FINAL REPORT

Behavioral Ecology of Deep-diving Odontocetes in The Bahamas

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14. ABSTRACT

This project has provided key baseline information on the behavioral ecology of six cetaceans known from the Bahamas (melon-headed whale, *Peponocephala electra*; short-finned pilot whale, *Globicephala macrorhynchus* (*Gm*); Blainville's *Mesoplodon densirostris*, Gervais' *Mesoplodon europaeus* and Cuvier's *Ziphius cavirostris* beaked whales; and sperm whale) to assess potential vulnerabilities to disturbance from Navy activities. All occur sympatrically in deep-water habitats that overlap with Navy sonar use, including at the U.S. Navy's Atlantic Undersea Test and Evaluation Center. Data acquired through photo-identification, molecular genetics and chemical biomarkers from tissue biopsies, satellite telemetry, and acoustic recordings were integrated to characterize their population structure and movement patterns, social organization, and foraging behavior. *Gm* exhibited the most widespread movements while beaked whales demonstrated high site fidelity on a small scale. Long-term and/or complex social structure was revealed for all species studied raising concern for activities that could disrupt key individuals within social units and their resultant effect on the entire unit. Variation across species in their vertical foraging habitat suggests diet differences while the diving capacity of beaked whales enabled them to access upper bathypelagic foraging niches despite their relatively small sizes, but at the cost of reduced dive efficiency. This study provides further support that beaked whales, due to their limited ranging patterns and foraging strategies, may be most vulnerable to disturbances.

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Table of Contents

List of Tables iii
List of Figures iv
List of Acronyms vi
Keywords viii
Acknowledgements ix
Abstract 1
Objectives 5
Background 6
Materials and Methods 9
Visual data collection 9
Acoustic data collection and analyses 9
Telemetry analyses 10
Tag deployments 10
Inferring diving behavior 11
Modeling movement 12
Dive bouts and foraging thresholds 12
Sex and demographic identification 13
Photo-identification analyses 13
Field sampling and processing 13
Association analyses 14
Chemistry analyses 17
Sample collection 17
Subset of biopsy samples analyzed for chemical tracers 17
Sample preservation and integrity 17
Analytes measured 18
Stable isotope analyses 18
Persistent organic pollutant analyses 18
Fatty acid analyses 19
Statistical analyses 19
Chemical tracers as indicators of short-/long-term foraging structure 19
Genetic analyses 20
Sample processing and molecular genetic marker amplification 20
Identifying duplicate samples, estimating genetic diversity and removal of close kin 21
Intraspecific genetic differentiation within Great Bahama Canyon 22
Results 23
SERDP field data collection 23
Acoustic detections 27
MELON-HEADED WHALE (*Peponocephala electra*) 28
Telemetry 28
Photo-identification 33
Movements 33
Social organization 34

Chemistry 35
SHORT-FINNED PILOT WHALE (*Globicephala macrorhynchus*) 40
Telemetry 40
Photo-identification 43
Movements 43
Chemistry 43
Genetics 46
Genetic diversity and differentiation in pilot whales 46
BLAINVILLE'S BEAKED WHALE (*Mesoplodon densirostris*) 51
Telemetry 51
Photo-identification 51
Movements 51
Social organization 52
Chemistry 56
GERVAIS BEAKED WHALE (*Mesoplodon europaeus*) 60
Photo-identification 60
Movements 60
Chemistry 60
CUVIER'S BEAKED WHALE (*Ziphius cavirostris*) 64
Telemetry 64
Photo-identification 64
Movements 64
Chemistry 65
SPERM WHALE (*Physeter macrocephalus*) 68
Telemetry 68
Photo-identification 70
Movements 70
Association analyses 71
Chemistry 74
Genetics 76
Genetic diversity and differentiation in sperm whales 76
Acoustics 81
Persistent organic pollutant concentrations in whales and prey 84
Discussion 88
Population structure and ranging patterns 88
Social organization 89
Foraging habitat and behavior 91
Diving 91
Foraging strategies 91
Inferring diet differences 93
Conclusions and Implications for Future Research 94
Literature Cited 97
Appendices 106
Appendix A – Supporting data 106
Appendix B – List of scientific publications 114

List of Tables

Table 1. Models fit to standardised lagged association rates from photo-identification data. 15
Table 2. Primers and annealing temperatures used to amplify the mitochondrial control region from skin biopsies. 21
Table 3. Summary of data collected from 1991 – 2014 in the northern Bahamas. 25
Table 4. Summary statistics of satellite tag deployments. 28
Table 5. Contingency table for melon-headed whale photo-identification data. 34
Table 6. Contingency table for short-finned whale photo-identification data. 43
Table 7. Frequency of short-finned pilot whale mtDNA control region haplotypes. 47
Table 8. Numbers of different mtDNA haplotypes and numbers of sampled pilot whale groups within each strata. 47
Table 9. Pilot whale genetic divergence among strata estimated from mtDNA control region sequence data. 48
Table 10. Nuclear genetic divergence among pilot whales. 48
Table 11. AMOVA results quantifying the partitioning of genetic variance for short-finned pilot whales among strata and encounter groups. 49
Table 12. Contingency table for Blainville's beaked whale photo-identification data. 52
Table 13. Model selection for the standardized null and lagged association rates of adult female Blainville's beaked whales. 53
Table 14. Model selection for the standardized null and lagged association rates of adult male Blainville's beaked whales associating with adult females. 54
Table 15. Permutation tests using association matrices and a mantel test for Blainville's beaked whale long-term preferred associations and avoidances. 55
Table 16. Contingency table for Gervais' beaked whale photo-identification data. 60
Table 17. Contingency table for Cuvier's beaked whale photo-identification data. 65
Table 18. Contingency table for sperm whale photo-identification data. 71
Table 19. Sperm whale social unit names and membership compositions. 71
Table 20. Sperm whale mitochondrial haplotype diversity, frequency and nucleotide diversity within each strata. 77
Table 21. Sperm whale genetic divergence among strata within the Bahamas estimated from mtDNA sequence data. 77
Table 22. Genetic divergence among strata estimated from sperm whale nuclear genotypes. 78
Table 23. Numbers of sperm whales genotyped per encounter group within each stratum. 80
Table 24. Concentrations of summed polybrominated biphenyls, summed DDTs, summed chlrodanes, summed hexochlorocyclohexanes, summed polybrominated diphenyl ethers measured in the blubber of the six species. 84
Table 25. Concentrations of summed polybrominated biphenyls, summed DDTs, summed chlrodanes, summed hexochlorocyclohexanes, summed polybrominated diphenyl ethers measured in potential prey. 87

List of Figures

Figure 1. Map of the study area. 7
Figure 2. Photographs documenting the deployment of a satellite transmitter tag on a sperm whale in the Bahamas. 11
Figure 3. Photo-identification images of a Blainville's beaked whale demonstrating the longevity of natural markings. 14
Figure 4. Photographs of an individual melon-headed whale of varying image quality, demonstrating how photographs were quality graded. 14
Figure 5. Visual and acoustic survey effort during surveys in the Great Bahama Canyon. 24
Figure 6. Map of encounter locations for the six priority species in the northern and central Bahamas from 1991-2014. 26
Figure 7. Locations of acoustic detections during ship surveys. 27
Figure 8. Movement tracks within the Great Bahama Canyon estimated from satellite transmitter tags. 29
Figure 9. Plots of estimated displacement away from the tagging site against time. 30
Figure 10. Scatterplots indicating the relationship of maximum depth to the duration of each dive recorded. 31
Figure 11. Boxplots comparing the proportion of each Time-at-Temperature histogram spent within presumed foraging strata. 32
Figure 12. Boxplot comparing the ratio of foraging dive depth to local bathymetric depth at estimated dive locations. 33
Figure 13. Dendrogram from photo-identification data, showing association indices between melon-headed whales. 35
Figure 14. Differences in epidermal stable isotope ratios among the six species. 36
Figure 15. PCA of dietary fatty acids in the blubber of the six species. 37
Figure 16. Differences in stable isotope ratios among melon-headed whales. 38
Figure 17. PCA and hierarchical cluster analysis of POP patterns measured in melon-headed whales. 39
Figure 18. Movement tracks of short-finned pilot whales. 41
Figure 19. Boxplots comparing the maximum depth of foraging dives for adult females and adult males for each study species. 42
Figure 20. Differences in stable isotope ratios among short-finned pilot whales. 44
Figure 21. PCA and hierarchical cluster analysis of POP patterns measured in short-finned pilot whales. 45
Figure 22. Differences in epidermal SI ratios among short-finned pilot whale groups. 46
Figure 23. Bar plot showing the assignment of individual short-finned pilot whale samples to genetic groups. 49
Figure 24. Mean genetic relatedness among pairs of short-finned pilot whales. 50
Figure 25. Standardized null and lagged association rates from photo-identification data for Blainville's beaked whale adult females. 53
Figure 26. Standardized null and lagged association rates from photo-identification data for Blainville's beaked whale adult males associating with adult females. 54
Figure 27. Frequency plot showing group composition when the focal Blainville's beaked whale adult female is with and without a calf. 56
Figure 28. Differences in SI ratios among Blainville's beaked whales. 57

Figure 29. PCA and hierarchical cluster analysis of POP patterns measured in Blainville's beaked whales. 59
Figure 30. Differences in the pattern of dietary fatty acids among Blainville's, Cuvier's, and Gervais' beaked whales. 62
Figure 31. Relationship between the fatty acid ratio and mean foraging dive depth. 63
Figure 32. Differences in SI ratios among Cuvier's beaked whales. 66
Figure 33. PCA and hierarchical cluster analysis of POP patterns measured in Cuvier's beaked whales. 67
Figure 34. Movement tracks of sperm whales showing movements generally within the Great Bahama Canyon. 69
Figure 35. Dendrogram showing association indices between sperm whales from photo-identification data. 72
Figure 36. Individual-level social network of seven sperm whale social units from photo-identification data. 73
Figure 37. Differences in SI ratios among sperm whales. 74
Figure 38. PCA and hierarchical cluster analysis of POP patterns measured in sperm whales. 75
Figure 39. Differences in epidermal SI ratios among groups of sperm whales. 76
Figure 40. Bar plot showing the assignment of all individual sperm whale samples to genetic groups. 79
Figure 41. Bar plot showing the assignment of individual female sperm whale samples to genetic groups. 79
Figure 42. Rates of association based on photographic re-sightings among pairs of sperm whales plotted against genetic relatedness for the same pair. 80
Figure 43. A plot of the range of pairwise coefficients of genetic relatedness among sperm whales within and between social units. 81
Figure 44. Plot showing length estimates of sperm whales calculated from acoustic recordings of each individuals' clicks. 82
Figure 45. Rhythm plot of 63 sperm whale codas. 83

List of Acronyms

ANOSIM – Analysis of Similarities
AMOVA - Analysis of Molecular Variance
ASE - Accelerated Solvent Extraction
AUTEC – Atlantic Undersea Test and Evaluation Center
BMMRO – Bahamas Marine Mammal Research Organisation
CHLRs – Chlordanes
CTCRW – Continuous Time Correlated Random Walk model
CU – Cul de Sac stratum
D – Distinctiveness rating
DDT – Dichlorodiphenyltrichloroethane
DoD – Department of Defense
DTAG – Digital acoustic recording tag
EA – East Abaco stratum
EABC – East Abaco stratum
EX – Exuma Sound stratum
FAME - Fatty acid methyl esters
GB – Grand Bahama stratum
Gm – Short-finned pilot whale, *Globicephala macrorhynchus*
FAs – Fatty acids
h - Haplotypic
HCHs – Hexachlorocyclohexanes
ICI – inter-click-interval
IPI – inter-pulse-interval
LD - Linkage disequilibrium
LIMPET – Low Impact Minimally Percutaneous External Transmitter
LOCPRIOR - Location prior
Md – Blainville's beaked whale, *Mesoplodon densirostris*
Me – Gervais' beaked whale, *Mesoplodon europaeus*
mtDNA – mitochondrial DNA
NAND - North Andros/South Berry Is. stratum
NE – North Eleuthera stratum
NEWL - Northwest Eleuthera
NOAA – National Oceanographic and Atmospheric Administration
nuDNA – nuclear DNA
NWSFC – Northwest Fisheries Science Center
ONR – Office of Naval Research
Pe – Melon-headed whale, *Peponocephala electra*
pi - nucleotide
Pm – Sperm whale, *Physeter macrocephalus*
PBDEs – Polybrominated diphenyl ethers
PCA – Principal component analyses
PCBs – Polychlorinated biphenyls
POPs – Persistent Organic Pollutants

Q – Quality rating
QAIC - quasi-Akaike Information Criterion
RHIB – Rigid-hulled inflatable boat
SA – South Abaco stratum
SD – standard deviation
SERDP – Strategic Environmental Research and Development Program
SGBA – South Grand Bahama stratum
SIs – Stable Isotopes
SLAR – Standardized lagged association rate
SRY – Sex-determining Region of the Y chromosome
SWFSC – Southwest Fisheries Science Center
TAT – Time-at-temperature
TDR – Time-depth recorder
TO – Tongue of the Ocean stratum
TOTO – Tongue of the Ocean
Zc – Cuvier's beaked whale, *Ziphius cavirostris*
ZFX – Zinc Finger protein, X linked

Keywords

Behavioral ecology, odontocete, social structure, residency patterns, reproductive biology, diet, foraging ecology, habitat use, population structuring

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Behavioral Ecology of Deep-diving Odontocetes in The Bahamas

Abstract

Objectives

Odontocete cetaceans are known for the diversity and complexity of behavioral ecology exhibited across this diverse taxonomic suborder. Characterization of such population-specific traits is required for assessing and mitigating the potential impacts of anthropogenic activities. The Great Bahama Canyon, in the northern Bahamas, was the site of a multi-species atypical stranding of cetaceans associated with the use of Navy sonar. More recently, dedicated studies of beaked whales (Family *Ziphiidae*) in this area documented behavioral responses of these deep-diving odontocetes to sonar exposure at the United States (U.S.) Navy's Atlantic Undersea Test and Evaluation Center (AUTEC). The AUTEC range, and the Great Bahama Canyon in general, is known to be used by a number of odontocete species in addition to beaked whales, requiring data on species-specific vulnerabilities.

In this study, an interdisciplinary set of individual-based data was used to provide baseline information on the behavioral ecology of six Department of Defense (DoD) priority species of odontocete cetaceans that occur sympatrically throughout the Great Bahama Canyon. The six species are taxonomically diverse and include two species of delphinids (melon-headed whales *Peponocephala electra, Pe*; short-finned pilot whales, *Globicephala macrorhynchus, Gm*), three species of beaked whales (Blainville's, *Mesoplodon densirostris, Md*; Gervais', *Mesoplodon europaeus, Me*; Cuvier's, *Ziphius cavirostris, Zc*) and the sperm whale (*Physeter macrocephalus, Pm*). The six study species range in adult size from less than 3 m to greater than 15 m, all are thought to be deep diving, and all are found in deep-water habitats that overlap with Navy sonar use. The project's goal was to characterize and compare habitat use and behaviors of these species and to assess potential vulnerabilities to disturbance from Navy activities.

Technical approach

Data acquired through individual photo-identification, molecular genetics and chemical biomarkers from tissue biopsies, satellite telemetry, and acoustic recordings were integrated to characterize the population structure and movement patterns, social organization, foraging behavior, and habitat of each species. Three month-long shipboard surveys of the Great Bahama Canyon were conducted annually between 2011 and 2013. Data were also leveraged from studies conducted prior to, and concurrent with the Strategic Environmental Research and Development Program (SERDP) project, resulting in a total dataset of over 60,000 photographs from 913 encounters, 407 biopsy samples, 95 acoustic detections comprising over 200 hours of recordings, and 74 tag deployments. Encounters were distributed across seven geographically-defined strata that divided the Great Bahama Canyon and surrounding waters.

Results

Photo-identification (over 24 years) and satellite telemetry (maximum deployment of 92 days) revealed ranging patterns that varied greatly across species. *Gm* exhibited relatively

widespread movements across strata throughout the canyon, and some groups were tracked into Gulf Stream waters off the coast of Florida. Together with an extremely low re-sighting rate over multiple years from photo-identifications (<0.01% of individuals re-sighted) and population genetic analyses, these data suggest a population that ranges well beyond the Bahamas and is likely part of a stock recognized in U.S. waters. The movements of *Pe* also were relatively expansive within the canyon, but the distinctly seasonal pattern to their encounters (April – September) and the anomalous signatures of persistent organic pollutants measured in blubber biopsies suggest they may be seasonal migrants into the study area from elsewhere. In contrast to these two delphinid species, *Pm* exhibited evidence of sex-based habitat partitioning. Genetically-confirmed and tagged sub-adult males ranged more widely than adult females with the majority of young males tracked primarily within the Tongue of the Ocean (containing the AUTEC range) either solitarily or in small bachelor groups, in contrast to adult female groups and their calves that rarely used this area. Photo-identification data documented multi-year re-sightings of individuals within both demographic groups, suggesting a vulnerability of the sub-adult males that may be repeatedly disturbed by sonar exposure at AUTEC. Genetic analyses revealed that bachelor males were more closely related to one another than to adult females, suggesting these males may be immigrants from areas outside the canyon rather than originating from local matrilines. In contrast to the other tagged species, telemetry data showed beaked whales (*Md* and *Zc*) exhibit a high level of site-fidelity on a small-scale (movements <100 km from the tagging site). This was strongly supported by photo-identification analysis for *Md*, which documented high site fidelity of adult females to local sampling strata, including AUTEC, spanning more than a decade. This suggests that beaked whales, particularly *Md*, may be vulnerable to repeated disturbances due to their limited ranging patterns.

Diverse patterns of social organization were found among species in the Bahamas, ranging from long-term associations of *Gm* of both sexes to a fission-fusion social structure found in *Pe.* Seven *Pm* social units were identified in the study area, consisting of adult female nursery groups and a single bachelor unit comprised of three males. *Md* was the only beaked whale species with sufficient data for detailed social structure analyses. Analyses revealed a generally fluid social structure with harem-like groups typically consisting of a single adult male and several reproductive females and their young. Males remained with the same group of females for up to a year while female associations persisted over multiple years and were driven by a common reproductive state. Of all six odontocete species studied, *Pe* have the most fluid social structure, though some dyadic bonds were suggested by similar persistent organic pollutant concentrations (which bioaccumulate over lifetimes) in associating males. Overall, evidence of long-term and/or complex social structure in all four species studied raises concern for anthropogenic activities that could disrupt key individuals within their social units and their resultant effect on the entire unit.

Diving capacity was generally found to scale with body size from the smallest species (*Pe*) to the largest (*Pm*); however, both tagged beaked whale species had maximum dive depths and durations that exceeded even those of the much larger sperm whales (dive maximums: *Md* 1888 m and 65 mins; *Zc* 1888 m and 100 mins; compared to 1344 m and 62 mins for *Pm*). These relatively long and deep foraging dives likely exceeded the aerobic dive limits for the smaller beaked whales and were followed by recovery periods of shallow non-foraging dives. This contrasted with the relatively continuous bouts of deep-diving exhibited by both delphinid species and sperm whales. This diving strategy enables beaked whales to access upper bathypelagic foraging niches despite their relatively small sizes, but at the cost of significantly

reduced dive efficiency (less than 30% of total time spent in target foraging depths). This foraging strategy induces a particular vulnerability to disturbance, as any disruption to normal behavior could constrain foraging opportunities that are already physiologically limited.

