods used in our study which involve observing known individuals in the field, it was not possible to record data blindly.

Dolphins with measured concentrations of THg in blood were divided into approximate exposure tertiles (low, medium, high) based on the distribution of their data. A total of 98 individuals had sufficient photo-identification histories (three or more sightings) for inclusion in the analysis. Associations among dolphins within each category of THg exposure were evaluated by measuring the number of sightings of each individual dolphin documented with another known individual (a dyad). The strength of the social relationship between dyads was calculated in SOCPROG 2.4 (Whitehead 2009) using the half-weight association index:

$$\text{HWI} = X/[X + Y_{ab} + \tfrac{1}{2}(Y_a + Y_b)],$$

where X is the number of times dolphins *a* and *b* were observed together, Y_{ab} is the total number of times dolphins *a* and *b* were identified in separate groups, Y_a is the number of times dolphin *a* was identified and Y_b is the number of times dolphin *b* was identified (Cairns and Schwager 1987, Whitehead 2008). The index is scaled from 0 (two individuals were never sighted together) to 1 (two individuals were always sighted together.) The HWI association index was calculated for each dyad in each THg category. The mean association index for all individuals in the category was then calculated and compared across THg categories using analysis of variance (ANOVA).

Social affiliations among dolphins were examined in order to determine whether individual dolphins in each of the three categories of THg concentrations were more likely to be associated with each other than individuals in the other categories of THg concentrations. To elucidate differences in social affiliation between categories of THg, network measures of strength, clustering coefficient, eigenvector centrality, and affinity were calculated in SOCPROG 2.4 in MATLAB 2014 (Whitehead 2009). Strength is the sum of the association indices for each individual; a high strength indicates that an individual is strongly associated with others in the population.

Eigenvector centrality is the weighted sum of direct and indirect connections and measures the influence of an individual within the network of the population. The clustering coefficient (calculated for weighted networks in SOCPROG using the matrix described by Holme *et al.* 2007) measures how well an individual's associates are themselves associated. Affinity measures the strength of an individual's associate connections. Mean THg, and the above network measures were compared between Hg categories using ANOVA. Statistical analysis was conducted using SPSS 23.0 (SPSS Inc., Chicago, IL). $P < 0.05$ was considered statistically significant.

To visualize the relationship between THg and social groups within the population, the social network structure of the THg concentration categories was illustrated in Gephi 0.8.2 (Gephi Consortium, 13 Rue de l'Université, Paris, France) and arranged using the Force Atlas algorithm, which interprets networks by attracting and repulsing nodes in proportion to the distance between them (Bastian and Heymann 2010). The relative distance between individual nodes in the figure represents the level of social affiliation within each THg group. Statistical analyses were conducted using IBM SPSS statistics 20 for Windows (IBM Corp., Armonk, NY) and MATLAB 2014 (MathWorks Inc., Natick, MA).

The spatial distribution of dolphin sightings in each category was mapped using the Kernel Density tool in the Spatial Analyst toolbox within ArcMap 10.4 which gives a 95% fixed kernel density estimate. To minimize observation bias when calculating the kernel densities, 10 random sightings of each individual in the category were used (Urian *et al*. 2009). The distribution of sightings of the high, medium, and low groups was expressed as kernels in order to establish home ranges for dolphins in each of the exposure categories.

RESULTS

The mean concentrations ± standard deviation (SD) for dolphins in the high, medium and low categories of THg concentration were 990.47 µg/L (487.02), 366.77 µg/L (53.88), and 199.73 µg/L (61.8) wet weight, respectively (Table 1). There was no statistically significant difference in ages between exposure groups ($P = 0.48$), which is in agreement with a previous analysis of THg concentrations in IRL dolphins (Schaefer *et al*. 2015*a*, Table 1) that found no statistically significant difference across age groups in either males or females. The difference between THg concentrations in males and females was also not statistically significant.

Association indices within each exposure category were measured by the HWI as defined above (Table 1). Dolphins in the highest exposure category had statistically significant differences in mean association indices ($P = 0.04$), with the highest HWI with other individuals in the highest exposure category (0.08). There were no significant differences in the mean association indices among dolphins in the middle and lowest THg groups.

The parameter means for social affiliation indices between categories of THg exposure were evaluated to determine whether dolphins in the highest exposure category were more likely to be associated with each other than dolphins in the lower exposure categories (Table 1). Individuals in the highest exposure category had a mean strength of 0.77, which was significantly higher than that for individuals in the medium and low exposure categories (0.34 and 0.45, respectively, ($P < 0.01$). Affinity was also significantly higher for individuals in the high exposure category (*P* < 0.02). There were no significant differences between categories of THg exposure for clustering coefficient or eigenvector centrality.

The social network of individual dolphins in the IRL is shown in Figure 2 with their corresponding assignment to categories of THg exposure. Some clustering can be seen among individuals with high and medium THg exposure (red and yellow nodes, respectively); a small cluster appears in the network on the left side and another large cluster on the right. Photo-identification data show the spatial distribution of the left cluster to be in the northern IRL and southern Mosquito Lagoon, while the right cluster is comprised of dolphins known to range in the southern reaches of the IRL, including the St. Lucie River.

The kernel density estimates of IRL dolphins with high, medium and low concentrations of THg were mapped (Fig. 3). The figure shows overlapping home ranges throughout the study area; there was no clear separation of home ranges according to the concentration of THg in blood. Home ranges of the high concentration animals were very dense in the northern area of the lagoon, with another large range in the southern half of the lagoon. The medium concentration animals had fairly even densities throughout the lagoon with the densest area located at Sebastian Inlet, which lies in the middle of the lagoon system. The low concentration animals ranged in the far northern areas and southern half of the lagoon, with the densest cluster located south of Sebastian Inlet.

DISCUSSION

Several indications of social affiliation among dolphins with high levels of exposure to mercury were found in these analyses, which have important implications for ecosystem health. Social affiliations as measured by the HWI index were significantly stronger among individuals within the highest THg exposure category; individuals were more likely to be associated with animals in the same exposure group compared to dolphins with lower THg exposure. The mean HWIs for all exposure categories (low THg = 0.07; medium THg = 0.05; high THg = 0.08) were higher than the overall HWI for the IRL population (0.01) reported previously but within the range of the means previously described for the five discrete IRL communities (0.02–0.09) (Titcomb *et al*. 2015). The difference in mean HWI between all individuals in the population and those within each THg exposure category suggests that the association of individuals within exposure categories is not random, but may be based on feeding patterns or prey species availability in specific locales within the IRL. The higher measure of strength among individuals in the highest THg group indicates that those individuals are more strongly associated with others in the same category compared to individuals in the lower and middle categories. Likewise, the strong measure of affinity within the highest THg category indicates that individuals with high THg levels have associates who are well-connected within the network. It is likely more beneficial for individuals to forage with others who share similar foraging techniques (deWaal and Luttrell 1986) and bottlenose dolphins are known to associate preferentially while foraging (Gero *et al*. 2005, Lopez and Shirai 2008). Similar prey preferences for dolphins inhabiting the IRL may indicate that microhabitats with varying concentrations of Hg in the biota could be driving exposure in certain areas.

Photo-identification studies of home ranges of individual

IRL dolphins show that they spend most of their time in individual geographic segments and do not move back and forth between the ocean and the estuary in significant numbers (Mazzoil *et al.* 2008). This is important since the concentration of THg in blood is a short-term measurement reflecting recent dietary intake. Therefore, the concentrations of THg are unlikely to be affected by movement and feeding in other areas.

There were no significant differences in the clustering coefficients or eigenvector centrality measures between THg categories. The lack of significant differences in these measures is most likely due to our analysis of all individuals in each THg category, without separating individuals in each THg category spatially. The linear nature of the study area restricts many of these animals (particularly those whose habitats are in the far northern or southern reaches of the lagoon) from associating with each other (Titcomb *et al*. 2015). Similarly, the lack of difference in centrality was expected. Centrality measures the scope of an individual’s interactions with the entire population; individuals that are exposed to THg are not necessarily more likely to be associated than other individuals in the population as a whole. In this case of mercury exposure, centrality is probably not as meaningful as it would be in an infectious disease epidemic, where the animals with the highest centrality can drive the spread of a disease in a population (Gomez *et al*. 2013, Rushmore *et al*. 2013).

Strong social affiliations suggest these individuals may be foraging together in the same areas and perhaps even feeding cooperatively (Daura-George *et al*. 2012). Dolphins routinely display differences in tactics and prey selection within populations that are adaptations to local conditions (Krutzen *et* *al*. 2005, Sargeant *et al*. 2007). For example, bottlenose dolphins in Belize were observed fishing more frequently in specific microhabitats within their particular home range; *e.g.*, areas where seagrass beds adjoined open salt flats (Eierman and Connor 2014). Such local differences could partially explain the variations and associations observed in this study and are supported by a previous stable isotope analysis of IRL dolphins (Browning *et al*. 2014). Isotopic signatures from 153 live dolphins were used to assign dolphins to one of three subpopulations within the IRL. However, the differences were not driven by the trophic level of feeding but rather by the proportions of specific prey consumed. Therefore, these differences in dietary structure may contribute to the observed results. In support of this hypothesis, stable isotope analysis detected fine scale differences in fatty acid signatures between dolphins inhabiting the northern and southern areas of the lagoon (Browning *et al*. 2014), suggesting that the diets of dolphins differ across the estuary.