Variation across species in their vertical foraging habitat suggests diet differences, which were supported by analysis of chemical tracer data from skin and blubber biopsies. Nitrogen and carbon stable isotope ratios indicated niche separation among all six species, with the two delphinid species (*Gm* and *Pe*) apparently feeding at a much lower mean trophic level ($\delta^{15}N_{mean}$ ~10.3) than any of the three beaked whale species studied ($\delta^{15}N_{mean}$ ~11.8). Conversely, *Pm* appear to be feeding at trophic levels intermediate between delphinids and beaked whales ($\delta^{15}N_{mean}$ ~11.3). The rather large differences observed in $\delta^{15}N$ values between these three groups suggest their diets are distinctly different, an observation supported by dietary fatty acid profiles that generally separated species into the same three groupings.

Species differences in diurnal patterns of diving, and diving relative to the available bathymetric depth provided insight into these diet differences. Beaked whales appeared to forage closest to the benthos, and were the least diurnal of the tagged species. Of these, *Zc* was most likely to feed on or close to the benthos, with *Md* possibly slightly higher in the water column. Although no direct dive data were recorded from the third species of beaked whale, *Me*, inference gleaned from a blubber fatty acid model developed as part of this study indicates that foraging depth is likely similar to both the other beaked whales. The other three species performed shallower dives (typically less than 1000 m for *Pm*, and less than 500 m for *Gm* and *Pe*) that showed distinct diurnality. *Pm* and *Gm* had deeper and longer daytime dives than night dives, presumably responding to the diurnal vertical migration of their prey in the water column. The only recorded dives for *Pe* at depths below surface waters occurred at night, suggesting they feed only at night when their prey are accessible within their dive range and that they may be unable to dive deep enough during the day to reach bathypelagic prey. These multiple lines of evidence indicate that, in addition to maintaining a moderately high degree of niche separation by foraging at different depths, these six sympatrically distributed species also maintain separation in sympatry by selectively foraging on different prey items.

Benefits and next steps

These new data fill key data gaps and provide necessary information for decision-making to mitigate impacts of Navy activities on vulnerable species and populations. Despite melon-headed whales being a highly mobile species, re-sightings across multiple years of over a third of individuals photo-identified at AUTEC suggests that ongoing monitoring is required to assess and identify population-level impacts from repeated disturbance at this site. Similarly, estimates of future Navy "takes" of the *Gm* stock off the U.S. southeast coast likely need to include takes that occur at AUTEC due to new data documenting the movement of individuals between regions. The integrated results for *Md* emphasize a particular vulnerability for these animals at AUTEC and a precautionary need for this distinct subpopulation to be considered a separate conservation unit. Although data are more limited, resource managers should also consider other beaked whales in the Bahamas particularly vulnerable to disturbance because of similar foraging constraints and apparently limited ranges. Future work in the Bahamas should focus on developing longitudinal datasets for *Zc* and *Me* in the Tongue of the Ocean (TOTO) and surrounding waters of sufficient resolution to allow monitoring of these potential effects. To develop an effective management strategy for sperm whales in the Bahamas, it is necessary to investigate the stock identity for whales using TOTO through an expanded study of population

structure and gene flow throughout the wider Caribbean. To this end, the sperm whale photo-identification catalogue and acoustic recordings of codas compiled during this project will be shared with collaborators in the North Atlantic, and genetic data could contribute to an expanded population study.

Objectives

Using an interdisciplinary set of individual-based data we provide quantitative baseline data on the behavioral ecology of six Department of Defense (DoD) priority species in the Bahamas: Blainville's beaked whales (*Mesoplodon densirostris*, *Md*), Gervais' beaked whales (*Mesoplodon europaeus*, *Me*), Cuvier's beaked whales (*Ziphius cavirostris*, *Zc*), sperm whales (*Physeter macrocephalus*, *Pm*), short-finned pilot whales (*Globicephala macrorhynchus*, *Gm)* and melon-headed whales (*Peponocephala electra*, *Pe*). Data acquired through individual photo-identification, molecular genetics, fatty acid, persistent organic pollutant and stable isotope profiles, satellite telemetry and acoustic recordings were integrated to characterize the population structure and movement patterns, foraging behavior and habitat, and social structure of these key cetacean species. These data are used to assess the potential vulnerabilities of each species to disturbance from Navy activities, guiding management decisions and informing conservation efforts.

Background

Odontocete cetaceans are well known for the diversity and complexity of social structure and behavioral ecology exhibited across this diverse taxonomic suborder (*e.g.*, Bigg *et al.* 1990, Amos *et al.* 1993, Christal *et al.* 1998, Gowans *et al.* 2007, Mahaffy *et al.* 2015). Identifying significant social units, ecological niches and critical habitats are key components for characterizing a population's social organization and patterns of habitat use, which in turn are critical for understanding the distribution, behavior and status of a species. Intra-specific social and ecological diversity exhibited by some odontocetes highlights the need for population specific studies (*e.g.*, Connor *et al.* 2000, Parsons *et al.* 2003a, Foote *et al.* 2009, Andrews *et al.* 2010). Adequate characterization of the structure and ecology of cetaceans has become a necessary component for both assessing and mitigating the potential impacts of anthropogenic activities (Cox *et al.* 2006).

Atypical strandings and behavioral responses of beaked whales have been correlated with navy sonar and air guns used during seismic exploration (*e.g.*, Frantzis 1998, Balcomb and Claridge 2001, Jepson *et al.* 2003, Peterson 2003, Cox *et al.* 2006, McCarthy *et al.* 2011, Tyack *et al.* 2011, DeRuiter *et al.* 2013), raising concern that beaked whales may be particularly vulnerable to anthropogenic sounds. However, other deep-diving odontocetes have also shown behavioral responses to sonar (Hohn *et al.* 2006, Southall *et al.* 2006, Miller *et al.* 2012, DeRuiter *et al.* 2013). This has highlighted the need for baseline data on the behavioral ecology of all deep-diving odontocetes with overlapping distributions with navy activities, to effectively mitigate potential effects.

Our study area is the site of a previous mass stranding of beaked whales associated with the use of navy sonar (Balcomb and Claridge 2001). Also, sonars are currently regularly used on the weapons range of the U.S. Navy's Test and Evaluation Center (AUTEC), within our study area in Tongue of the Ocean (Figure 1), and recent data have documented beaked whales at AUTEC to exhibit behavioral responses to sonar exposure (McCarthy *et al.* 2011, Tyack *et al.* 2011, Moretti *et al.* 2014). The AUTEC range, and our study area in general, is known to be used by a number of odontocete species, requiring more data on their vulnerabilities. The six species of priority in this study are taxonomically diverse, including two species of delphinids (*Pe* and *Gm*), three species of beaked whales (*Md, Me, Zc*) and the sperm whale (*Pm*), which range in size from <3m to >15m maximum length (Jefferson *et al.* 2011). All are found in deep-water and pelagic habitats that overlap with navy sonar use, and all are known, or assumed, to be deep-divers (Miller *et al.* 2004a, Miller *et al.* 2004b, Watwood *et al.* 2006, Baird *et al.* 2006, Tyack *et al.* 2006; Aguilar de Soto *et al.* 2008; Schorr *et al.* 2014). As such, understanding their movement and diving behavior is key to understanding and comparing their vulnerabilities, and we used direct data from satellite telemetry and photo-identifications, along with indirect inference from chemical tracers in their tissues to describe and compare the habits and habitats of these sympatric species.

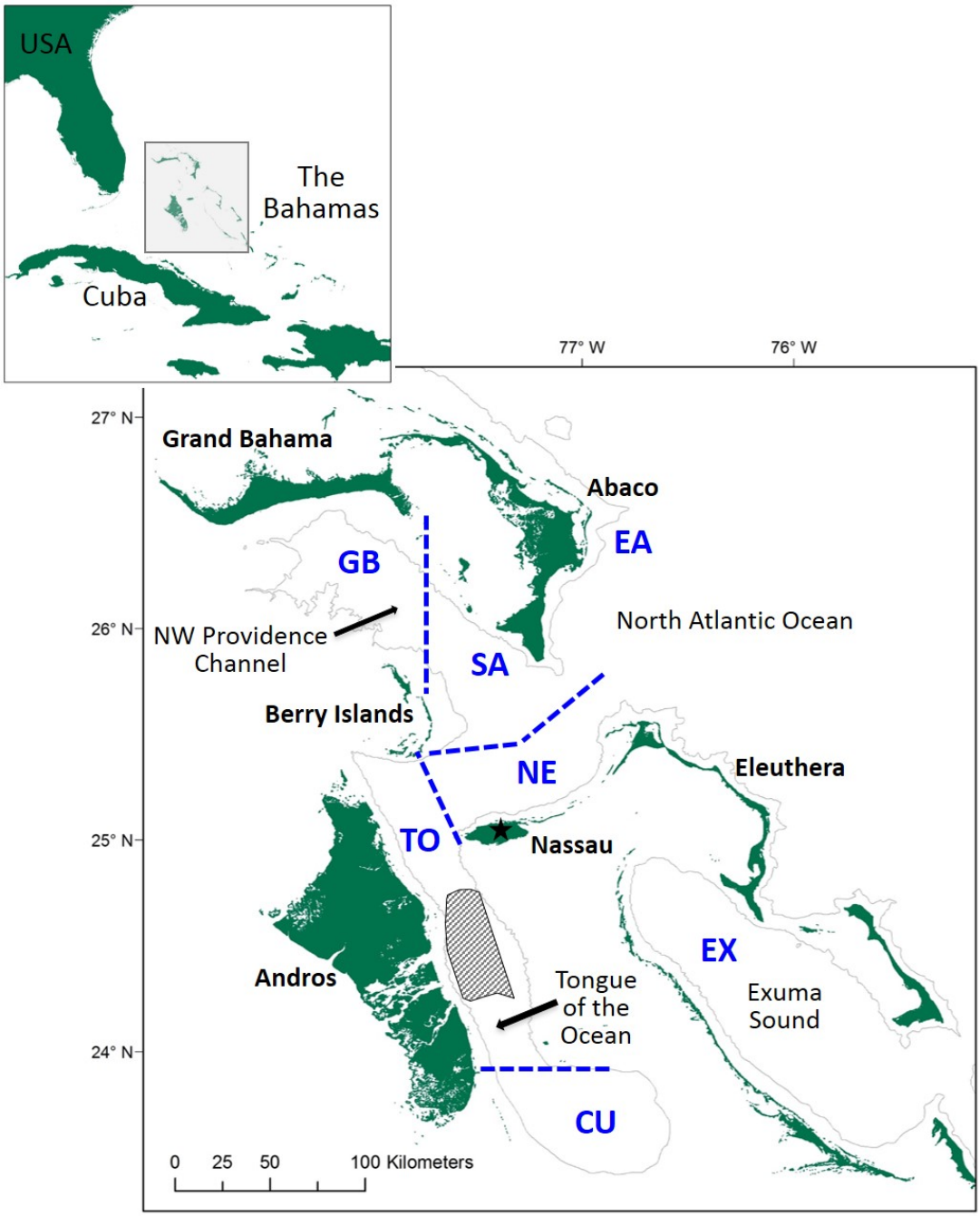


Figure 1. Map of the study area; the Great Bahama Canyon is located in the northern Bahamas and has two branches; NW Providence Channel and Tongue of the Ocean. The names of the main islands surrounding the canyon are shown. The AUTEC weapons range located in the Tongue of the Ocean is represented by the hashed area, and the 1000 m isobath by the gray line. The blue dashed lines and abbreviated names show the boundaries of the strata used in data analyses; GB = Grand Bahama, SA = South Abaco, EA = East Abaco, NE = North Eleuthera, TO = Tongue of the Ocean, CU = Cul de Sac, and EX = Exuma Sound.

We also adopted an integrated suite of research tools to investigate key structural processes within the populations of these priority species. Social-constraints, such as group living or mating systems can affect the distribution of individuals based on their specific age and/or sex classes within populations, which can render certain age and/or sex classes more vulnerable to anthropogenic activities. Moreover, social organization is also an important determinant of the genetic structure of natural populations. Work in other regions has suggested a degree of matrilineal structuring within both pilot (Amos *et al.* 1993, Fullard *et al.* 2000) and sperm whale (Richard *et al.* 1996, Lyrholm *et al.* 1999, Engelhaupt *et al.* 2009) populations, where stable social units are often comprised of maternally-related kin. Claridge (2006) described a harem-type social structure in Blainville's beaked whales from the Bahamas and suggested that a dominance hierarchy driven by female defense polygyny was influencing the spatial distribution and occupancy patterns of individuals. McSweeney *et al.* (2007) reported similar findings in Hawaii. However, little is known about social and population structuring within the two other species of beaked whales in our study area, or within melon-headed whales aside from recent dedicated efforts around the Hawaiian Islands (Aschettino *et al.* 2012, Woodworth *et al.* 2012). We combined the use of molecular genetics, acoustics, chemistry and photo-identification to fill key data gaps on the social structuring and population consequences for these sympatric species, providing highly-resolved baseline data for understanding their occupancy and vulnerability in this strategically-important region.

Materials and Methods

Visual data collection

An 18 m diesel-powered catamaran was used to conduct 30-day visual and acoustic surveys of the Great Bahama Canyon (Figure 1) annually between 2011 and 2013 using standardized ship survey methods (Thomas *et al.* 2006, Zerbini *et al.* 2006). Surveys were designed to cover the full extent of the study area, with additional effort focused in areas of known high cetacean density to increase individual-based sampling opportunities.

The visual survey team consisted of six marine mammal observers using binoculars to search for cetaceans. Three observer positions included two primary observers positioned on opposite sides of the observation platform (7.64m above sea level) using 15 X 80 Fujinon binoculars to scan from 90° on their side and overlap 10° in front to provide greater coverage of the ship's track line. The third observer was responsible for scanning the centerline (track-line) using 7 X 50 reticule binoculars and searching the near view by eye, and also served as data recorder. The team was responsible for confirming species identification and group size, and providing reticules and bearing data (using 15 X 80 binoculars) that was needed to calculate distance to sightings from the track line. To minimize fatigue, the 3-person visual team rotated through 30 minute shifts in each position, totaling 1.5 hours on, followed by 1 hour off.

After recording sightings, the vessel broke off the survey track-line for a close approach on the group. Closing mode was adopted, when needed, to confirm species identification and to better estimate group size. During sightings of the six priority species, a 6.8 m RHIB was deployed for photo-identification, biopsy sampling and satellite tagging when weather permitted. When close approaches were successful in allowing the collection of individual-based data, these events were termed encounters. The survey vessel remained in the area to provide visual support for the RHIB and/or to track the whales acoustically and make acoustic recordings.

Data were collected prior to this SERDP award from a wide variety of ship and boat platforms, ranging from 6 to 83 m in length. Previous efforts included vessel surveys throughout the Great Bahama Canyon, Exuma Sound and off Abaco Island, which provided the majority of tissue samples analyzed during this study. Additionally focused research on the weapons range at AUTEC has been conducted since 2005, with the survey vessel being vectored to animals by real-time acoustic detections using a network of bottom-mounted hydrophones (Moretti *et al.* 2006). Much of the previous work was shore-based and limited in the area covered by the use of small boats so encounters tended to occur closer to shore. Even during ship surveys work tended to focus in the same small area while a favorable weather opportunity lasted. For analysis purposes, it seemed reasonable to recognize the limitation in our area coverage and so we separated the entire study area into seven different geographic strata acknowledging that survey effort was neither uniform throughout any one strata, nor across strata. This approach allowed us to investigate movement patterns, compare genetic relatedness and population genetic structure, and data from chemical tracers within and between strata, and formed an important basis for understanding species-level differences in behavioral ecology.

Acoustic data collection and analyses

A 2-element 200 m hydrophone was towed from the ship's stern to aid in the detection of deep-diving cetaceans during surveys and also to record vocalizations whilst among animals. An RME Fireface 800 sound card (Audio AG, Haimhausen, Germany) was used and recordings

made using PAMGUARD software (www.pamguard.org, Gillespie *et al.*, 2008) with a sample rate of 192 kHz and written to disk as 16-bit wav files. PAMGUARD provided a real-time interface, with click classification functions that could be specified for a focus species. The real-time display also provided a bearing and distance estimate to vocalizing animals, which was used to track groups.

Recordings were analyzed distinctly for each species. For the delphinids, recordings with a single species and a good signal-to-noise ratio were identified and provided to institutions managing detection software, for their catalogue of species-specific sounds, for this geographical region. Beaked whale vocalizations were analyzed for species determination where visual species identification could not be confirmed. This was possible real-time in most cases by investigating the spectrum of the click in the PAMGUARD software. Finally, sperm whale vocalizations were analyzed to provide size estimates of the whales (Rhinelander and Dawson 2004), to look for possible vocal clans from coda clicks (Rendell & Whitehead, 2003), and to investigate for the presence of clangs (Gordon 1987).

Inter-pulse-intervals (IPI's) from sperm whale echolocation clicks can be used to acoustically estimate the size of sperm whales (Goold 1996, Gordon 1991, Rhinelander and Dawson 2004). Echolocation clicks were recorded immediately following a whale fluke up, i.e. when the whale commences a foraging dive. This allows for photo-identification of the whale producing the clicks and good signal-to-noise ratio in recordings, as the whale will typically be the closest whale to the hydrophone. Finally, recording the first clicks following the initiation of a whales' dive reduces the possible effects of off-axis clicks that can be present in clicks from a whale in different aspects. It has been shown that the best way to ensure good click structure for the measurement of IPI's is to measure clicks from either the posterior or anterior axis to the whale (Zimmer *et al.* 2005). As the whale begins producing clicks during its descent, recordings are made from the anterior axis of the whale.

Coda clicks are stereotyped patterns of clicks that the whales' produce, often while they are at the surface, and are thought to have a communicative function (Schulz *et al.* 2008, Watkins and Schevill 1977, Weilgart and Whitehead 1993). Coda clicks and clangs were identified using Rainbow Click software (www.ifaw.org/ifaw/general/default.aspx?oid=25653; Gillespie 1997), which allows for both visual and aural identification of codas. Custom-written Matlab scripts were used to calculate the inter-click-intervals (ICI's) between coda clicks and the total duration of each coda. Codas and clangs were not attributed to individual whales, but to the unit of whales the ship was with at the time.

Telemetry analyses

Tag deployments

Between 2009 and 2014, satellite transmitter tags were deployed on the dorsal fin or surrounding dorsal ridge of cetaceans using a crossbow bolt fired from 5-25 m from either a black-powder gun (Tyack *et al.* 2011) or crossbow (*e.g.*, Durban and Pitman 2012). The crossbow bolt rebounded upon contact with the whale, leaving the tag attached by two 4-6.5 cm surgical-grade titanium darts (Andrews *et al.* 2008; Figure 2). Two models of tags were used: both SPOT (AM-S240, Wildlife Computers Inc.; *e.g.*, Andrews *et al.* 2008) and SPLASH (Mk-10, Wildlife Computers Inc.; *e.g.*, Schorr *et al.* 2014) tags transmitted a series of messages to overhead Argos satellites (www.Argos-system.org) when the whales surfaced to breathe, which permitted the calculation of location estimates with associated error ellipses and also contained a stream of dive behavior information summarized internally within the tags.