The clustering of individuals with high THg exposure shown in Figure 2 who are routinely sighted in the northern IRL is consistent with a previous report which documented higher concentrations of THg in dolphins inhabiting the northern segments of the lagoon (Schaefer *et al*. 2015*a*). These findings add to the evidence that concentrations of mercury in the IRL are not homogenous and that the social structure and feeding ecology of the population contributes to bioaccumulation of mercury through the food chain in local habitats. Differences in THg concentration have been reported on fine scales that are related to differences in microhabitat type and other ecological factors (Chumchal *et al*. 2008). Failure to discriminate between exposure groups according to their home ranges as shown in maps of kernel density estimates suggests that ranges of these apex predators overlap at the level of the entire estuary.

Mercury exposure among IRL dolphins is due primarily to dietary sources of Hg (Stavros *et al*. 2007). Tremain and Schaefer (2015) reported significantly higher THg concentrations in silver perch (*Bairdiella chrysoura*), Irish pompano (*Diapterus auratus*), pinfish (*Lagodon rhomboids*), and striped mullet (*Mugil cephalus*) sampled from the northern Indian River than from the southern reaches of the estuary. Within the IRL, silver perch contained the highest Hg levels among the common dolphin prey species examined (0.222 mg/kg) and striped mullet the lowest (0.015 mg/kg), a 15 fold difference (Tremain and Schaefer 2015). Silver perch have been documented in the diets of IRL dolphins (Barros 1993, Luczkovich *et al*. 2000). Atlantic croaker (*Micropogonias undulates*) and striped mullet are also an important prey biomass for IRL dolphins; their diets also include spot (*Leiostomus xanthurus*) in smaller quantities (Barros 1993). Additional foraging ecology studies are needed to determine whether the differences in THg concentrations among social clusters are driven by differential prey selection and availability in local areas within the lagoon.

Environmental and hydrological characteristics are not homogeneous within the lagoon. The IRL is ecologically diverse and spans a major biogeographic boundary between the subtropics and temperate zones (U.S. EPA 1996). The large latitudinal range, the extensive canal system draining into the IRL and the location of rivers and inlets contribute to variations in water temperature, salinity, and currents (Woodward-Clyde Consultants 1994). Shallow depths and the limited tidal exchange between the lagoon and the Atlantic Ocean result in minimal flushing (Smith 1993); therefore, chemical and microbial agents may become concentrated within areas of the lagoon with limited tidal movement. This is particularly true in the northern areas of the IRL where the dolphin groups with the highest THg concentrations were routinely observed. Further evaluation of local biogeochemistry and accumulation of mercury in prey species is needed to better understand factors influencing the distribution of Hg in the apex predator.

The current study is the first of its kind to utilize social networks in a coastal dolphin population to evaluate shared environmental exposures among groups of individuals. The approach described has the potential to be applied to other populations and wildlife species in order to understand exposures among social groups. Additionally, data on social affiliations and habitat use combined with environmental exposures have the potential to identify environmental hotspots that represent hazards to both wildlife and public health. For example, the identification of the northern IRL as a hotspot of Hg accumulation and exposure in dolphins has environmental implications as well as significance for other species that consume fish from the IRL including humans. We recently showed that hair mercury concentrations in coastal residents along the IRL were higher among those who obtained a substantial portion of their seafood from local, recreational sources (Schaefer *et al.* 2015*b*). The current study adds to the evidence that the bottlenose dolphin represents an excellent sentinel for ecosystem and public health.

ACKNOWLEDGMENTS

The authors would like to acknowledge the staff, veterinarians, and volunteers who make the HERA and Photo Identification projects possible. This research was conducted under National Marine Fisheries Service (NMFS) General Authorization No. 32, Letter of Confirmation File Nos. 1025-1670 and 998–1678. All animal capture and sampling protocols were conducted under National Marine Fisheries Permits No. 998-1678-00 and 14352 and approved by Harbor Branch Oceanographic Institute’s Institutional Animal Care and Use Committee (IACUC). Support was provided by Florida’s “Protect Wild Dolphins” specialty license plate program. This publication is HBOI contribution no. 2062.

LITERATURE CITED

Barros, N. B. 1993. Feeding ecology and foraging strategies of bottlenose dolphins on the central east coast of Florida. Ph.D. dissertation, University of Miami, Miami, FL. 328 pp.

Bastian, M., and S. Heymann. 2010. Gephi: An open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media. Available at http://www.aaai.org/ocs/index.php/ICWSM/09/paper/view/154.

Bossart, G. D. 2006. Marine mammals as sentinel species for ocean and human health. Oceanography 19(2):134–137.

Browning, N. E., S. D. McCulloch, G. D. Bossart and G. A. J. Worthy. 2014. Fine-scale population structure of estuarine bottlenose dolphins (*Tursiops truncatus*) assessed using stable isotope ratios and fatty acid signature analyses. Marine Biology 161:1307–1317.

Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. Animal Behaviour 35:1454–1469.

Cantor, M., L. L. Wedekin, P. R. Guimarães, F. G. Daura-Jorge,

M. R. Rossi-Santos and P. C. Simões-Lopes. 2012. Disentangling social networks from spatiotemporal dynamics: The temporal structure of a dolphin society. Animal Behaviour 84:641–651.

Chilvers, B. L., and P. J. Corkeron. 2001. Trawling and bottlenose dolphins' social structure. Proceedings of the Royal Society of London Series B: Biological Sciences 268:1901–1905.

Chumchal, M. M., and K. D. Hambright. 2009. Ecological factors regulating mercury contamination of fish from Caddo Lake, Texas, USA. Environmental Toxicology and Chemistry 28:962–972.

Chumchal, M. M, R. W. Drenner, K. D. Hambright and L. W. Newland. 2008. Habitat-specific differences in mercury concentration in a top predator from a shallow lake. Transactions of the American Fisheries Society 137:195–208.

Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91–126 *in* J. Mann, R. C. Conner, P. L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL.

Daura-Jorge, F. G., M. Cantor, S. Ingram, D. Lusseau and P. C. Simões-Lopes. 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8:702–705.

de Waal, F. B. M., and L. M. Luttrell. 1986. The similarity principle underlying social bonding among female rhesus monkeys. Folia Primatologica 46:215–234.

Díaz López, B., and J. A. Bernal Shirai. 2008. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. Behavioral Ecology and Sociobiology 62:887–894.

Eierman, L. E., and R. C. Connor. 2014. Foraging behavior, prey distribution, and microhabitat use by bottlenose dolphins (*Tursiops truncatus*) in a tropical atoll. Marine Ecology Progress Series 503:279–288.

Fair, P. A., J. D. Adams, E. Zolman, *et al*. 2006. Protocols for conducting dolphin capture-release health assessment studies. NOAA Technical Memorandum NOS NCCOS 49. 83 pp.

Fair, P. A., J. Adams, G. Mitchum, *et al.* 2010. Contaminant blubber burdens in Atlantic bottlenose dolphins (*Tursiops truncatus*) from two southeastern US estuarine areas: Concentrations and patterns of PCBs, pesticides, PBDEs, PFCs, and PAHs. Science of the Total Environment 408:1577–1597.

Gero, S, L. Bedjer, H. Whitehead, J. Mann and R. C. Connor. 2005. Behaviorally specific preferred associations in bottlenose dolphins, *Tursiops* spp. Canadian Journal of Zoology 83:1566–1574.

Gómez, J. M., C. L. Nunn and M. Verdú. 2013. Centrality in primate–parasite networks reveals the potential for the transmission of emerging infectious diseases to humans. Proceedings of the National Academy of Sciences of the United States of America 110:7738–7741.

Guentzel, J. L., W. M. Landing, G. A. Gill and C. D. Pollman. 2001. Processes influencing rainfall deposition of mercury in Florida. Environmental Science and Technology 35:863–873.

Hohn, A. A., M. D. Scott, R. S. Wells, J. C. Sweeny and A. B.

Irvine. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Marine Mammal Science 5:315–342.

Holme, P., S. M. Park, B. J. Kim and C. R. Edling. 2007. Korean university life in a network perspective: Dynamics of a large affiliation network. Physica A 373:821–830.

King, S. L., and V. M. Janik. 2015. Come dine with me: Food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). Animal Cognition 18:969–974.

Krützen, M., J. Mann, M. R. Heithaus, R. C. Connor, L. Bejder and W. B. Sherwin. 2005. Cultural transmission of tool use in bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America 102:8939–8943.

Lee, P. C. 1994. Social structure and evolution. Pages 266–303 *in* P. J. B. Slater and T. R. Halliday, eds. Behaviour and evolution. Cambridge University Press, Cambridge, U.K.

Lopez, B. D., and J. A. B. Shirai. 2008. Marine aquaculture and bottlenose dolphins' (*Tursiops truncatus*) social structure. Behavioral Ecology and Sociobiology 62:887–894.