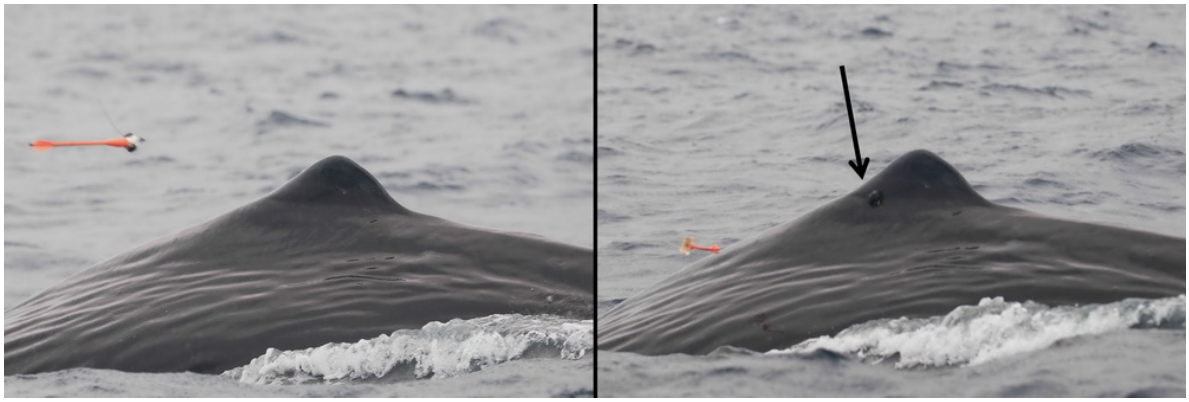


Figure 2. Photographs documenting the deployment of a satellite transmitter tag on the dorsal hump of a sperm whale in the Bahamas. The tag is projected on a crossbow bolt (left), which rebounded upon contact with the whale (right), leaving the tag attached (as indicated by the black arrow) by two titanium darts.

Inferring diving behavior

Dive information recovered from SPOT tags was transmitted in the compressed format of time-at-temperature (TAT) histograms, which consisted of the proportion of thermistor readings collected at 10 second intervals over a typically 6-hour sampling period that fall within 12 temperature categories (<4ºC, 4-6ºC, 6-8ºC, 8-10ºC, 10-12ºC, 12-14ºC, 14-16ºC, 16-18ºC, 18-20ºC, 20-22ºC, 22-24ºC and ≥24ºC). Six-hour sampling periods were programmed to begin at 01:00, 07:00, 13:00, or 21:00 local time, which were selected so that the majority of sampling contributing to any given TAT histogram fell within either daytime or nighttime periods over the course of seasonal variation in day length. To interpret the behavioral information encoded in TAT histograms on a scale of depth comparable to SPLASH tag records for each species, we applied a process detailed in Joyce *et al.* (in review) of assimilating hydrographic data and estimating the climatological depth of the isotherms dividing TAT bins at the mean estimated location of TAT-recorded dive activity using standard oceanographic interpolation methods.

SPLASH tags, which at the time of our study cost 1.64x times more than SPOT tags, used pressure measurements to provide a direct record of dive behavior. Pressure transducer observations (accuracy: +/- 1% of reading) were summarized internally within the tag and were uploaded, as satellite bandwidth and surface interval duration allowed, in the form of 3 logs. The "time series" log consisted of time-depth recorder (TDR) observations logged at 2.5 minute intervals, which were used to look at sequence of dives, and in aggregate were also used to look at the proportion of time spent in different depth strata at a finer depth resolution than available via TAT. A second "behavior" log summarized the vertical ranging activity of the tagged whales as a sequence of surface intervals and dives, which were each described by a duration and maximum depth. "Dives" were defined as exceeding a threshold of 15 m depth in a high-resolution time series of depth readings archived temporarily within an internal memory cache, and the maximum depth of each of these dives was recorded. The duration of each of these qualifying dives was defined by successive activation of the salt-water switch on the tag when it switched between wet to dry states during surfacing by the whale. The final log consisted of "depth histograms" which summarized counts of dive maxima that fell within 14 depth intervals (15-50m, 501-200, 201-300, 301-400, 401-500, 501-1000, 1001-1200, 1201-1400, 1401-1600,

1601-1800, 1801-2000, 2001-2500, 2501-3000, >3000 m) over twelve hour sampling periods. Twelve hour sampling periods were programmed similarly to TAT histograms with start times at 07:00 or 21:00 local time, which were selected to approximately coincide with sunrise and sunset times over as wide a range of seasonally varying day lengths as possible.

Modeling movement

Tags for this study were scheduled to transmit up to 700 times during 12-18 hours of each day, timed to coincide with passes of satellites from the Argos satellite system. Location estimates from the Argos system were therefore irregularly spaced, and each had an associated error ellipse, and we used a movement model to predict the maximum likelihood movement path at regular hourly increments over the duration of each track. We fit a Continuous Time Correlated Random Walk model (CTCRW, Johnson *et al.* 2008) using the *R* package *crawl* (Johnson *et al.* 2013), modified to include an observation model for the full extent of the Argos error ellipses (e.g. Ford *et al.* 2013). After fitting an initial movement model to all the available location estimates for a given individual, significant outliers were identified and removed on the basis of the measurement error shock diagnostic (p-value ≤ 0.01, de Jong and Penzer 1998) and the maximum likelihood path for each whale was subsequently refitted using the remaining data.

The estimation of movement tracks from irregularly spaced Argos estimates of varying precision was necessary to predict isotherm boundaries at the mean locations of TAT histograms and estimate the approximate bathymetric depth corresponding to dives in behavior and time series logs. The CTCRW model was used to predict maximum likelihood locations at hourly intervals over the duration of TAT and dive depth histogram sampling periods and at the precise date-time stamps of dives and time-series observations. To incorporate spatial uncertainty into hourly and specific predictions, we used 50 correlated random walks simulated from the posterior distribution of the CTCRW model to calculate the range and standard deviations of latitude and longitude associated with each timestamp.

Bathymetric depths were subsequently extracted from a 0.0083 º latitude and longitude resolution bathymetric digital elevation model at CTCRW maximum likelihood locations and simulated prediction locations using the function *extract* from the R library *raster* (Hijmans and van Etten 2012). Bottom depth uncertainty was estimated by calculating the range and standard deviation of bathymetric depth estimates at the locations simulated hourly and/or at specific timestamps from the CTCRW posterior distribution for each tracked individual. Local sunrise and sunset times were calculated at the ML coordinates and date-time stamps of each histogram, dive, and time series observation using the function *sunriset* from the R library *maptools*. Because the start and end times of TAT and dive depth histograms were fixed but the duration of daylight varied seasonally, exact proportion of each histogram occurring before or after sunset ranged from 82-100% depending on the time of year over which the tag was transmitting.

Dive bouts and foraging thresholds

Despite the compression of dive behavior and time series logs, uploading these data still necessitated significant bandwidth relative to the limitations of the Argos satellite system and the short surfacing intervals. Consequently dive behavior and time series logs both provided discontinuous records of vertical ranging over the durations of tag deployments. To compare the proportion of each dive cycle spent on foraging dives and/or the proportion each dive cycle spent within presumed foraging strata we identified complete dive cycles within each message: these were preceded and followed by dives that reached minimum foraging depth thresholds and we

separated these complete cycles from fragments collected at the beginnings and ends of messages. Depth and corresponding temperature thresholds used to discriminate between presumed foraging and non-foraging dives were 50 m and 24ºC for the delphinids *Pe* and *Gm*, 600 m and 14ºC for the sperm whale (*Pm*), 650 m and 10ºC for *Md*, and 800 m and 8ºC for *Zc*. These thresholds were identified on the basis of published acoustic records of foraging behavior (*e.g.*, echolocation clicks and "buzzes" associated with prey capture attempts, Gordon *et al.* 1987) generated by digital acoustic recording tags (DTAG) available for each tagged species except *Pe* from separate study locations (Madsen *et al.* 2002, Miller *et al.* 2004a, Tyack *et al.* 2006, Watwood *et al.* 2006, Aguilar de Soto *et al.* 2008, Teloni *et al.* 2008), as well as the visual examination of histograms of time series, behavior log, and time-at-temperature observations. In both beaked whale species and sperm whales a clear depth/temperature threshold could be defined that distinguished a deeper peak of foraging dive activity from a near-surface peak of surface intervals and/or short, non-feeding "bounce" dives associated with physiological recovery. Both species of delphinids however made rapid dives with limited bottom time, and thus the distribution of dive activity, particularly at night, were contiguous with surface time. For these species all time spent below the upper depth-temperature bin of TAT (i.e., <24ºC or ~100 m) and > 50 m in behavior and time series logs was considered foraging dive activity.

Sex and demographic identification

Sex determination of tagged individuals based on external morphology was highly reliable in species that display distinctive sexually dimorphic adult characteristics such as dorsal fin size and shape in *Gm*, erupted teeth in male beaked whales and also jawline shape in *Md* (as described in Claridge 2013). In individuals that were both tagged and successfully biopsied, genetic sex identification (see Genetics methods) provided independent confirmation. Similarly, age-class was assessed both in situ during tagging events and later using photographs, based on field-approximated size and features such as tooth eruption in male *Md* that show a strong ontogenetic progression.

Photo-identification analyses

Field sampling and processing

When a cetacean group was sighted, close approaches were typically made using small vessels (<9 m) only. When approaching whales, the vessel was maneuvered alongside or behind the group depending on whether the intention was to obtain dorsal fin or fluke photographs, deploy tags or remotely biopsy individuals (see below). Between 1991 and 2003, black and white film (Ilford HP5 or Fujifilm) was shot using Nikon 35 mm cameras. The film was later push-processed to 1600 ASA to increase contrast and help reveal markings on the whale's dorsal fin and body. Between 2004 and 2014, Nikon digital SLR cameras were used to shoot high-resolution images of at least 6 megapixels. With both film and digital cameras, either a fixed 300 mm F4 lens or 80-200 mm F2.8 zoom lens was used. When possible, photographs were taken of both the right and left sides and the flukes (sperm whales only) of all individuals within a group.

Each identification image was visually examined either using a light table and magnifying eyepiece (for the black and white negatives) or a high-resolution computer monitor (for the digital images). Individual whales were identified using the unique pattern of scarring on the body and nicks in the dorsal fin (*e.g.*, Figure 3) or flukes (sperm whales).

Figure 3. Photo-identification images of Md091, an adult female Blainville's beaked whale from the South Abaco (SA) study area, taken 10 years apart demonstrating the longevity of natural markings. Oval marks are scars from bites attributed to cookie cutter sharks (*Isistius* sp.).

To increase accuracy in matching individuals across encounters, each individual was given a distinctiveness rating (*D*) ranging from 0 to 3 (3 being the most distinct) based on the extent of scarring and severity of its marks, and only individuals deemed distinctively-marked ($D > 0$) were used in the analyses. For melon-headed whales, individual photo-identifications were further limited to include only individuals with distinctiveness rating (*D*) >1 to overcome potential misidentifications due to very large group sizes (up to 500 individuals) resulting in over 30,000 photographs to analyze. Identification photographs were assigned a quality grade (*Q*) ranging from 0 to 3 (3 being the highest quality photograph) based on the image size, focus, lighting, angle, and exposure (Figure 4), and only high quality images ($Q > 1$) were used in subsequent analyses to prevent misidentifications. To further limit identification errors, at least two researchers separately confirmed all identifications of new whales.

Figure 4. Four photographs of the same individual melon-headed whale (Pe273), but of varying image quality (*Q*), demonstrating how photographs were graded from very poor quality (0, on far left) to excellent quality (3, on far right). Only images with quality 2 and 3 were included in any of the analyses for any species.

Association analyses

Melon-headed whales

Animals were considered to be associated if they were photo-identified on the same day. We used SOCPROG 2.6 (Whitehead & James, 2015) for Matlab 2014a to analyze associations between animals. We used a sampling period of one day, and only individuals seen in more than four days were included in the analysis, to ensure associations were meaningful. Only good quality photographs ($Q > 1$) were used, and only animals that had nicks and were very distinctive ($D > 1$). We used the half-weight index to calculate associations (Cairns & Schwager, 1987). Using the average-linkage method (Milligan & Cooper, 1987), we performed a hierarchical

agglomerative cluster analysis of the association data to look for some structure in the population.

Blainville's beaked whales

Using the simple-ratio association index, we calculated the mean and maximum pair-wise association indices within and between all sex and age-classes. We used Mantel permutation tests to test correlations between association matrices and binary 1/0 matrices that indicated whether pairs of individuals belonged (1) or did not belong (0) to the same sex/age-class. Rejecting the null hypothesis of no correlation in these tests would show that individuals were more (or less, in the case of significant negative correlations) likely to associate with others of the same age-sex class than expected by chance. These tests were run with 10,000 permutations using a two-tailed significance test.

To investigate associations temporally, we used standardized lagged association rates (SLARs) to look at the probability that individuals seen together at a given time would still be associated at some time lag (τ) in the future (Whitehead 1995, 2008). Standardizing the lagged association rate accounts for the possibility that not all associates of an individual, for a particular sampling period, are included in the dataset. The analysis was carried out for all individuals in the population, as well as for adult female associations with other adult females, and adult male associations with adult females, to provide some idea of the timespans of these bonds. A null association rate, the association rate expected if there were no preferred associations, was also calculated to compare to the observed SLARs, and a jackknife process estimated the precision of the SLARs (Whitehead 1995, 2007). Models were fit to the SLARs of how an association rate changed with time (Table 1), and the model with the best fit was chosen using the quasi-Akaike Information Criterion (QAIC) (Whitehead 2007). The model with the lowest QAIC was selected as the best model (Burnham and Anderson 2002), and ΔQAICs between each model's QAIC value and that of the best model were calculated to measure model selection uncertainty (where ΔQAIC from 0 to 2 indicates neither model can be preferred with certainty; ΔQAIC from 4 to 7 shows some uncertainty and ΔQAIC > 10 indicates considerable certainty in the preference of the model with the lower QAIC value).

Table 1. Models that are fit to standardized lagged association rates from photo-identification data, by the SOCPROG software (Whitehead 2008).

Model name	Model	Description
1. Preferred companions	$g(\tau) = a$	Association rate between individuals that does not change over time
2. Casual acquaintances	$g(\tau) = a \cdot e^{-b\tau}$	Short term associations a, for the duration $1/b$
3. Preferred companions + casual acquaintances	$g(\tau) = a + c \cdot e^{-b\tau}$	Short term associations ($a + c$), for the duration $1/b$, levelling off at association rate a
4. Two levels of casual Acquaintances	$g(\tau) = a \cdot e^{-b\tau} + c \cdot e^{-d\tau}$	Short term associations ($a + c$), with different durations ($1/b$ and $1/d$)

To investigate whether associations between individuals were different from random, we created association matrices for a set sampling period, and assigned a 1 for each pair of whales that were associated within the period, and a 0 for those that were not. The sampling period was chosen as the time when the SLARs began to decline. This allowed enough time for group compositions to switch, and different associations to occur, as well as associations across sampling periods to be meaningful. These matrices were permuted by inverting the association values between randomly chosen rows, whilst keeping constant both the number of identified individuals in a group, and the number of groups in which each individual was observed (Bejder *et al.* 1998). A Mantel test was run to determine the similarity of the matrices with the null hypothesis that associations between sampling periods were no greater or less than random. The number of permutations was chosen when *p*-values indicating the test significance become stable (Whitehead *et al.* 2005).

The analysis for preferred or avoided associations included adults only, as the sub-adult age-classes had only a small number of whales (<5), and calf preference will obviously be for their mother. We tested for long-term companionship by permuting associations within samples, as recommended by Whitehead (2009), testing whether individuals associated in different sampling periods more than would be expected by chance. Preferred long-term associations would be represented by significantly high standard deviations (SD) of the real association indices (Whitehead *et al.* 2005), and evidence of avoidance indicated if the proportion of zero association indices was higher in the real dataset than the randomized version.

Where there was evidence for preference or avoidance from significant *p*-values, we ran Mantel permutation tests to compare between 1/0 matrices that indicated whether a group had a calf (1) or did not (0), and matrices detailing the measured distances (in kilometers) between these groups. Rejecting the null hypothesis of no correlation in these tests would show that groups with a calf were more (or less, in the case of significant negative correlations) likely to be sighted in a similar area. These tests were run with 10,000 permutations using a two-tailed significance test. This Mantel test for location preference was performed on matrices using the 'ape' package (Paradis *et al.* 2004) in the statistical software R software version 3.0.3 (R Development Core Team 2012), with all other tests having been performed using Matlab as part of the SOCPROG software package.

Sperm whales

We used SOCPROG 2.5 (Whitehead 2009) for Matlab R2014a (8.3.0.532) to analyze associations amongst whales within species. For sperm whales, we focused on identifying separate units of whales that are typically made up of one or more matrilines. Units are defined as pairs of whales that were associated across two separate years (Gero *et al.* 2014; Whitehead *et al.* 1991). Association was defined as being photo-identified on the same day. Boat surveys did not cover large areas intra-day, therefore animals seen on the same day were likely to be associated. Only individuals seen in more than one year and whose fluke had at least one nick ($D > 0$) were included in the analysis. Additionally, only high quality photographs ($Q > 1$) were used, therefore some associations may have been missed due to poor quality pictures of an individual, i.e. $Q = 0$ or 1, or not all individuals in an encounter being photographed. Supplementary data describing the individual's genetic sex were included. To calculate associations, we used the simple ratio association index ($x/(x + y_{AB} + y_A + y_B)$), as recommended by Ginsberg and Young (1992) and Whitehead (2009).

For our investigation into unit membership, we used the average-linkage method for hierarchical clustering analysis. The cophenetic correlation coefficient was calculated to determine how well the cluster dendrogram represented the data. A cophenetic correlation coefficient of over 0.8 is considered a 'good' representation of the associations (Bridge 1993). We used 'Type 1' modularity to identify significant divisions (Whitehead 1997; Whitehead 2009), as it controls for gregariousness. A Q-value greater than 0.3 suggests that the population has a modular structure (Newman 2004).

Chemistry analyses

Sample collection

Tissue samples collected for chemistry and molecular genetic analyses included both skin biopsies collected by remote dart biopsy (*e.g.,* Barrett-Lennard *et al.* 1996, Parsons *et al.* 2003b), as well as free-floating sloughed skin samples (for *Pm*). Presumed prey samples were collected opportunistically when fragments, fecal remains or whole bodies were found during encounters with cetaceans.

Subset of biopsy samples analyzed for chemical tracers

A subset consisting of 237 skin/blubber biopsy samples collected from 2007 – 2014 (using ONR and SERDP funding) were analyzed for a full suite of chemical tracers at the Northwest Fisheries Science Center (NWFSC). These biopsy samples generally represented blubber tissues ranging from 5 to 30 mm in depth below the epidermal layers with the majority being at least 15 mm in length (not including epidermis). For this reason, and because it is well known that both fatty acids (FAs) and persistent organic pollutants (POPs) are highly stratified in the blubber of most/all cetaceans, it became necessary to standardize the length of all blubber samples to a constant length of 12 mm (3 mm-15 mm depth) so as to consistently represent the same blubber depth for all samples. In addition, two opportunistically collected rough-tooth dolphin (*Steno bredanensis*) biopsy samples were acquired from the study area and their skin/blubber tissues measured for all three chemical tracers solely for the purpose of testing the FA-depth model described below. Finally, ten opportunistically collected presumed prey samples were also collected and analyzed for their chemical tracers. Because the number of presumed prey species is very low and several could not be identified genetically to the species level, these data are of limited utility at present and therefore will not be reported here but can be made available to any interested parties as NWFSC unpublished results. A list of all biopsy and prey samples analyzed for chemical tracers can be found in Appendix A, Table A1 along with information about their genetically-determined sex, biopsy locations, and collection dates.

Sample preservation and integrity

Samples were placed in a liquid nitrogen dewar in the field, and shipped in a charged dry shipper; as such they were stored frozen near -80º C until analyzed. Blubber samples containing less than 5% total wet weight lipid were assumed to be non-representative as the result of excessive lipid loss during biopsy dart recovery efforts in the field (Krahn *et al.* 2004). Thus, in general, blubber biopsy samples having in their outer blubber layers <5% total lipid should be excluded from all models and statistical summaries. The gravimetric procedure used in this study to measure total lipid is described in Sloan *et al.* 2014. Whereas none of the *Md, Zc, Me, Pe,* or *Gm* biopsy samples received had total lipid values <5%, numerous *Pm* samples (34 of 67) had

total lipid values less than this lower limit with some samples exhibiting lipid values as low as 0.27%. Thus, there is a clear recognition that the quality of the *Pm* biopsy blubber samples was poorer (lower lipid) than those collected from the other five Bahamas cetaceans studied and this observation must always be kept in mind when interpreting chemical tracer results for this particular species. In order to retain as many *Pm* whales in the chemistry dataset as possible, we elected to lower the minimum total lipid requirement for *Pm* to ≥1%. Using this lower total lipid criteria, 48 of the 67 *Pm* whales listed in Appendix A, Table A1 produced FA and POPs results deemed to be of adequate quality to evaluate in a manner similar to that of the other remaining five species. Skin stable isotope results are presumably not affected by poor blubber quality.