Luczkovich. J. J., H. J. Daniel, M. Hutchinson, T. Jenkins, S. E. Johnson, R. Pullinger and M. W. Sprague. 2000. Sounds of sex and death in the sea: Bottlenose dolphin whistles suppress mating choruses of silver perch. Bioacoustics 10:323–334.

Lusseau, D., and M. E. J. Newman. 2004. Identifying the role that animals play in their social networks. Proceedings of the Royal Society of London 271:S477–S481.

Lusseau, D., B. Wilson, P. S. Hammond, *et al.* 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75:14–24.

Mann, J., M. Stanton, E. M. Patterson, E. J. Bienenstock and L. O. Singh. 2012. Social networks reveal cultural behavior in tool-using dolphins. Nature Communications 3:980.

Mazzoil, M., J. S. Reif, M. Youngbluth, *et al.* 2008. Home ranges of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida: Environmental correlates and implications for management strategies. EcoHealth 5:278–288.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, *et al.* 2014. The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. Behavioral Ecology 25:242–255.

Pouilly, M., D. Rejas, T. Pérez, J. L. Duprey, C. I. Molina, C. Hubas and J. D. Guimarães. 2013. Trophic structure and mercury biomagnifications in tropical fish assemblages, Iténez River, Bolivia. PLoS ONE 8(5):e65054. http://dx.doi.org/10.1371/journal.pone.0065054.

Reddy, M. L., J. S. Reif, A. Bachand and S. H. Ridgeway. 2001. Opportunities for using navy marine mammals to explore associations between organochlorine contaminants and unfavorable effects on reproduction. Science of the Total Environment 274:171–182.

Reif, J. S., A. M. Schaefer and G. D. Bossart. 2015. Atlantic bottlenose dolphins (*Tursiops truncatus*) as a sentinel for exposure to mercury in humans: Closing the loop. Veterinary Sciences 2:407–422.

Rushmore, J., D. Caillaud, L. Matamba, R. M. Stumpf, S. P. Borgatti and S. Altizer. 2013. Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. Journal of Animal Ecology 82:976–986.

Sargeant, B. L., and J. Mann. 2009. Developmental evidence for foraging traditions in wild bottlenose dolphins. Animal Behaviour 78:715–721.

Sargeant, B. L., A. J. Wirsing, M. R. Heithaus and J. Mann. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? Behavioral Ecology and Sociobiology 61:679–688.

Schaefer, A. M., H. W. Stavros, J. S. Reif, P. A. Fair and G. D. Bossart. 2011. Effects of mercury on hepatic, renal, endocrine and hematological parameters in Atlantic bottlenose dolphins (*Tursiops truncatus*) along the eastern coast of Florida and South Carolina. Archives of Environmental Contamination and Toxicology 61:688–695.

Schaefer, A. M., E. Murdoch Titcomb, P. Fair, *et al*. 2015*a*. Mercury concentrations in Atlantic bottlenose dolphins (*Tursiops truncatus*) inhabiting the Indian River Lagoon, Florida: Patterns of spatial and temporal distribution. Marine Pollution Bulletin 97:544–547.

Schaefer A. M, E. Jensen, G. D. Bossart and J. S. Reif. 2015*b*. Hair mercury concentrations and fish consumption patterns in Florida residents. International Journal of Environmental Research and Public Health 11:6709–6726.

Smith, N. 1993. Tidal and non-tidal flushing of Florida’s Indian River Lagoon. Estuaries 16:739–746.

Stavros, H. C., G. D. Bossart, T. C. Hulsey and P.A. Fair. 2007. Trace element concentrations in skin of free-ranging bottlenose dolphins (*Tursiops truncatus*) from the southeast Atlantic coast. Science of the Total Environment 388:300–315.

Stavros, H. C., G. D. Bossart, T. C. Hulsey and P. A. Fair.

2008. Trace element concentrations in blood of free-ranging bottlenose dolphins (*Tursiops truncatus*): Influence of age, sex and location. Marine Pollution Bulletin 56:348–379.

Stavros, H. C., M. Stolen, W. N. Durden, W. McFee, G. D. Bossart and P. A. Fair. 2011. Correlation and toxicological inference of trace elements in tissues from stranded and free-ranging bottlenose dolphins (*Tursiops truncatus*). Chemosphere 82:1649–1661.

Titcomb, E. M., G. O'Corry-Crowe, E. F. Hartel and M. S. Mazzoil. 2015. Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins. Marine Mammal Science 31:1314–1337.

Tremain, D. M., and A. M. Schaefer. 2015. Mercury concentrations in the prey of apex piscivores from a large subtropical estuary. Marine Pollution Bulletin 95:433–444.

Trivers, R. L. 1985. Social evolution. Benjamin/Cummings, Menlo Park, CA.

Urian, K. W., S. Hofmann, R. S. Wells and A. J. Read. 2009. Fine scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science 25:619–638.

U.S. EPA (U.S. Environmental Protection Agency). 1996. National Estuary Program, Indian River Comprehensive Conservation and Management Plan. Available at http://www.epa.gov/owow/estuaries/programs/irl.htm.

U.S. EPA (U.S. Environmental Protection Agency). 2007. Method 7473. Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry. Available at http://www.epa.gov/wastes/hazard/testmethods/sw846/pdfs

/7473.pdf.

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199–225 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Discoveries and puzzles. University of California Press, Berkeley, CA.

Wells, R. S., H. L. Rhinehardt, L. J. Hansen*, et al.* 2004. Bottlenose dolphins as marine ecosystem sentinels: Developing a health monitoring system. Ecohealth 1:246–254.

Weiss, J. 2006. Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs. Aquatic Mammals 32:10–19.

Whitehead, H. 2008. Analyzing animal societies: Quantitative methods for vertebrate social analysis. Chicago University Press, Chicago, IL.

Whitehead, H. 2009. SOCPROG programs: Analyzing animal social structures. Behavioral Ecology Sociobiology 63:765–778.

Woodward-Clyde Consultants. 1994. Biological resources of Indian River Lagoon. Indian River Lagoon National Estuary Program. Final Technical Report. Project Number: 92F274C, Melbourne, FL.

Received: 15 June 2016
Accepted: 17 December 2016

Figure 1. The Indian River Lagoon, Florida, subdivided into six segments based on hydrodynamics and geographic features.

Figure 2. Social affiliation and clustering among individual IRL dolphins by categories of total mercury concentration in blood (High-Red, Medium-Yellow, Low-Blue). Lines between nodes represent individuals sighted together. The relative distance between individual nodes represents the level

of social affiliation.

Figure 3. Kernel density estimates of the home ranges of individual dolphins in the three THg categories: high (a), medium (b), and low (c).

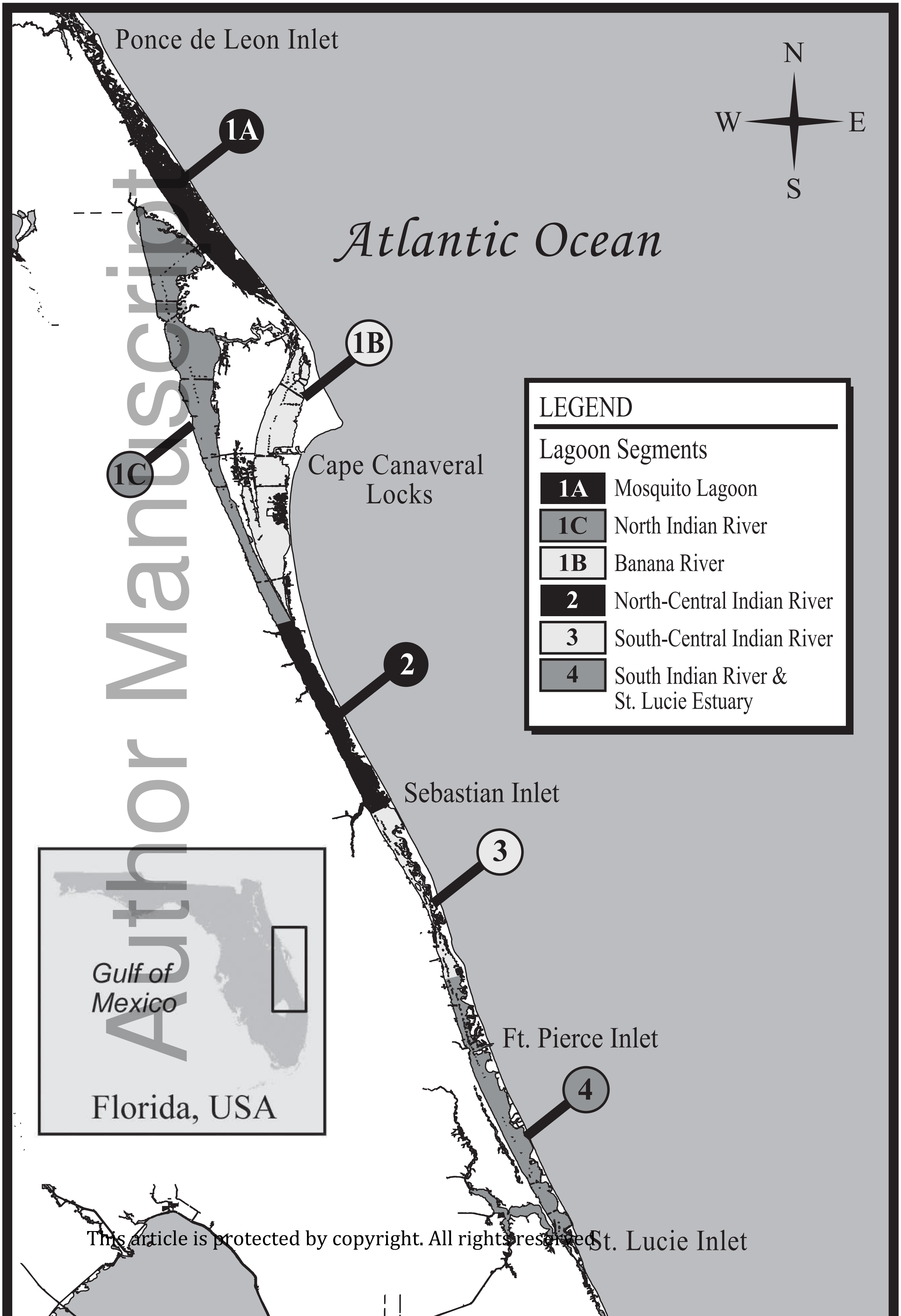
[1] Corresponding author (e-mail: mmurdoch@fau.edu).