Analytes measured

Each animal listed in Appendix A, Table A1 had their 3-15 mm blubber depth tissues analyzed for total lipid (n=1), individual fatty acids (n_{total}=80), and persistent organic pollutants (n_{total} = 73) which consisted primarily of individual organochlorines (*e.g.*, Dichlorodiphenyltrichloroethanes (DDTs), Chlordanes, etc., n=19), individual polychlorinated biphenyl (PCB) congeners (n=39) and individual polybrominated diphenyl ether (PBDE) congeners (n=15). Moreover, skin tissues from each animal were analyzed for both their nitrogen and carbon stable isotope (SI) ratios using the procedure outlined below. A complete list of all individual fatty acids and POP compounds routinely measured in marine biota at the NWFSC can be found in Sloan *et al.* 2006, 2014. Individual PCB, PBDE, and organochlorine congeners were reported both on an absolute concentration basis (ng/g lipid) and a weight percent composition basis (wt%) and used to evaluate contaminant levels and provide complex patterns of chemical tracers suitable to study the population structuring among selected groups of whales, respectively. Samples that had concentrations of PCB and PBDE congeners that fell below method detection limits were excluded from all subsequent statistical summaries and multivariate analyses.

In addition to these individual POP analytes, additional POP variables (n=19) were constructed from these individual values (usually as a sum of individuals of similar class (*e.g.*, ΣPCBs) or as a ratio of two independent variables (*e.g.*, ΣPCBs/ ΣDDTs) and these constructed variables also entered into the various multivariate POPs models described below. A full list of the 32 "detectable" individual PCB congeners as well as the 19 constructed POP ratios variables entered into these models are listed in Appendix A, Table A2.

Stable isotope analyses

Cetacean epidermal tissues were analyzed for nitrogen and carbon stable isotope ratios following the procedure outlined in Herman *et al.* (2005) and Sloan *et al.* (2006). In short, the skin tissue was: sliced into small pieces, freeze-dried, lipid removed using Accelerated Solvent Extraction (ASE) with methylene chloride, air dried and pulverized to a powder in a micro ball-mill, loaded into micro tin cups, and then analyzed using an Thermal Electron Delta Plus stable isotope ratio mass spectrometer. Stable isotope ratios are reported as per mille (‰) using standard delta notation ($\delta^{15}N$ and $\delta^{13}C$).

Persistent organic pollutant analyses

Blubber biopsy samples were analyzed for POP contaminants following laboratory procedures described in detail elsewhere (Sloan *et al.* 2006, 2014). Briefly, the procedure involves: extraction of POPs by ASE using methylene chloride, removal of extraneous polar

biogenic using a stacked silica gel/alumina column, removal of bulk lipid using high performance size exclusion liquid chromatography, and finally analysis of POPs by low resolution GC-MS (SIM-mode). A full list of all POPs measured as part of this study (both detectable and undetectable), their abbreviations, systematic & trivial names, and lists of compounds comprising the summary quantities, as well as quality assurance procedures can be found in Sloan *et al.* 2006, 2014.

Fatty acid analyses

FA concentrations in blubber were measured as previously described (Krahn *et al.* 2004; Herman *et al.* 2005) and their weight percent compositions (concentration of each individual fatty acid methyl esters (FAME) relative to the sum of all FAMEs, wt (%) were expressed in units of FAMEs. In short, the procedure includes: ASE extraction of lipid with methylene chloride, transesterification of lipids to FAMEs using 3% sulphuric acid in methanol, addition of water followed by liquid-liquid extraction of the FAMEs into isooctane, and finally analysis by low resolution GC-MS (SIM-mode). The n-number standard nomenclature system was used for abbreviating the names of these FAs, where the number following the 'n' symbol appearing in the abbreviation refers to the carbon position of the first double bond relative to the alkyl end of the molecule. A full list of all 83 FAs measured as part of this study (of which three were added as internal standards), their abbreviations, systematic and trivial names, and lists of compounds comprising the summary quantities, as well as quality assurance procedures can be found in Sloan *et al.* 2006, 2014.

Statistical analyses

All multivariate and univariate analyses described herein were conducted using either JMP Statistical Discovery Software (PC profession edition, version 5.01) or Primer-E statistical software package (Version 6.1.6). Unless otherwise stated, all univariate comparisons between 2 group means were significant tested (α=0.05) using a simple two-sample Student's t-test assuming equal variances. Multivariate comparisons of fatty acid profiles among individuals and/or groups of whales were conducted using a combination of principal component analyses (PCA) and Analysis of Similarities (ANOSIM). PCA analysis of FAME results for both exogenous "dietary only" fatty acids and PCA analysis of "all fatty acids" (endogenous and exogenous) were conducted by performing the analyses on the correlation matrices of their standardized wt% composition results. Prior to PCA and ANOSIM multivariate analyses of the 13 fatty acids deemed to be primarily of dietary origin (see list in Appendix A, Table A2), the wt% composition results for the 13 dietary fatty acids were re-standardized by expressing their concentrations relative to the sum of the wt% compositions of all dietary fatty acids rather than the sum of all detectable fatty acids. It is the pattern of these standardized dietary fatty acids that will be used in this study to assess differences in perceived prey preferences among individual whales and among pre-defined groups of whales. Finally, all hierarchical cluster analyses reported herein were computed based on the distribution of their Ward Distances.

Chemical tracers as indicators of short-/long-term foraging structure

Assuming the turn-over rates (half-lives) of nitrogen and carbon isotopes in the epidermis tissues of all six DoD-priority species are similar to those reported in other cetacean species ($t_{1/2}$ ~ 14-17 days, Browning *et al.* 2014), the SI ratio signals measured in the skin of these whales should reflect their integrated diets over a period of about 2 months. Thus, SI ratios are indicators

of short-term (seasonal durations) foraging behavior. Unlike SIs, exact turn-over rates of fatty acids in the blubber of cetaceans have not been directly reported, but are generally assumed to be comparable to SI turn-over rates; thus also rendering exogenous blubber fatty acids as potential indicators of short-term foraging. Conversely, strongly lipophilic persistent organic pollutants measured in the blubber of marine mammals have been shown to bioaccumulate over a life-time with as little as 2% of their total body burdens of ΣPCBs being eliminated/metabolized each year (Hickie *et al.* 2007; Mongillo *et al.* 2012). However, unlike SIs and FAs, POP concentrations (and patterns) measured in the blubber of these whales are reflective of both the integrated average of prey consumed, and most importantly, their primary foraging habitats over their lifetimes. Thus, in combination, these three independent chemical tracers can provide useful insights into both the short- and long-term prey preferences and foraging habitats of live, free-ranging cetaceans that are not easily accessible by other means over these timeframes. The foraging structure (short/long-term) of each of the six priority species were evaluated using all three of these chemical tracers with specific emphasis on assessing the extent to which these whales exhibit strong foraging site-fidelity to any one of the six defined strata depicted in Figure 1. Solely for the purpose of interpreting our chemical tracer data, we have sub-divided the area depicted as TO in Figure 1 into two separate substrata (re-designated as TO and NA) where the new NA substrata encompasses the segment of the original TO strata beginning at 25ºN latitude and extending north to/including the areas directly offshore of the Berry Island group. Division of the original defined TO strata into two substrata is warranted owing to the fact that we observe moderate to large differences in the quantities of all three chemical tracers between these two adjoining regions for some species, most notably the two delphinids (*Gm* and *Pe*).

Genetic analyses

Sample processing and molecular genetic marker amplification

Samples were stored frozen in salt-saturated DMSO solution until the time of processing. Total genomic DNA was isolated from skin biopsy subsamples using either silica-based filter membranes (Qiagen, Valencia, CA) or lithium chloride (Gemmell and Akiyama 1996) standard extraction procedures. DNA concentrations were determined using a QuBit (Invitrogen) fluorometer and normalized to a working concentration of 2 ng/µl.

Individual samples were genetically sexed by PCR amplification of the sex-determining region of the Y chromosome (SRY) and the zinc finger protein, X linked (ZFX) genes following Rosel (2003). The mitochondrial control region sequence was amplified from *Pm* and *Gm* samples via PCR in two overlapping fragments in 20 ul reaction volumes using oligonucleotide primers and annealing temperatures specified in Table 2. Amplicons were sequenced both forward and reverse on model 3100 Applied Biosystems Inc. sequencer. Sequences were manually checked for sequencing errors or questionable base calls, aligned and contiguous sequences created in CodonCode Aligner (CodonCode Corp., Dedham, MA). Control region haplotypes were assigned with reference to published sequences deposited in GenBank. Haplotypic (*h)* and nucleotide (pi) diversities were estimated according to Nei (1987) to describe the control region sequence divergence and haplotype frequency differences using Arlequin v3.5 (Excoffier and Lischer 2010).

Table 2. Primers and annealing temperatures used to amplify the mitochondrial control region from skin biopsies collected from short-finned pilot whales and sperm whales in the Bahamas.

Species	Primer set #1	Annealing Temp (ºC)	Primer set #2	Annealing Temp (ºC)	Reference
Globicephala macrorhynchus	H16498 & L15812	56	DL3c & 12SC	60	Zerbini *et al.* (2007)
Physeter macrocephalus	PmacD & TRO	48	DL3c & 12SC	60	Mesnick *et al.* (2011)

Samples were genotyped at 22 (*Gm*) or 18 (*Pm*) nuclear microsatellite loci using conditions and multiplex complexes specific to each species/locus combination (Appendix A - Table A3). Loci were amplified in groups of 2 to 5 multiplexed loci with non-overlapping allele sizes using the Qiagen Multiplex PCR Kit. Each multiplex PCR was performed according to the conditions suggested by Qiagen Multiplex PCR Kit handbook in a reduced total reaction volume of 20uL. Additional PCR conditions are described in Appendix A, Table A3. Amplified products were analyzed using an ABI 3100 automated DNA sequencer and allele sizes were determined using ABI LIZ500 as the internal size standard. GeneScan v3.7 and Genotyper v3.7 (ABI) software were used to collect and analyze microsatellite data.

Genotyping quality control measures included negative control reactions at each step including DNA extraction, PCR, and sequencing, as well as replicate genotyping of multiple samples. An overall genotyping replication rate of ≥11% of samples allowed us to empirically estimate the per allele genotyping error rate (Hoffman and Amos 2005; Morin *et al.* 2010). In addition, each PCR set included at least two samples previously genotyped to provide cross-plate controls and ensure consistent allele binning throughout the study.

Identifying duplicate samples, estimating genetic diversity and removal of close kin

DROPOUT (McKelvey and Schwartz 2005) and GenAlEx (Peakall and Smouse 2006) were used to examine the microsatellite genotype dataset for potential errors and to identify duplicate genotypes by comparing all multilocus genotypes to one another. All pairs of genotypes that mismatched at three or fewer loci were rechecked for potential scoring errors by re-examining the electropherograms for those loci. Pairs of samples that were identified as genetic matches were further examined by comparing control region haplotypes and genetic sex. Duplicate genotypes were removed from the dataset and all further analyses were conducted on a data restricted to only a single representation of each genotyped whale. Departures from Hardy-Weinberg equilibrium expectations using the Fisher's exact test (Guo and Thompson 1992) and tests for genotypic disequilibrium among the loci were assessed using GENEPOP v4.0 (Raymond and Rousset 1995). Multiple tests error rate was adjusted using the sequential Bonferroni correction (Rice 1989).

Intraspecific pairwise estimates of genetic relatedness were calculated in KINGROUP (Konovalov *et al.* 2004) using a maximum likelihood estimator and the observed microsatellite allele frequencies (Konovalov and Heg 2008). Both sperm whales and pilot whales are known from other studies to exhibit high site fidelity and fidelity to social groups sometimes spanning multiple years. Such characteristics increase the likelihood of incidentally sampling multiple

related individuals within the life of a study which has the potential to impact estimates of population structure and inflate measures of genetic distance through violations of model assumptions due to allelic enrichment (Amos *et al.* 1993). To account for the possible over-representation of 'kin' within the datasets putative genetic kin were identified using hypothesis testing in KINGROUP (Konovalov *et al.* 2004) for given genetic relationships. Statistical significance of the null hypothesis was estimated empirically through simulations for a given hypothesis given the observed allele frequencies and 10,000 random permutations of the dataset. Pairs of statistically significant 'kin' (*i.e.*, parent-offspring, full-sibs, or half-sibs) were compared to those identified as falling within 95% CI's for given genetic relationships using ML-RELATE (Kalinowski *et al.* 2006).

Intraspecific genetic differentiation within Great Bahama Canyon

Intraspecific genetic structure within the Bahamas was examined by estimating genetic differentiation among *a priori* subdivisions. Putative geographic strata were defined based on the location in which individuals were biopsied and individuals were assigned to the stratum in which they were sampled. Genetic differentiation among these strata was quantified through pairwise comparisons among strata and an Analysis of Molecular Variance (AMOVA, Excoffier *et al.* 1992). To test hypotheses of divergence between putative populations, the pairwise divergence metrics F_{ST} (Wright 1931, Weir and Cockerham 1984) and F'_{ST} (Hedrick 2005) were calculated from nuclear genotypic data using the R package "strataG" (R Development Core Team 2011, Martien *et al.* 2014) and 5,000 permutations of the dataset to calculate the p-value. Both F_{ST} and Phi_{ST} overall, as well as pairwise comparisons among strata, were estimated for mtDNA sequence data as implemented in Arlequin 3.5.x (Excoffier *et al.* 1992). For Phi_{ST} estimates, the Tamura-Nei (Tamura and Nei 1993) model of sequence evolution with α=0.47 was used. A hierarchical AMOVA was also used to examine the partitioning of genetic variance among strata and among encounter groups within strata for pilot whales.

To explore the data for evidence of genetic structuring without imposing *a priori* subdivisions, the Bayesian clustering algorithm implemented in STRUCTURE 2.3 (Pritchard *et al.* 2000) was employed to estimate the number of genetically distinct subpopulations, assuming the admixture model with correlated allele frequencies. In light of photo-documented movements of individual whales among neighboring strata, and the generally weak signals of population genetic structure resolved for other cetacean populations, it is reasonable to expect relatively weak signals of genetic differentiation. Therefore, we applied the model of Hubisz *et al.* (2009), incorporating general sample locations to inform cluster assignments. The sampling location prior (LOCPRIOR) was assigned according to the *a priori* geographic strata described above. We executed five independent runs of 10^5 MCMC iterations (after burn-in of 10^5 iterations) for each model to estimate the support for each number of candidate clusters, *k*, from 1 to 6. The most likely number of clusters, *k*, was compared using both methods of Pritchard *et al.* (2000) and the statistic Δk which quantifies the second order rate of change in log-likelihood across the range of *k* values as described by Evanno *et al.* (2005).

All estimates of genetic differentiation and STRUCTURE runs were calculated for the full dataset, as well as a restricted dataset from which one individual from each pair of identified likely genetic kin was removed for analyses of spatial genetic patterns to minimize the impact of inclusion of kin in the dataset. For sperm whales, the model was also fit to a dataset comprising only adult females to examine the matrilineal structure often ascribed to this species.

Results

SERDP field data collection

Three month-long visual and acoustic surveys were conducted in the Great Bahama Canyon during June 2011, 2012 and 2013, which were used as platforms for individual-based sampling. A team of six observers visually surveyed 7,367 km of ship track-line, resulting in 92 sightings of our six priority species (Figure 5). Data were collected from each of the 5 strata within the canyon as intended but additional time was designated during surveys south of Grand Bahama Island (GB) and the Cul de Sac (CU) to increase sampling in those areas, with mixed success. Although we adequately sampled all six priority species in GB, the exposed nature of the CU limited our sampling in that strata. Furthermore, efforts tended to be focused in several coastal areas in SA, NE and TO where close proximity of deep water allowed us to work in a lee shore during windy periods.

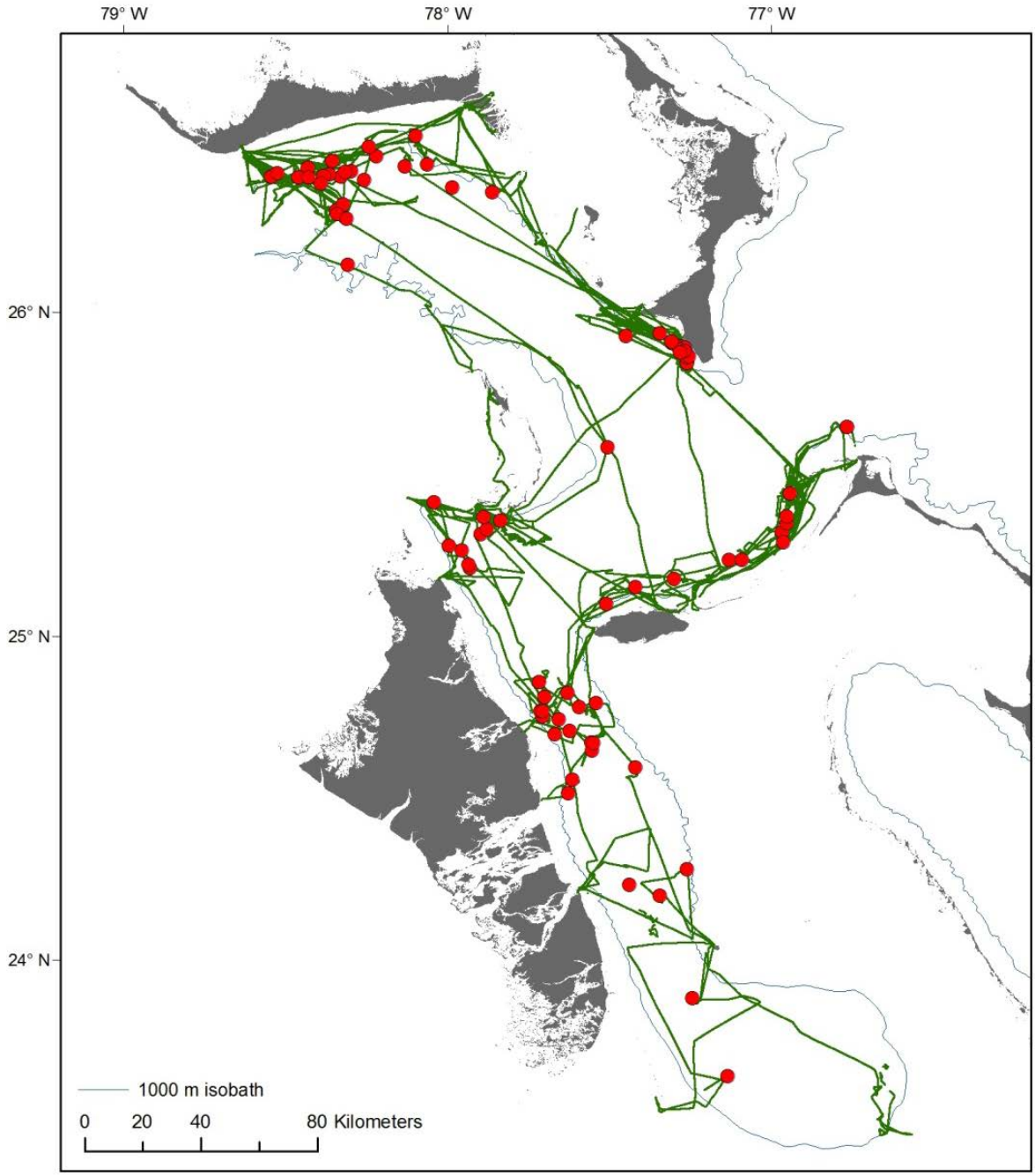


Figure 5. Visual and acoustic survey effort during three month-long surveys in the Great Bahama Canyon conducted annually from 2011 – 2013. Green lines represent the track of the survey vessel (18 m power catamaran) while the red circles represent locations of sightings of the six priority cetacean species.

When sea conditions allowed, a 6.8 m rigged-hulled inflatable boat (RHIB) was launched for close approaches to obtain photographs, biopsy samples and deploy satellite tags. More than 20,000 photographs were taken and 79 tissue samples were collected, including from all priority species as well as from potential prey species. During these surveys, 39 satellite Low Impact

Minimally Percutaneous External Transmitter (LIMPET) tags were deployed on five of the six priority species, including sperm whales (*n*=15), pilot whales (*n*=7), melon-headed whales (*n*=7), Blainville's beaked whales (*n*=5) and Cuvier's beaked whales (*n*=5). These data were greatly augmented by existing data collected before this project commenced, and during concurrent projects, all of which have been included in the analyses (Table 3). For example, data from a further 35 tags were available to effectively double the sample size of movement and dive data.

Table 3. Summary of all data collected from 1991 – 2014 in the northern Bahamas that was used in this study to investigate the behavioral ecology of six odontocete species. Photo-identifications shown only include high quality photographs of distinctively-marked individuals.

Whale Species	Encounters	Photo IDs	Biopsy Samples	Tags Deployed	Acoustic Detections
Melon-headed *Peponocephala electra*	40	740	42	13	3
Short-finned pilot *Globicephala macrorhynchus*	37	626	62	15	2
Blainville's beaked *Mesoplodon densirostris*	458	321	96	12	22
Gervais' beaked *Mesoplodon europaeus*	27	47	15	0	2
Cuvier's beaked *Ziphius cavirostris*	89	89	61	7	6
Sperm *Physeter macrocephalus*	262	184	131	27	20

The locations of all encounters for all six species combining both the existing data and SERDP-data are shown in Figure 6, revealing differences in their distribution and habitat use in the northern Bahamas.

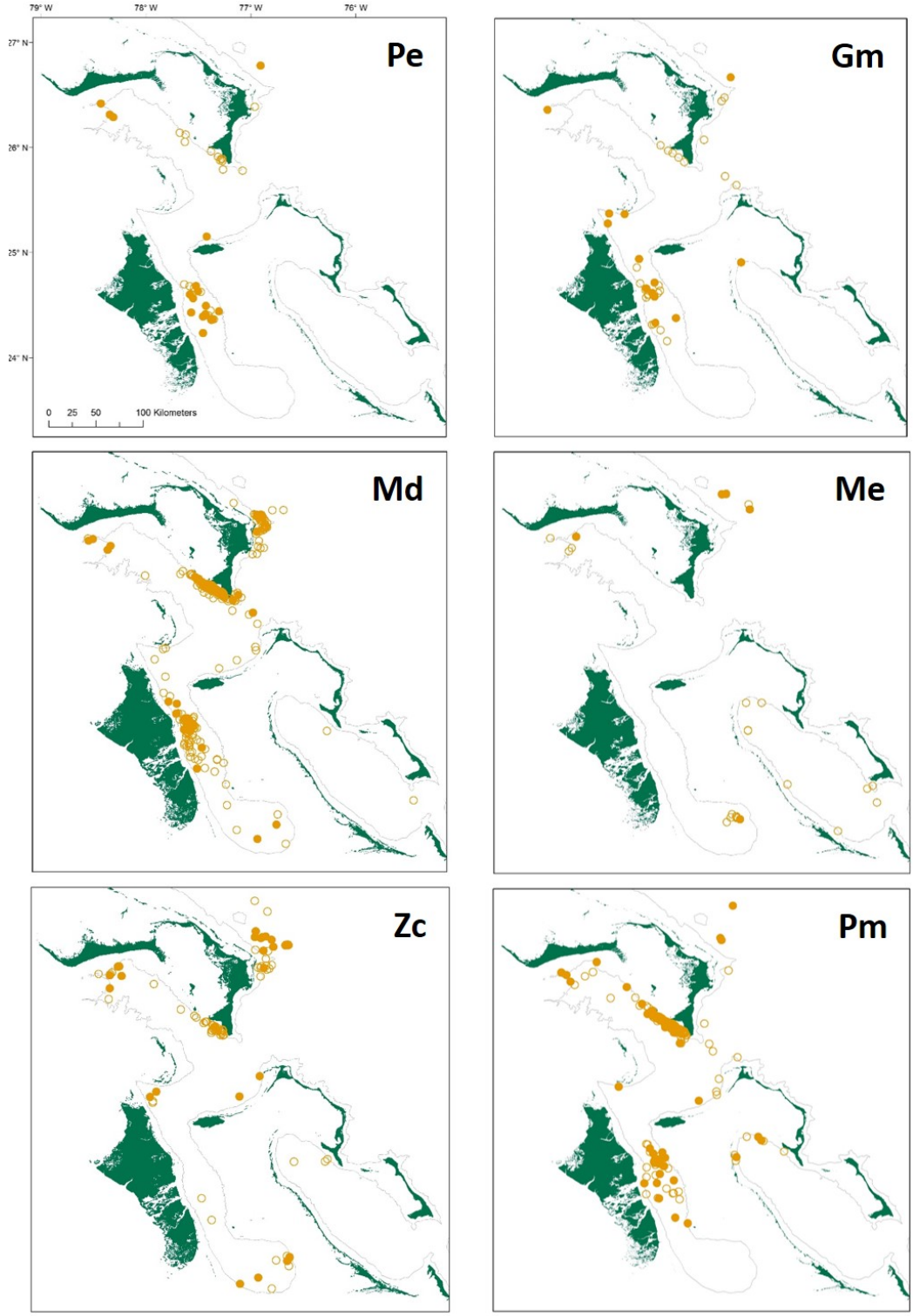


Figure 6. Locations for encounters (open circles) of the six priority species during the study in the northern and central Bahamas from 1991-2014. Closed circles are locations when biopsy samples were collected. Species are: melon-headed whale (Pe, *n*=40 encounters) short-finned pilot whale (Gm, *n*=37), Blainville's beaked whale (Md, *n*=458), Gervais' beaked whale (Me, *n*=27), Cuvier's beaked whale (Zc, *n*=89), and sperm whale (Pm, *n*=262).

Acoustic detections

Ninety-five acoustic detections were made during SERDP ship surveys, including detections of all six priority species (Figure 7). More than half (60%) of acoustic detections led to subsequent visual sightings of the animals, demonstrating the utility of this approach. Recordings were augmented by additional collections during the ONR ship surveys, and opportunistic RHIB surveys. In total, from 2007 - 2013, acoustic recordings were collected for 10 species, including 3 beaked whales species, 6 oceanic dolphin species, and sperm whales. Only data collected from sperm whales were analyzed here; recordings were used to measure the size of individuals and to associate social vocalizations (codas) with particular social units.

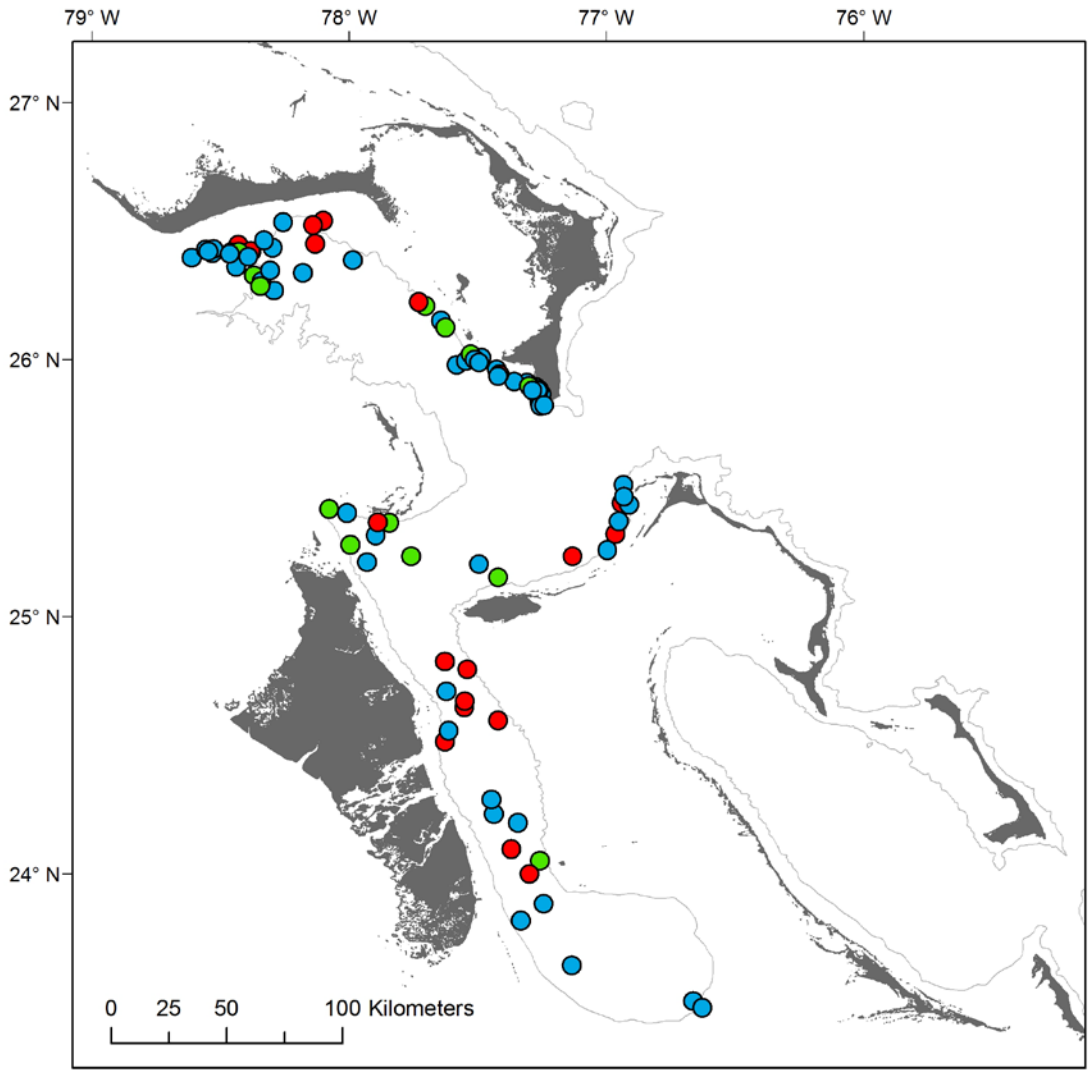


Figure 7. Locations of acoustic detections of 10 cetacean species from a 200m towed array used during ship surveys between 2009 and 2012 in the Great Bahama Canyon. Blue circles represent Ziphiids (3 beaked whales species), green circles represent Delphinids (6 oceanic dolphin species), and red circles represent sperm whales.

MELON-HEADED WHALE (*Peponocephala electra*)

Telemetry

A total of 13 tags were deployed on melon-headed whales, resulting in 1150 location estimates (Table 4). These estimates were moderately precise, compared to other species, with an average error radius of 3.5 km. Although this species surfaces regularly and tags therefore potentially could communicate frequently with satellites, these were the smallest animals tagged in this study and exhibited rapid surfacings that limited tag transmissions and the subsequent precision of location estimates. Transmissions were received during tag durations up to 43 days, but deployment durations averaged 1-2 weeks (median = 13 days) – limited by the requirement to use short (4.5cm) attachment darts for this species' small dorsal fin.

Table 4. Summary statistics of satellite tag deployments on deep-diving odontocete cetacean species in the Great Bahama Canyon 2009-2014. Tags is the total number of Argos transmitter tags deployed, "depth" indicates the number of SPLASH tags that had depth-rec recording capabilities and "Dives" are the number of dives recorded by SPLASH tags below a qualifying depth of 15 m. Error Radius is the average error associated with location estimates from the Argos satellite system across tags for each species; *Md* = Blainville's beaked whale, *Zc* = Cuvier's beaked whale, *Pe* = melon-headed whale, *Gm* = short-finned pilot whale, *Pm* = sperm whale.

Whale Species	Tags (# depth)	Days (median/max)	Location Estimates	Error Radius (m)	Dives
Md	12 (9)	19/47	1442	3322	2157
Zc	7 (6)	26/92	594	5624	532
Pe	13 (4)	11/43	1150	3549	75
Gm	15 (3)	17/42	3001	2319	1580
Pm	27 (6)	10/19	1449	3278	480

Movement tracks showed individuals remained within the Great Bahama Canyon during the tag deployments, but melon-headed whales did travel relatively widely between different areas (across strata) of the Canyon (Figure 8); individuals typically remained within 200 km of the tagging location for the duration of the tags (Figure 9). Biopsy samples were not collected from any of the tagged melon-headed whales, so genetic determination of sex was not possible.

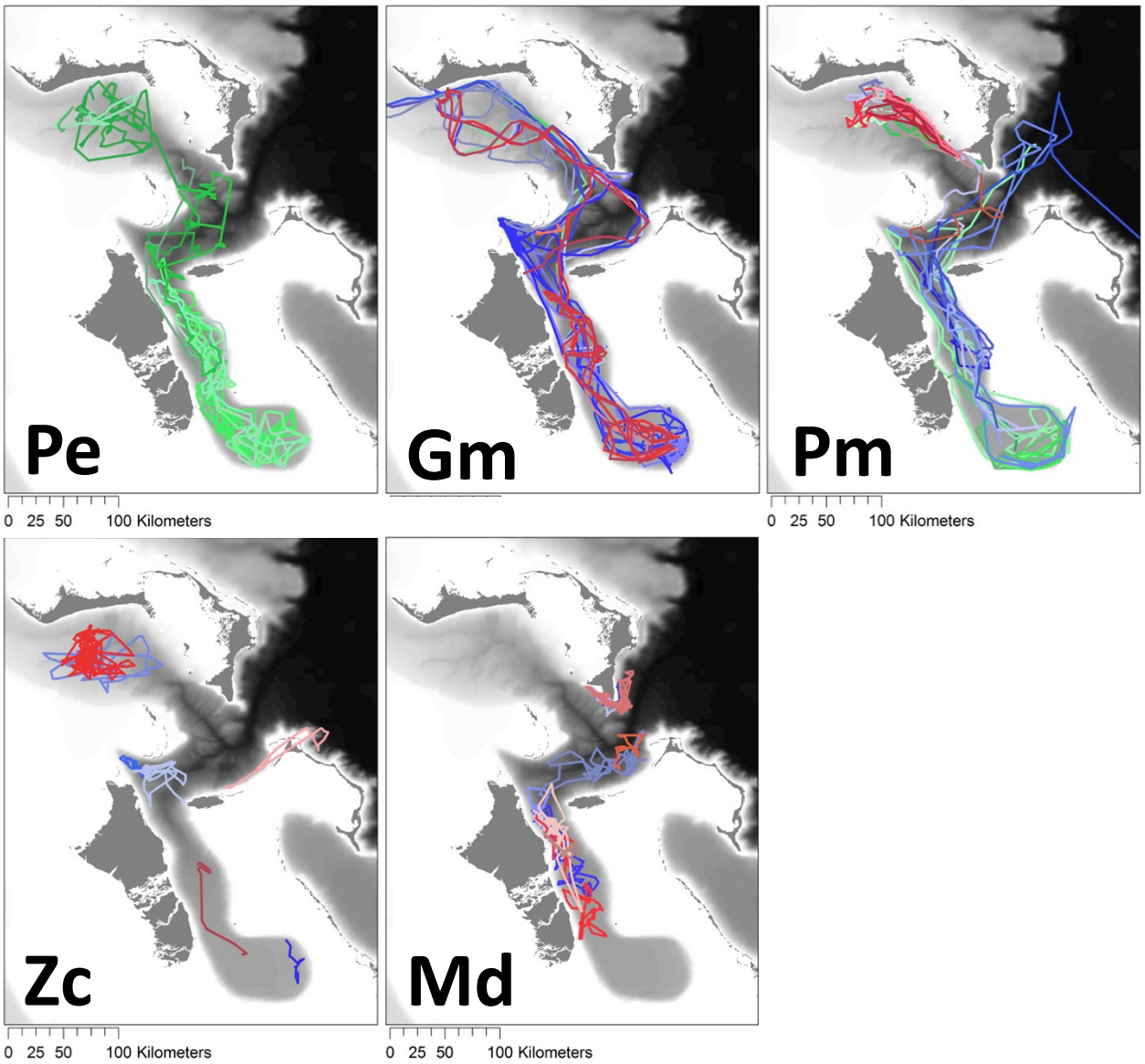


Figure 8. Movement tracks within the Great Bahama Canyon for melon-headed whales (*Pe*, *n*=13) short-finned pilot whales (*Gm*, *n*=15), sperm whales (*Pm*, *n*=27), Cuvier's beaked whales (*Zc*, *n*=7) and Blainville's beaked whales (*Md*, *n*=11) and estimated from satellite transmitter tags deployed between 2009 and 2014. Tracks represent the maximum likelihood fit of a continuous-time correlated random walk model (Johnson *et al*. 2008) to location estimates from the Argos satellite system; colors reflect sex of tagged whales (red = females, blue = males, green = unknown) with shading to identify individual tracks.

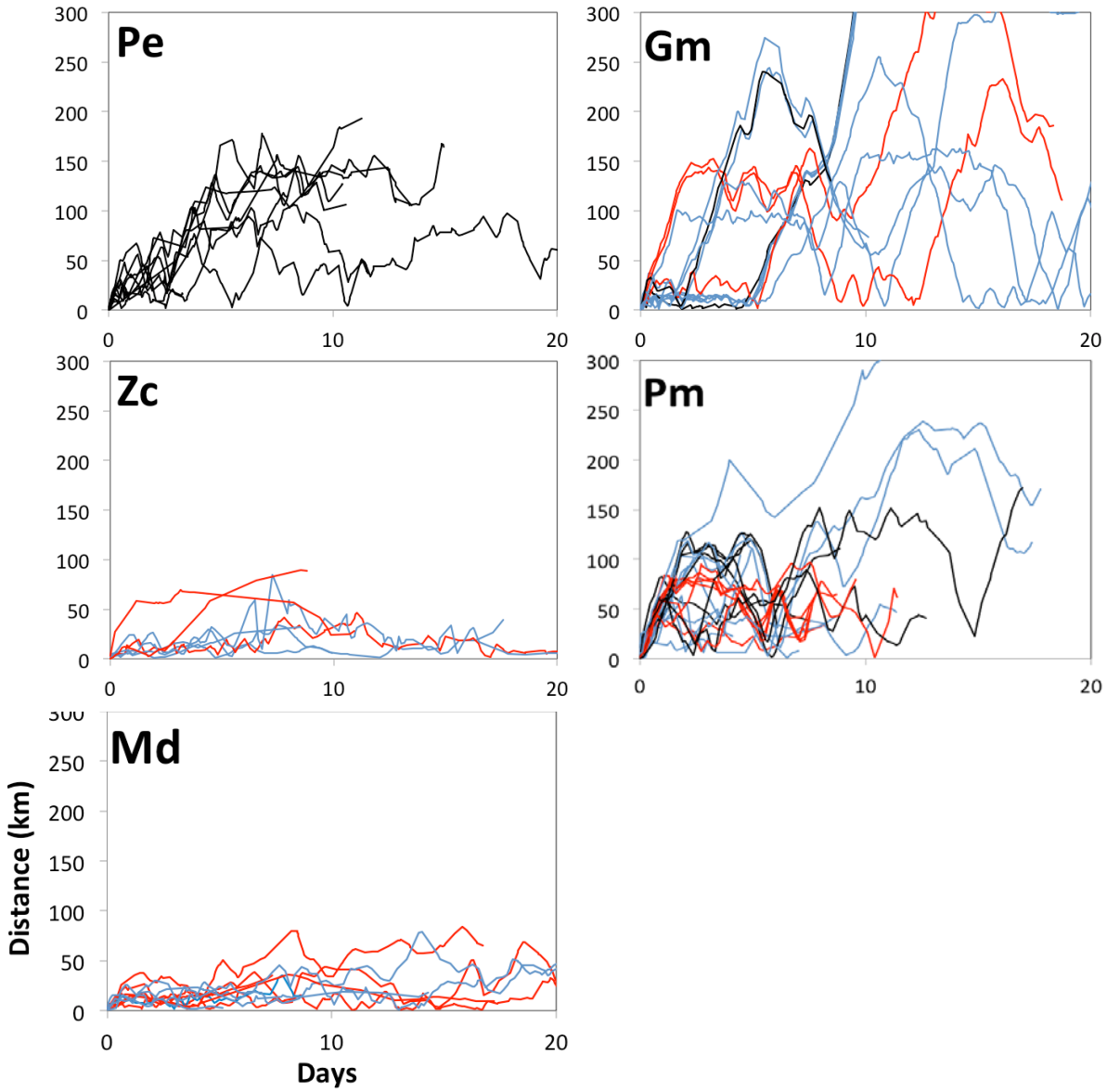


Figure 9. Plots of estimated displacement (straight line distance) away from the tagging site against time, standardized for the first 20 days of deployments of transmitter tags on melon-headed whales (*Pe*, *n*=13) short-finned pilot whales (*Gm*, *n*=15), sperm whales (*Pm*, *n*=27), Cuvier's beaked whales (*Zc*, *n*=7) and Blainville's beaked whales (*Md*, *n*=11). Displacement is to hourly maximum likelihood predictions of a continuous-time correlated random walk model (Johnson *et al.* 2008) fit to location estimates from the Argos satellite system; colors reflect sex of tagged whales (red = females, blue = males, black = unknown).