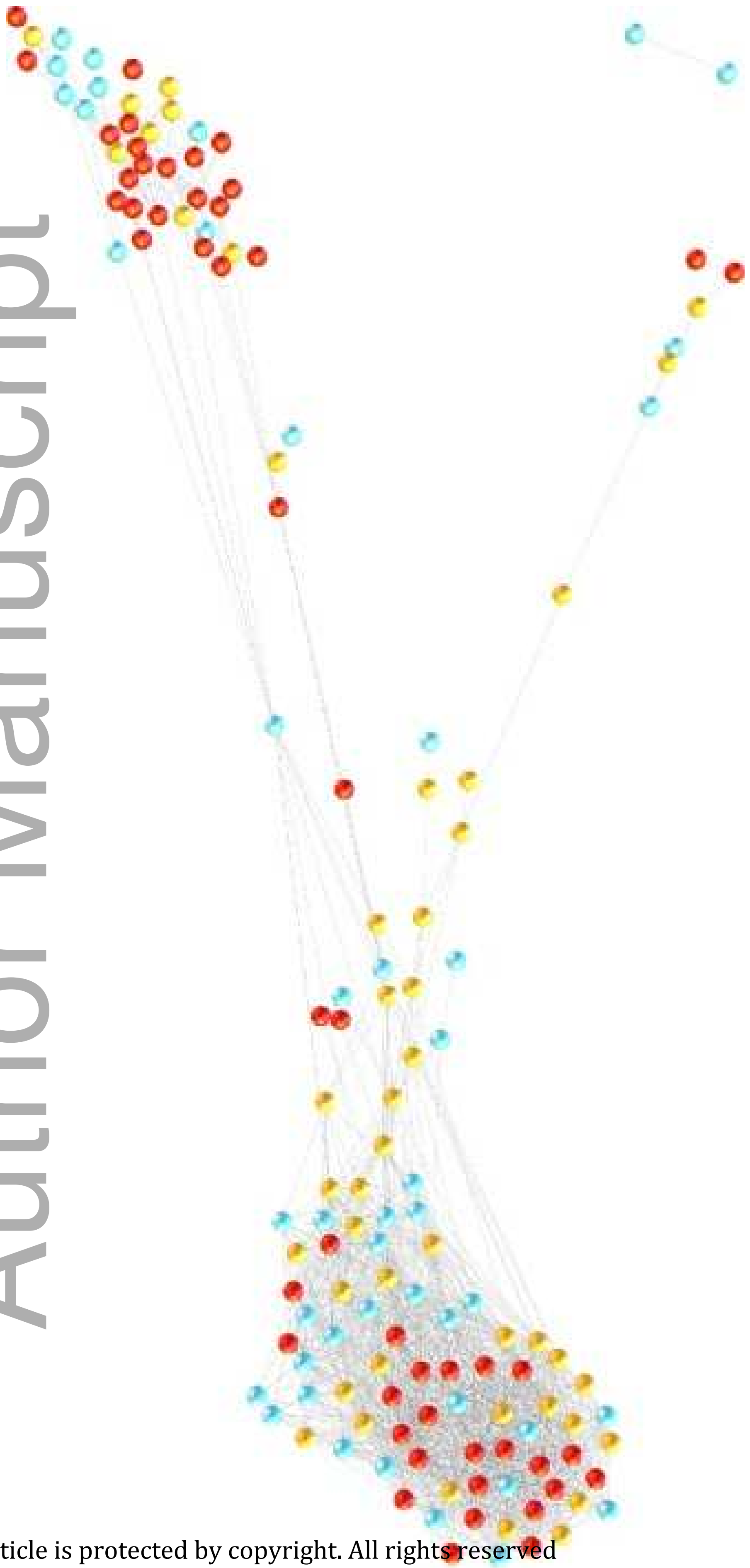
Table 1. Mean associations (HWI) and network measures of social affiliation (± standard deviation) for categories of blood THg concentration (µg/L wet weight) among IRL dolphins.[1]