Melon-headed whales remained in surface waters (<50 m) during the day and only undertook deeper foraging dives at night (Figure 10; median night foraging dives of 336 m, max = 504 m). Direct dive data from SPLASH tags was limited (75 dives, Table 4), but this inference is supported by TAT data from SPOT tags, which suggest this species only dive into waters colder than 24ºC (deeper than ~100 m) at night (Figure 10).

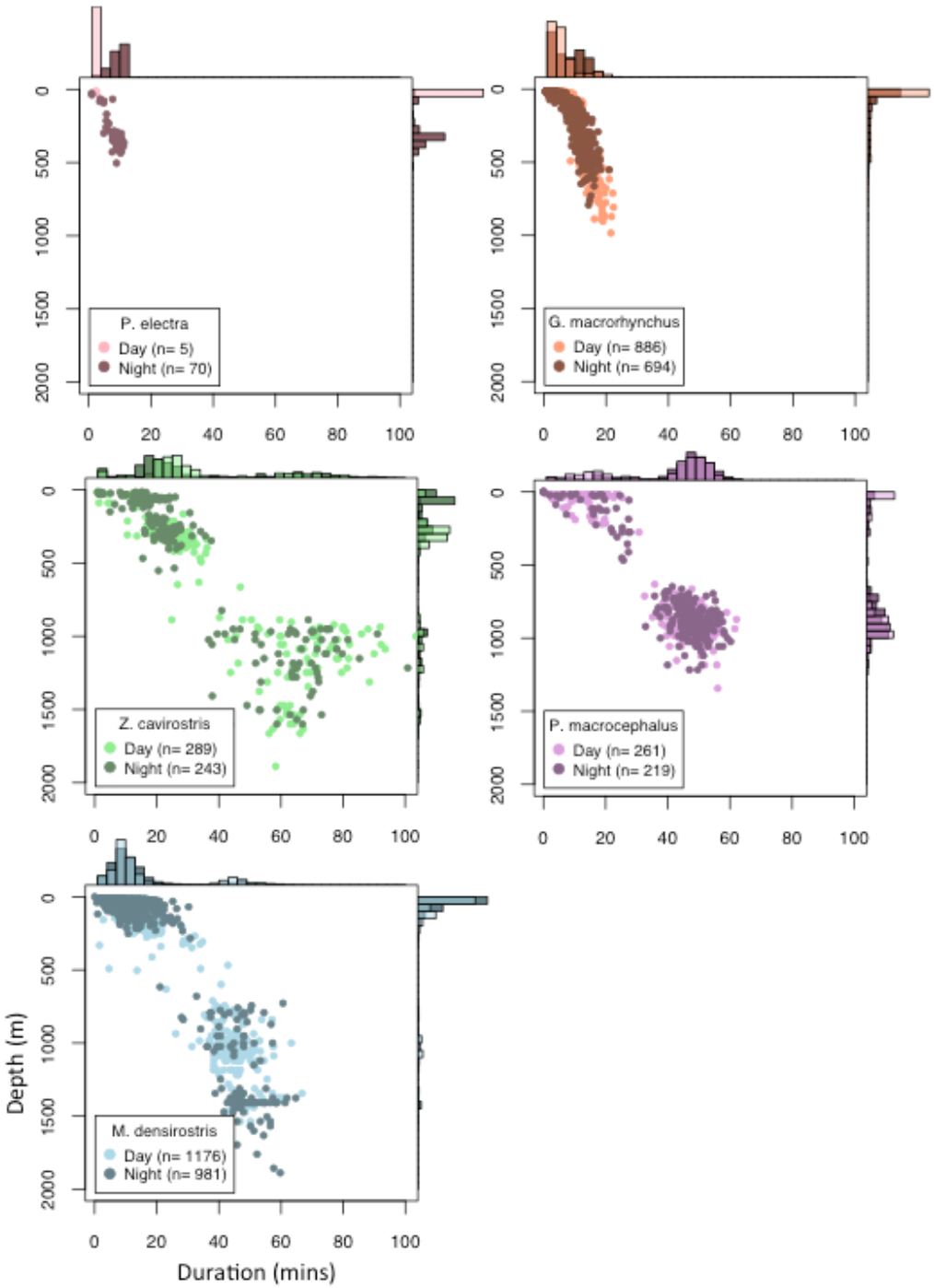


Figure 11. Scatterplots indicating the relationship of maximum depth to the duration of each dive recorded in the behavior log for each tagged species in this study (melon-headed whales, *P. electra*; short-finned pilot whales, *G. macrorhynchus*; sperm whales, *P. macrocephalus*; Cuvier's beaked whales, *Z. cavirostris*; Blainville's beaked whales, *M. densirostris*). Histograms along the vertical and horizontal margins of each plot represent the distribution of depth and duration of dives, respectively. Daytime and night-time dives within each species are represented by light and dark shades respectively.

These night dives were of typical duration 8.9 mins (max = 11.3 mins; Figure 10), and were frequent during night-time hours resulting in more than 75% of the time spent in foraging strata (the highest for any of the species; Figure 11).

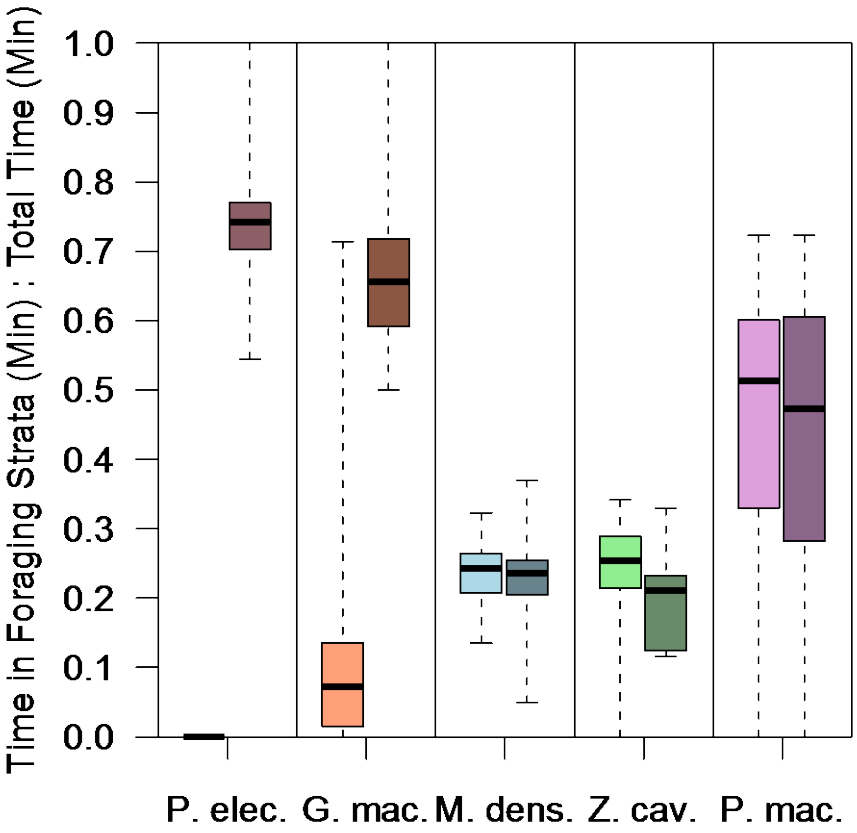


Figure 12. Boxplots comparing the proportion of each Time-at-Temperature histogram spent within presumed foraging strata (see methods for strata definitions). Daytime and night-time dives are represented by light and dark shades respectively for each study species (melon-headed whales, *P.elec*; short-finned pilot whales, *G.mac*; Blainville's beaked whales, *M.dens*; Cuvier's beaked whales, *Z.cav*; sperm whales, *P.mac*). Boxes show 25% to 75% intervals of the sampling distributions, horizontal line shows the median and whiskers represent the full extent of the distributions.

Even though melon-headed whales occurred in deep water, their dive depth was only a fraction of the available bathymetric depth (~20% of the water column on average; Figure 12).

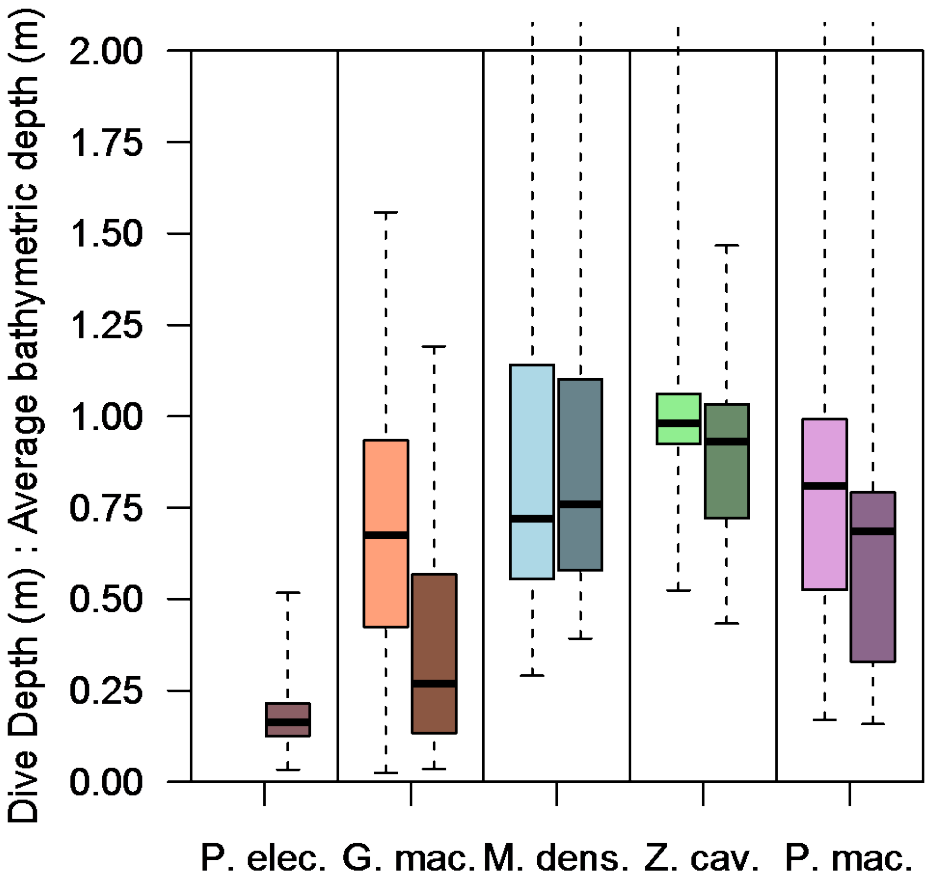


Figure 13. Boxplot comparing the ratio of foraging dive depth to local bathymetric depth at the estimated maximum likelihood locations of dives for each study species (melon-headed whales, *P.elec*; short-finned pilot whales, *G.mac*; Blainville's beaked whales, *M.dens*; Cuvier's beaked whales, *Z.cav*; sperm whales, *P.mac*). Location estimates from a continuous-time correlated random walk model (Johnson *et al.* 2008). Theoretically this ratio should not exceed 1.0, however sampling of the bathymetric depth raster at erroneous locations caused by Argos observation error and resultant movement model process error resulted in ratios implying dive depths in excess of bottom depth. Boxes show 25% to 75% intervals of the sampling distributions, horizontal line shows the median and whiskers represent the full extent of the distributions.

Photo-identification

Movements

Photo-identification data were collected for melon-headed whales from 1995 – 2013 in five of the seven strata (Table 5). Using only high quality photographs (Q>1) of very distinctive individuals (D>1), a total of 740 individuals were photo-identified. The majority of individuals were found in the TO stratum, and in fact on the AUTEC Weapons Range (see Figure 6 for encounter locations). Movements were found between all five strata, supporting shorter-term telemetry data that *Pe* range throughout the Great Bahama Canyon but also documenting

movements outside the canyon as well. Re-sightings across multiple years were documented in three strata, with the highest percentage of re-sightings found in the TO strata (34% of total individuals in TO strata), suggesting long-term use of the AUTEC area by some whales.

Table 5. Contingency table for melon-headed whale photo-identification data collected from 1995 – 2013 in each strata in the Bahamas using high quality photographs (*Q*>1) of very distinctively-marked individuals (*D*>1). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as all movements between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	**GB**	**SA**	**EA**	**NE**	**TO**	**CU**	**EX**
GB	203 (23)	24	0	29	64	0	0
SA		260 (2)	2	11	59	0	0
EA			23 (0)	1	0	0	0
NE				86 (0)	49	0	0
TO					363 (124)	0	0
CU						0	0
EX							0

Social organization

From 740 individuals in the photo-identification catalogue for this species, a total of 62 individuals remained in the dataset for analysis after additional filtering to include only animals seen on more than 4 days. A cophenetic correlation coefficient of 0.82 from our clustering analysis provided confidence in the representation of associations shown in the dendrogram (Figure 13), as coefficients > 0.8 indicate a good match (Bridge, 1993). All but four individuals were assigned to two main clusters identified in the dendrogram, and the mean association index within clusters was 0.51 (SD = 0.12), and 0.20 (SD = 0.07) between clusters. Therefore, although individuals did associate between clusters, and all clusters were linked, we found that there is some degree of structure within the social organization of *Pe* in the Bahamas.

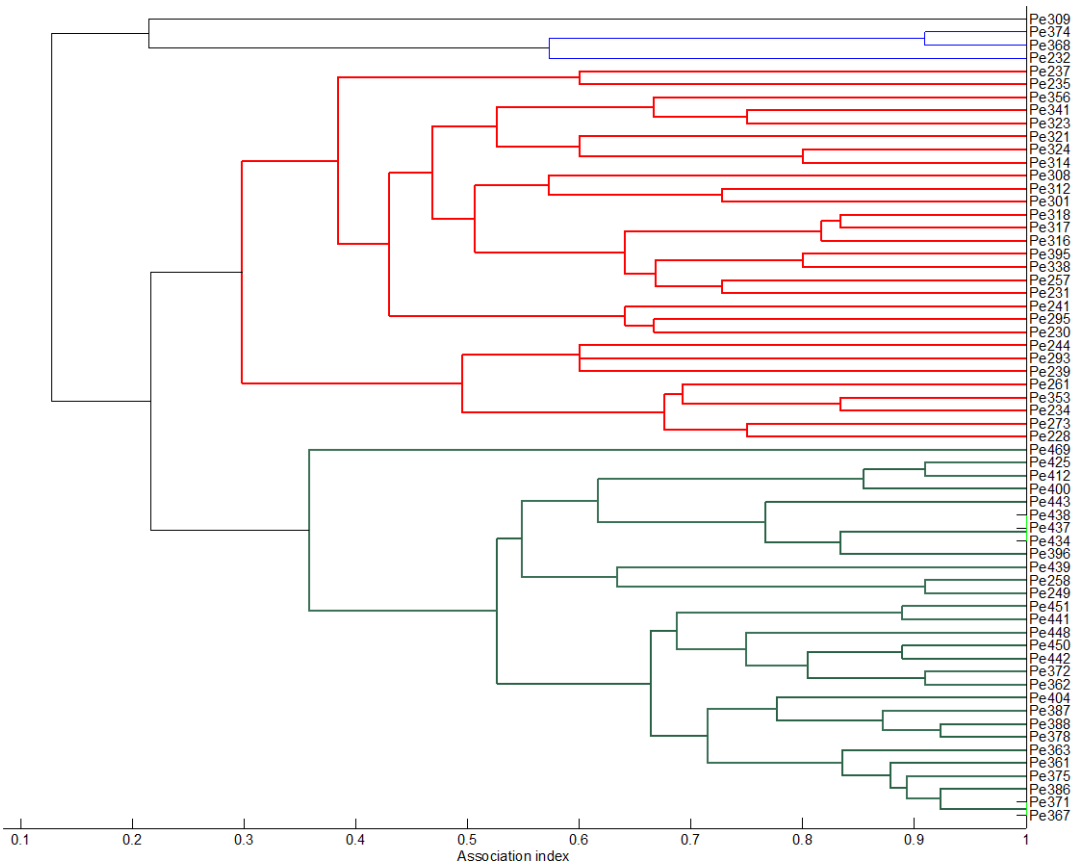


Figure 14. Dendrogram from photo-identification data of good quality photographs ($Q > 1$), showing the association index between 62 melon-headed whales that were seen on more than 4 days, were distinctive by nicks in their dorsal fins ($D > 1$), showing two main clusters of animals.

Chemistry

The two delphinid species (*Pe* and *Gm*) were found to be feeding at a much lower mean trophic level ($\delta 15N_{mean}$~10.3) than any of the other species as shown by separation between all six species in nitrogen and carbon stable isotopes results (Figure 14).

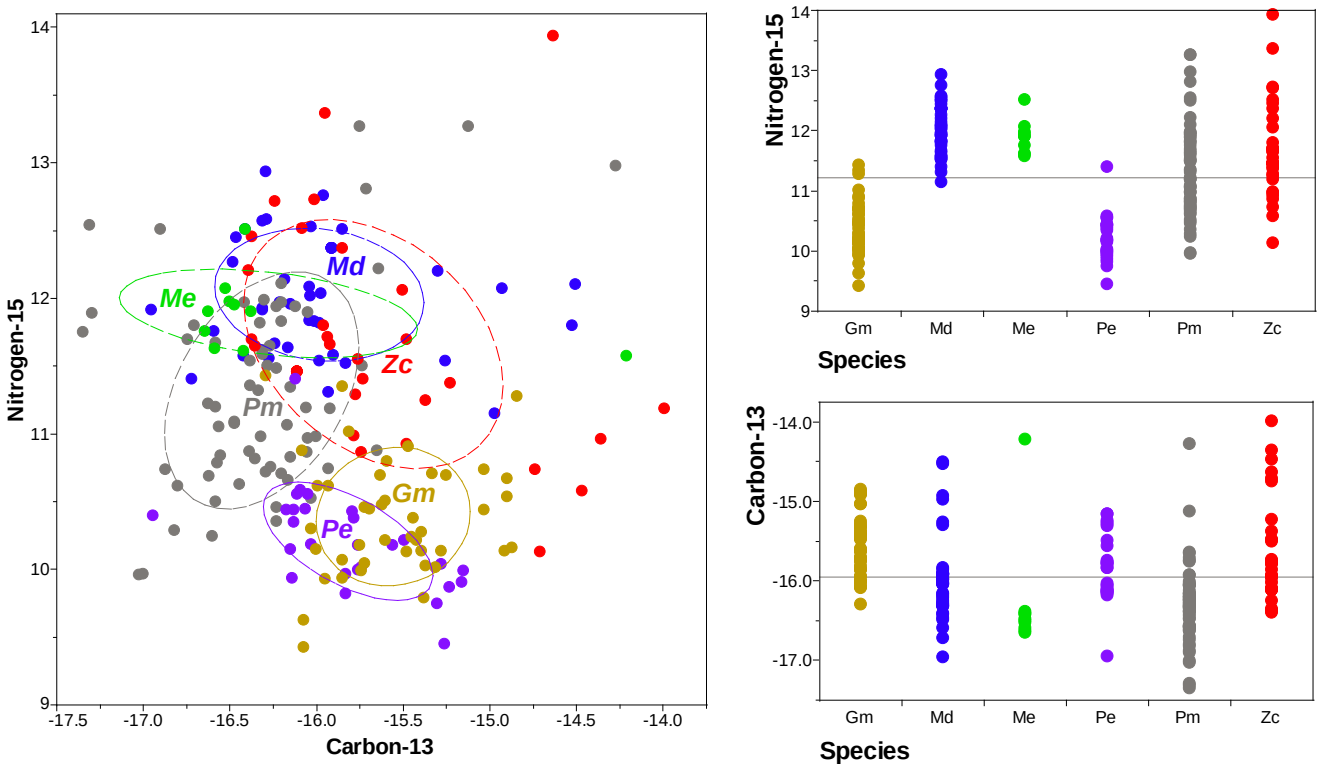


Figure 15. Differences in epidermal stable isotope ratios among the six color-coded priority cetacean species (both sex) from biopsy samples collected in the northern Bahamas from 2007-2014. Ovals represent the 50% probability density intervals of the distribution of isotopes for the species shown. Species abbreviations: short-finned pilot whale (*Gm*, in gold); Blainville's beaked whale (*Md*, in blue); Gervais' beaked whale (*Me*, in green); melon-headed whale (*Pe*, in purple); sperm whale (*Pm*, in grey); Cuvier's beaked whale (*Zc*, in red); colors are matched across panels.

We also observed that the dietary fatty acid (see Appendix A, Table A2) profile data generally separated into the same three general groupings with distinct separation among the delphinids, sperm, and beaked whales (Figure 15).

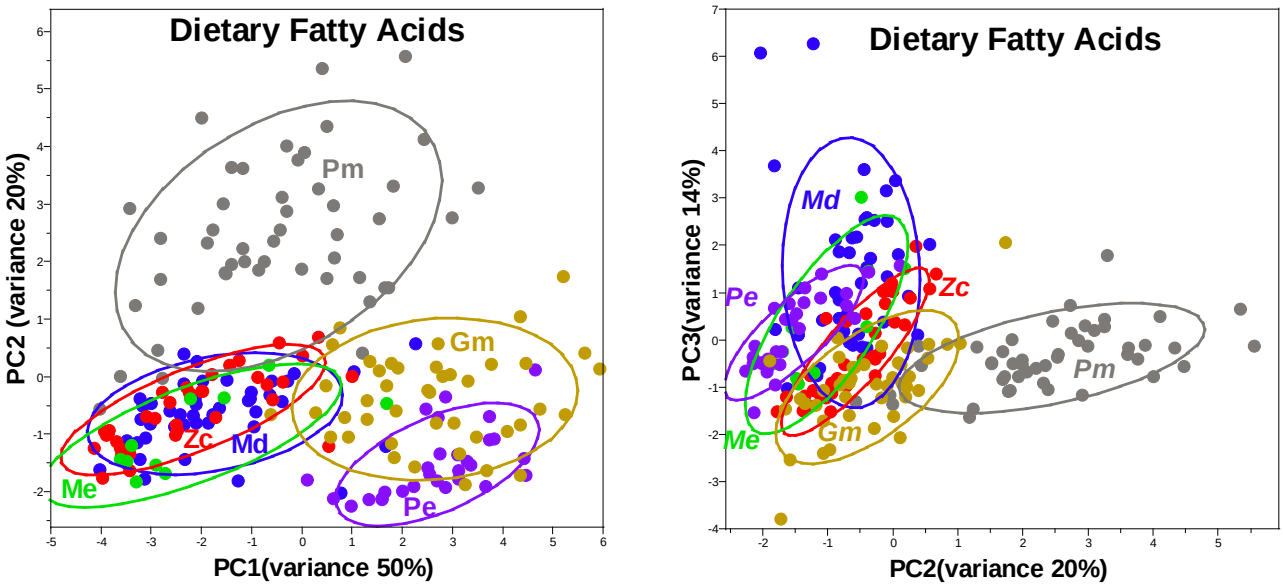


Figure 16. Using Principal Component analyses of dietary fatty acids in the blubber of the six priority cetacean species of both sex to qualitatively infer perceived differences in the preferred prey. The identity of the 13 dietary fatty acids used in this analysis are listed in Appendix A, Table A2. Ovals represent the 50% probability density intervals of the distribution of isotopes for the species shown. Species abbreviations: short-finned pilot whale (*Gm*, in gold); Blainville's beaked whale (*Md*, in blue); Gervais' beaked whale (*Me*, in green); melon-headed whale (*Pe*, in purple); sperm whale (*Pm*, in grey); Cuvier's beaked whale (*Zc*, in red); colors are matched across panels.

The foraging structure of melon-headed whales (with emphasis on their short- and long-term foraging site fidelity) was evaluated from measurements of stable isotope ratios, dietary fatty acids, and POP patterns in their tissues. In Figure 14, we show the stable isotope ratio results for all *Pe* analyzed as part of this study where individual whales are grouped by their four strata (biopsy locations). With the exception of the single *Pe* animal biopsied at EA, some separation is observed among the remaining 3 strata suggesting that the foraging movements of these whales may be restricted somewhat within the 2-3 month time period required for their nitrogen and carbon isotopes to turn-over in the skin. This hypothesis of restricted short-term foraging movements of Bahamas *Pe* whales is also partially supported by the corresponding dietary FA results for *Pe* (data not shown) in which some differences are observed in the patterns of dietary FAs when comparing among the four *Pe* sampling strata; however, resolution of strata via dietary fatty acid analysis is substantially less pronounced than that observed for stable isotopes (Figure 16). In combination, these two findings provide some initial indications that *Pe* whales may exhibit some small degree of short-term (2-3 months) foraging site fidelity limiting predation to within a single stratum (or a pair of adjoining strata). Some additional support for this limited short-term site-fidelity hypothesis is provided by the satellite tag results obtained for *Pe* whales (Figure 8) wherein it was observed that all eight *Pe* whales either remained within a single stratum or at most moved into an adjoining stratum during the relatively short periods of time the satellite tags were deployed.

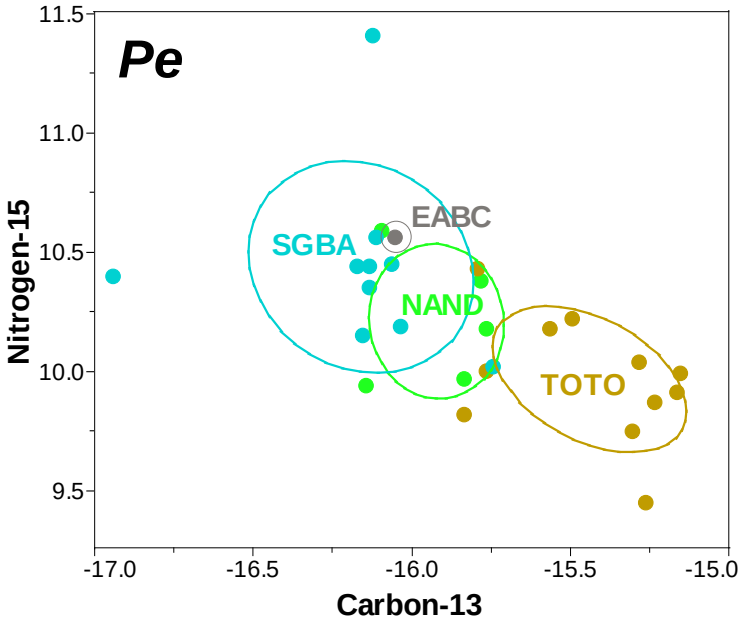


Figure 17. Differences in stable isotope ratios among melon-headed whales (*Pe*) of both sexes biopsy sampled in the northern Bahamas in the four color-coded strata indicated from 2007 - 2014. Ovals represent the 50% probability density intervals of the distribution of isotopes within the regions indicated. Strata abbreviations: South Grand Bahama (SGBA); North Andros/South Berry Is. (NAND); East Abaco (EABC), and Tongue of the Ocean (TOTO).

In contrast, the POP patterns obtained for *Pe* depict differences in the patterns of POPs among the four strata (Figure 17). POP analyses were restricted to samples genetically confirmed to be males. These patterns suggest that long-term foraging movements may be much more extensive than their short-term foraging bouts with Bahamian *Pe* whales probably foraging over the entirety of the Bahamas study area within their lifetimes. This conclusion is based on the observation that the differences in POP patterns measured among *Pe* encounter groups biopsied within the same strata [*e.g.*, GB(12) and GB(13)] are quite large. Although animals within these two particular encounter groups seemingly have fed in rather similar habitats over their lifetimes thus explaining their highly similar POP profiles, the large difference in POP profiles observed between the GB(12) and GB(13) encounter groups in turn implies their primary lifetime foraging habitats must be substantially different from one another despite all animals having been biopsied in the same strata. A similar argument can also be advanced from the TO and NA substrata POP pattern data presented in Figure 17. Thus, whereas our SI and FA results have hinted that *Pe* whales may be exhibiting some small degree of short-term foraging site fidelity, our POP results suggest that Bahamas *Pe* whales likely forage over their lifetimes throughout the entire Bahamas study area (and perhaps beyond) with minimal long-term site-fidelity.

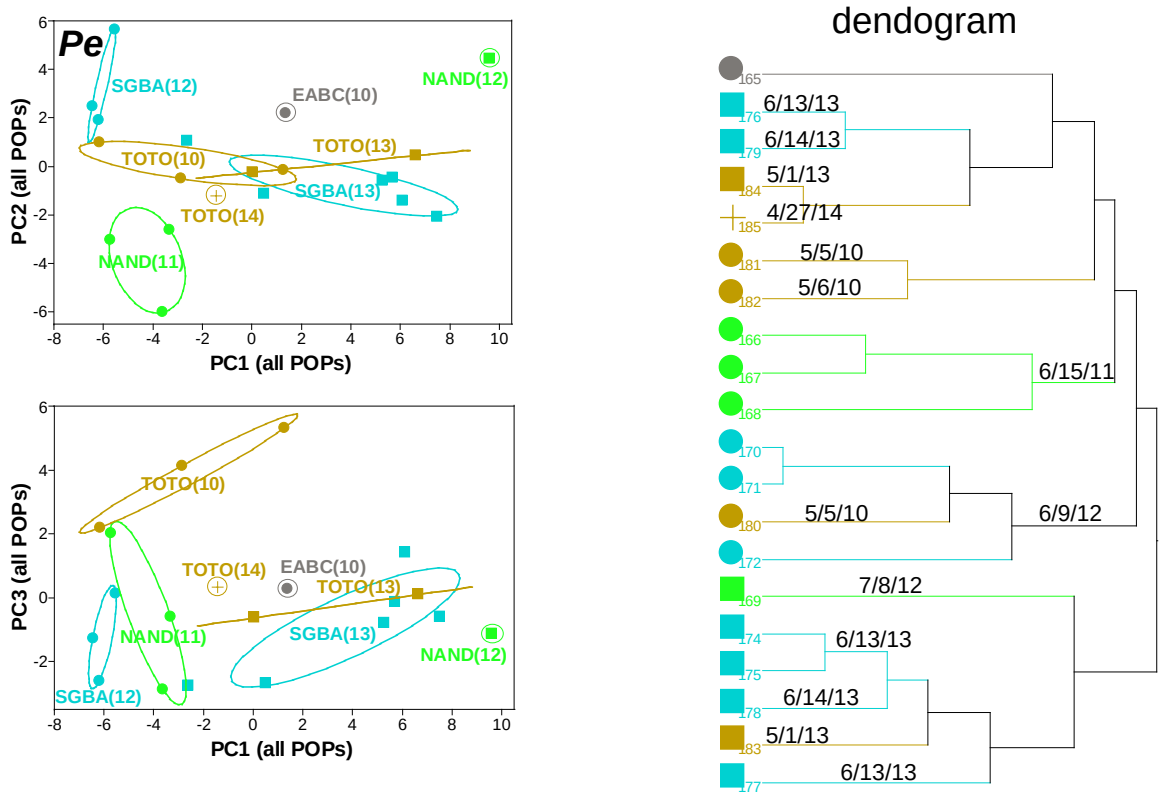


Figure 18. Principal Component and hierarchical cluster analysis of POP patterns measured in the epidermal tissues of melon-headed whales (*Pe*, males only) with whales grouped by their four color-coded sampling strata in the northern Bahamas. Ovals represent the 50% probability density intervals of the distribution of POPs within the strata indicated. Strata abbreviations: South Grand Bahama (SGBA); North Andros/South Berry Is. (NAND); East Abaco (EABC), and Tongue of the Ocean (TOTO). Biopsy collection dates of each individual whale are indicated in the dendrogram plot. Numbers appearing in parentheses at the locations depicted in the PCA plots represent a group of individual whales biopsied on the same date/location in the year indicated.

SHORT-FINNED PILOT WHALE (*Globicephala macrorhynchus*)

Telemetry

A total of 15 tags were deployed on short-finned pilot whales, resulting in 3001 location estimates (Table 4). These estimates were precise compared to other species, with an average error radius of 2.3 km, due to the frequent and slow surfacing behavior of this species, particularly during daytime resting, which enabled frequent tag transmissions. Transmissions were received during tag durations up to 42 days, and deployment durations averaged 2-3 weeks (median = 17 days). Movement tracks showed individuals to move rapidly and widely across strata within the Great Bahama Canyon (Figures 8 and 9) but also revealed long-range movements by two groups (five individuals) into Gulf Stream waters off the coast of Florida; one tagged whale ranged as far North as 32º N, off the coast of South Carolina (Figure 18). Tags were distributed among adult males (*n*=6), large sub-adult males (*n*=3) and adult females (*n*=4), with only four whales of unknown sex (these being either adult females or smaller sub-adult males). Multiple whales were tagged in the same groups for 3/5 groups tagged, and tracking showed these whales to stay together for the duration of the tag deployments, implying social cohesion. As such, the movement patterns of males and females were similar.

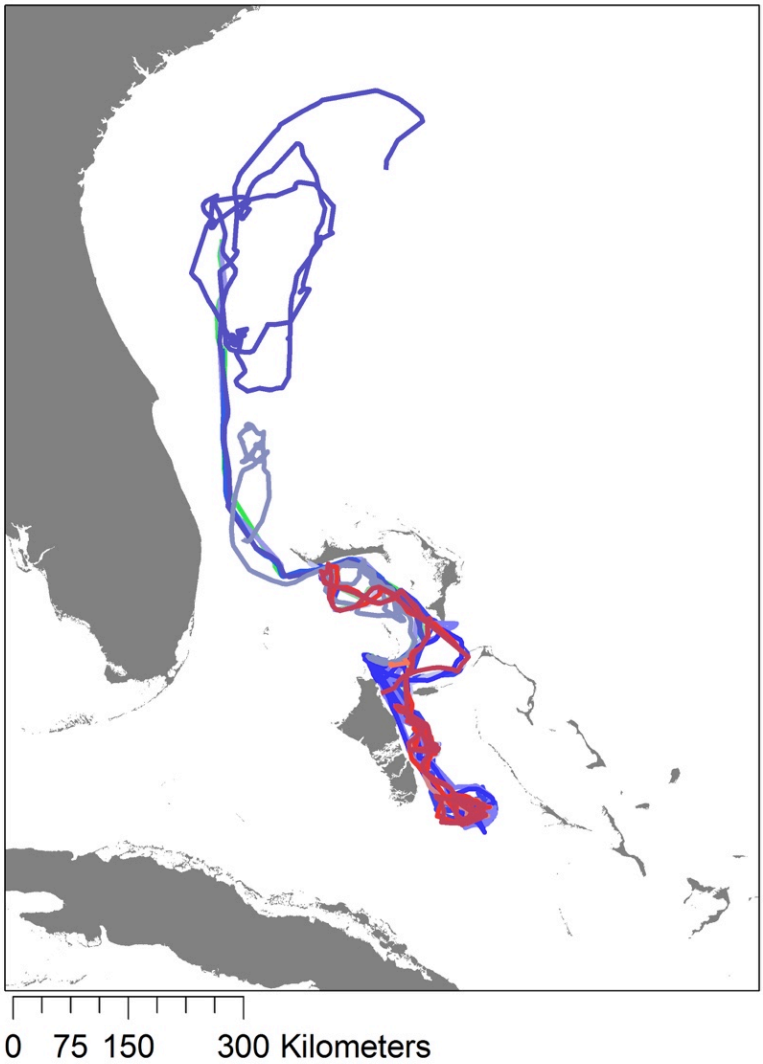


Figure 19. Movement tracks of short-finned pilot whales (*n*=15) showing widespread movements within the Great Bahama Canyon but also revealed long-range movements two of groups (five individuals) into Gulf Stream waters off the coast of Florida; one tagged whale ranged as far north as 32 ºN, off the coast of South Carolina. Tracks represent the maximum likelihood fit of a continuous-time correlated random walk model (Johnson *et al.* 2008) to location estimates from the Argos satellite system; colors reflect gender of tagged whales (red = females, blue = males, green = unknown) with shading to identify individual tracks.

Night diving of short-finned pilot whales was similar to that of melon-headed whales, with some deeper dives (Figure 10; median night dives of 234 m, max = 792 m). Unlike melon-headed whales, pilot whales also dove into mesopelagic waters during the day and these daytime dives were typically deeper than night dives (median day dives = 520 m, max = 984 m). Night-time dives were of typical duration 10.6 minutes (max = 21.0 mins) and the deeper daytime dives were slightly longer (median = 14.8 mins, max = 22.4 mins). However, these relatively deep

daytime dives were infrequent, and pilot whales spent much more time on foraging dives during the night (60-70% time foraging at night vs. 20-30% during the day; Figure 11). The deeper daytime dives used more of the water column than the shallower night dives (Figure 12), but pilot whales were not foraging close to the sea floor (~ 60% of available depth during the day, 30% at night).

Pilot whales are extremely sexually dimorphic, with adult males growing much larger than females, and we might expect size differences to translate into differences in diving capability. Direct dive data from SPLASH tags was limited for pilot whales, with no tags on genetically-confirmed adult females. Nonetheless, we do have tag data from a presumed adult female, of adult female size, providing evidence for variance diving between whales of different sizes (Figure 19). Although there were not clear differences in the median depth (male = 244 m, "female" = 308 m) or median duration (male = 11.8 mins, "female" = 10.9 mins), the maximum depth (male 984 m, "female" = 792 m) and duration (male = 22.4 mins, "female" = 18.7 mins) of dives were deeper and longer for the adult males compared to the whale of adult female size.