	Low Thg	Medium Thg	High THg	*P*
n	27	37	34	
Mean THg (µg/L)	199.73 (61.80)	366.77 (53.88)	990.47 (487.02)	<0.01
Range	34.90–279.46	285.01–480.00	494.05–2,750.02	
Mean age (years)	13.77 (6.34)	11.36 (4.24)	12.41 (6.65)	0.48
Gender				
Male (*n*, %)	20 (74.1)	23 (62.1)	18 (52.9)	0.07
Sampling period				
2003–2007	18 (66.7)	27 (73.0)	30 (88.2)	0.12
2010–2012	9 (33.3)	10 (27.0)	4 (11.8)	
Mean association (HWI)				
Low THg	0.07 (0.07)	0.06 (0.05)	0.06 (0.02)	0.90
Mid THg	0.05 (0.03)	0.05 (0.02)	0.07 (0.07)	0.15
High Thg	0.05 (0.03)	0.05 (0.03)	0.08 (0.07)	0.04

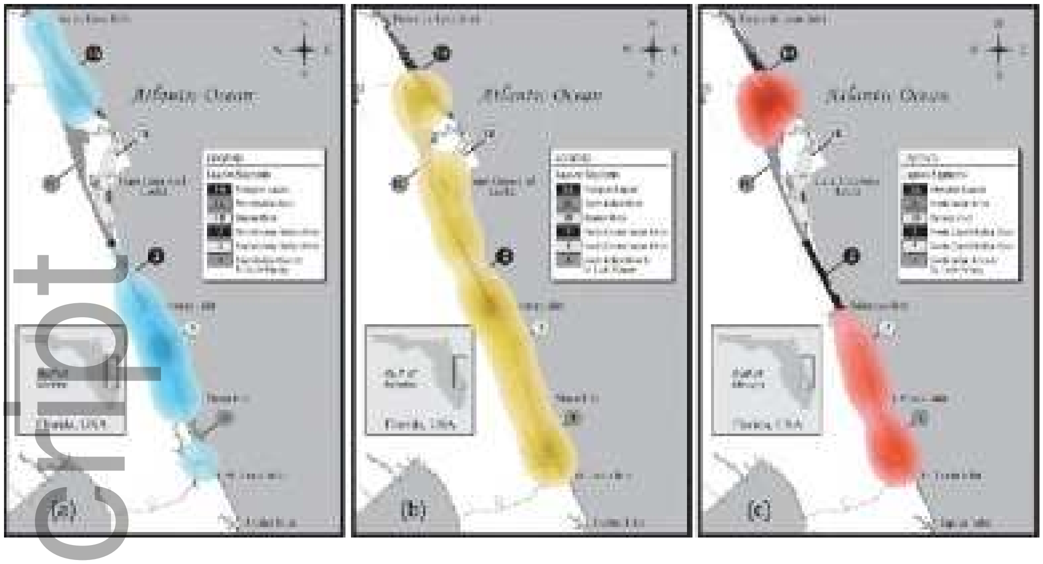
Network measures				
Strength	0.45 (0.35)	0.34 (0.30)	0.77 (0.56)	<0.01
Clustering coefficient	0.06 (0.06)	0.10 (0.06)	0.09 (0.05)	0.70
Eigenvector centrality	0.06 (0.14)	0.07 (0.12)	0.08 (0.12)	0.83
Affinity	0.60 (0.24)	0.50 (0.21)	0.99 (0.35)	0.02

[1] From SOCPROG 2.4 MATLAB.


Ponce de Leon Inlet
N
W
E
S
1A
Atlantic Ocean
1B
1C
Cape Canaveral Locks
LEGEND
Lagoon Segments
1A Mosquito Lagoon
1C North Indian River
1B Banana River
2 North-Central Indian River
3 South-Central Indian River
4 South Indian River & St. Lucie Estuary
2
Sebastian Inlet
3
Gulf of Mexico
Florida, USA
Ft. Pierce Inlet
4
St. Lucie Inlet



mms_12390_f2.tif



mms_12390_f3.tif