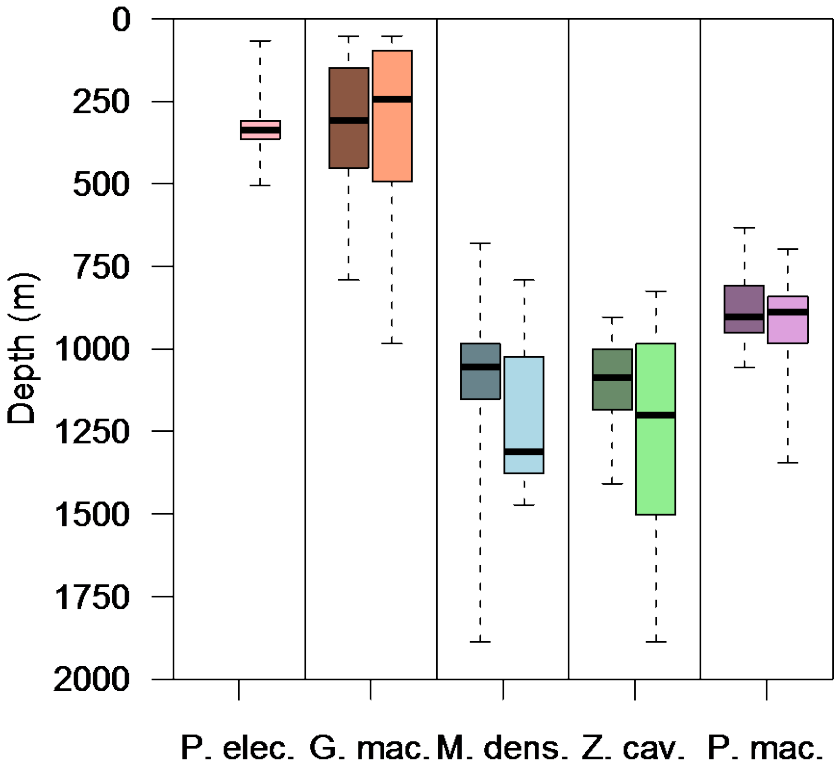


Figure 20. Boxplots comparing the maximum depth of foraging dives for adult females (darker box on left) and adult males (lighter box on right) for each study species (melon-headed whales, *P.elec*; short-finned pilot whales, *G.mac*; Blainville's beaked whales, *M.dens*; Cuvier's beaked whales, *Z.cav*; sperm whales, *P.mac*). Note, no sex data were available for melon-headed whales (*P.elec*); pilot whale "females" box comprises a single "presumed" adult female, of adult-female size, that was not confirmed though biopsy-genetics, sperm whale (*P.mac*) males are represented by sub-adults and not full adults. Boxes show 25% to 75% intervals of the sampling distributions, horizontal line shows the median and whiskers represent the full extent of the distributions.

Photo-identification

Movements

Photo-identification data were collected for short-finned whales from 1993 – 2014 in five of the seven strata (Table 6). Using only high quality photographs (*Q*>1) of distinctively-marked individuals (*D*>0), a total of 626 individuals were photo-identified. Almost 80% of individuals were found on the AUTEC Weapons Range in the TO stratum (see Figure 6 for encounter locations). Unlike *Pe*, pilot whale movements appeared limited; only one whale was seen in more than one strata (TO and GB). However, again unlike *Pe*, there were very few re-sightings with only 4 whales ever being re-sighted across multiple years, all in TO strata. These results suggest that *Gm* use of the Great Bahama Canyon, including the AUTEC Weapons Range is transient, and support shorter-term telemetry data that showed ranging patterns extending well beyond the Bahamas.

Table 6. Contingency table for short-finned whale photo-identification data collected from 1993 – 2014 in each strata in the Bahamas using high quality photographs (Q>1) of distinctively-marked individuals (D>0). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as the limited movement between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	GB	SA	EA	NE	TO	CU	EX
GB	38 (0)	0	0	0	1	0	0
SA		21 (0)	0	0	0	0	0
EA			70 (0)	0	0	0	0
NE				0	0	0	0
TO					486 (4)	0	0
CU						0	0
EX							12 (0)

Chemistry

In Figure 20, we provide results for nitrogen and carbon SI ratios measured in the skin of *Gm* whales (both sex) where the individual whales are shown grouped into one of their four designated biopsy locations (EA, GB, TO, and NA). In this analysis, the area corresponding to the TO strata was sub-divided into two locations with the northern/southern sections of this sub-division re-designated as NA and TO, respectively. Whereas some small offsets in SIs are observed between some strata (most notably δ13C) suggesting that some groups of *Gm* may

linger and forage in a common strata location for brief periods of time (days/weeks), the largely similar SI ratio values measured in *Gm* among the four strata suggests that these whales do not exhibit strong short-term site-fidelity but rather migrate over relatively large distances over short periods of time (2-3 months) feeding from multiple locations within the study area. This conclusion was further substantiated from the dietary FA results obtained for *Gm* wherein the patterns of dietary FAs among the four *Gm* strata were all highly similar with some small offsets also being observed (data not shown).

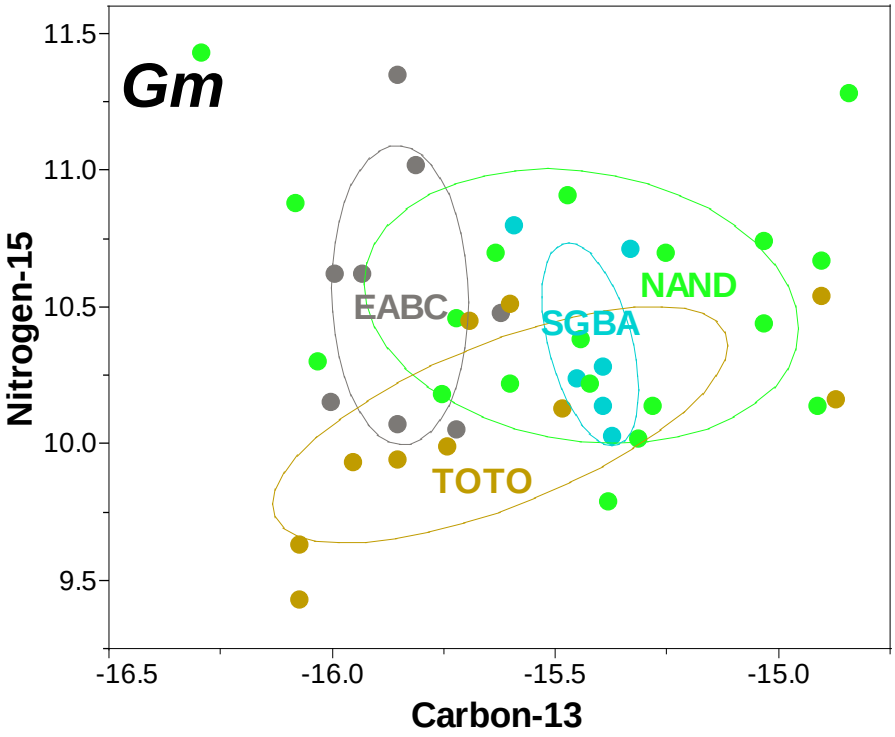
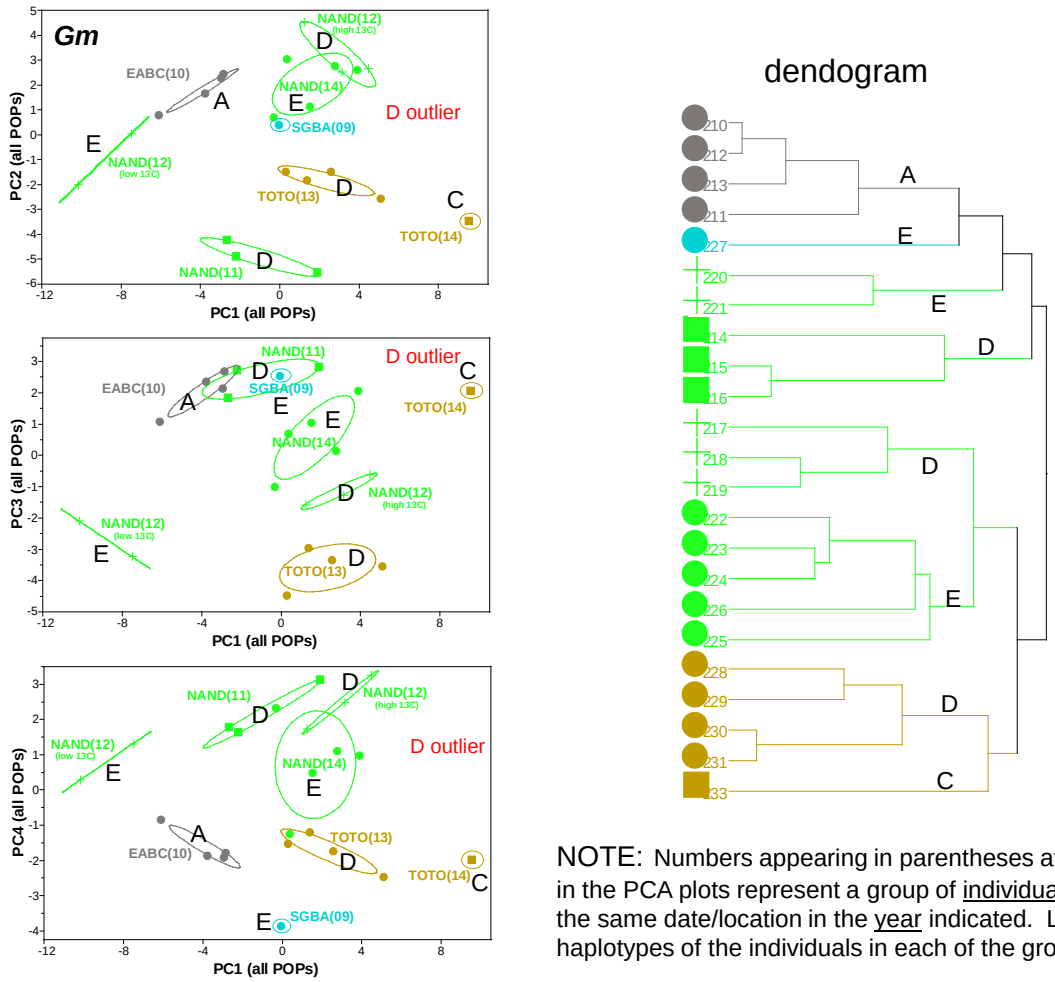


Figure 21. Differences in stable isotope ratios among short-finned pilot whales (*Gm*) of both sex biopsy sampled in the northern Bahamas in the four color-coded strata indicated from 2007 - 2014. Ovals represent the 50% probability density intervals of the distribution of isotopes within the regions indicated. Strata abbreviations: South Grand Bahama (SGBA); North Andros/South Berry Is. (NAND); East Abaco (EABC), and Tongue of the Ocean (TOTO).

The long-term foraging structure of Bahamas *Gm* whales was similarly evaluated by comparing POP patterns measured in the blubber of male *Gm* among the same four strata locations as listed below. Specifically, in Figure 21 we provide the POPs results of both a principal component and a hierarchical cluster analysis where all groups are denoted by their biopsy locations/strata, encounter group date/locations, and genetically-determined mtDNA haplotypes. Whereas there is a high degree of similarity among individuals within each of the eight encounter groups, large differences are observed between all encounter groups including those biopsied in the same strata.



NOTE: Numbers appearing in parentheses at the locations depicted in the PCA plots represent a group of individual whales biopsied on the same date/location in the year indicated. Letters (A-E) denote the haplotypes of the individuals in each of the groups.

Figure 22. Principal Component and hierarchical cluster analysis of POP patterns measured in the epidermal tissues of short-finned pilot whales (*Gm*, males only) with whales grouped by their four color-coded sampling strata. Ovals represent the 50% probability density intervals of the distribution of POPs within the regions indicated. Letters (A-E) represent the haplotypes of the individuals in each of the groups. Biopsy collection dates of each individual whale are indicated in the dendrogram plot. Numbers appearing in parentheses at the strata depicted in the PCA plots represent a group of individual whales biopsied in the same encounter in the year indicated. Strata abbreviations: South Grand Bahama (SGBA); North Andros/South Berry Is. (NAND); East Abaco (EABC), and Tongue of the Ocean (TOTO).

Finally, the chemical tracer data collected for *Gm* whales can provide some further insight into the foraging structure of *Gm* not only at the species and strata level, but also to some degree at the encounter group level. For example, in Figure 22 we provide a plot identical to the SI plot shown in Figure 16, but now where animals are grouped into one of nine different *Gm* encounter groups rather than their designated strata and show high degree of similarity in SI ratios among individuals within the individual encounter groups.

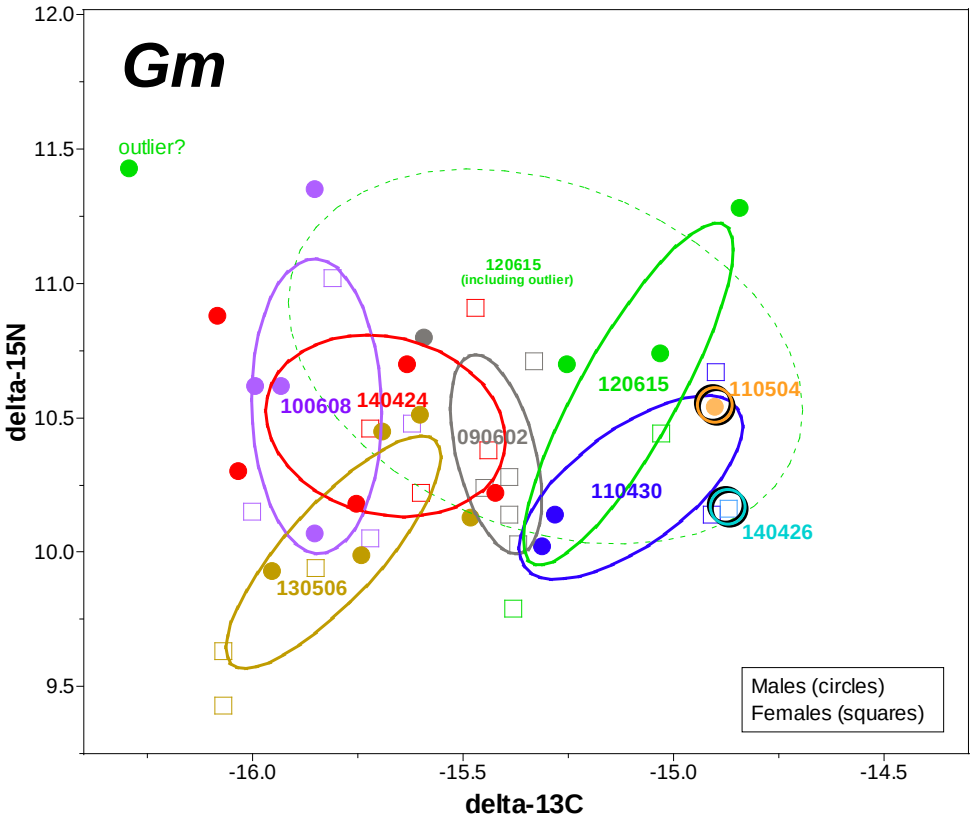


Figure 23. Differences in epidermal stable isotope ratios among encounter groups of short-finned pilot whales (*Gm*) of both sexes biopsied on the dates indicated (YYmmDD). Ovals represent the 50% probability density intervals of the distribution of isotopes within the encounter groups indicated. Symbols: Males (circles); Females (squares); colors represent whales sampled within the same encounter.

Genetics

Genetic diversity and differentiation in pilot whales

Seventy-two samples were collected and genotyped from pilot whales biopsied within the Bahamas. A genotyping error rate of 0.9% was empirically estimated from independent replicate genotyping of 15 samples. Four samples failed to yield DNA of sufficient quality and quantity and were dropped from the dataset. Two samples were identified as genetic duplicates indicating that the same whale had been biopsied twice. The final dataset included 67 unique, high quality pilot whales genotyped at a minimum of 17 loci (mean 21.74 ± 0.854).

Across the entire *Gm* dataset, no significant deviations from Hardy-Weinberg equilibrium were found (chi^2 = 58.392, df = 44, P = 0.0718), however significant deviations were observed at three loci (Ttr11, 468469 and MK8). Tests for linkage disequlibium for all pairs of loci revealed no significant deviations from expected after Bonferroni correction for multiple tests. Five unique mtDNA haplotypes (Table 7) were identified based on nucleotide differences across the

entire mitochondrial control region (1030bp), four of which have been previously sequenced from North Atlantic short-finned pilot whales (P. Rosel, *pers. comm.).*

Table 7. Frequency (n) of short-finned pilot whale mtDNA control region haplotypes among SERDP strata. Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

Haplotype	n	EA	EX	GB	SA	TO	Genbank accession
Gm_a	9	8				1	FJ513328
Gm_b	3					3	
Gm_c	1					1	
Gm_d	29			7	1	21	FJ513331
Gm_e	27		10	3		14	

Multiple biopsies were obtained from 17 *Gm* encounter groups. Of those groups, we collected genetic data from an average of 3.82 biopsies/group. A single mtDNA haplotype comprised most groups (mean = 1.235 haplotypes/group) with only two groups being represented by multiple mtDNA haplotypes. The greatest diversity of *Gm* haplotypes among the strata was found in TO where the largest number of groups was biopsied (Table 8).

Table 8. Numbers of different mtDNA haplotypes and numbers of sampled pilot whale (Gm) encounter groups within each of the five SERDP strata. Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

	# Haplotypes	# Groups	Notes
GB	2	2	*stranding
SA	1	1	*only 1 whale sampled
EA	1	3	
TO	5	15	
EX	1	2	*stranding

Global tests of genetic differentiation revealed significant genetic divergence among strata in both the mtDNA (F_{ST} = 0.390, P =0.0001; Phi_{ST} = 0.390, P =0.0001) and nuclear DNA (nuDNA) (F_{ST} = 0.025, P <0.0001; F'_{ST} = 0.075, P < 0.0001) datasets, indicating the presence of significant genetic structuring among *Gm* in the Bahamas. Using mtDNA sequence data, significant pairwise comparisons were found for four out of six pairs of strata (Table 9).

Table 9. Pilot whale genetic divergence among strata within the Bahamas estimated from mtDNA control region sequence data. Conventional FST below diagonal, PhiST above diagonal (yellow cells indicate p<0.001). Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

	EA	**EX**	**TO**	**GB**
EA		1	0.197	0.194
EX	1.000		0.512	0.667
TO	0.552	0.393		-0.060
GB	0.743	0.667	-0.029	

All pairwise comparisons revealed significant differentiation based on nuDNA genotype data (Table 10). However, after removal of 24 individuals to eliminate the effect of over-representation of kin in the nuDNA dataset, all metrics of (global and pairwise) genetic divergence were no longer significant.

Table 10. Nuclear genetic divergence (pairwise divergence metrics, F_{ST} and F'_{ST}) among pilot whales (*Gm*) sampled within the Bahamas. Strata and sample sizes are indicated. Statistical significance (p.val) is based on 10,000 random permutations of the dataset. Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

	n			**n**	**F_{ST}**	**F_{ST} p.val**	**F'_{ST}**	**F'_{ST} p.val**
EA	8	v.	**EX**	10	0.045	0.002	0.132	0.002
EA	8	v.	**GB**	9	0.038	0.015	0.114	0.014
EA	8	v.	**TO**	39	0.013	0.037	0.040	0.037
EX	10	v.	**GB**	9	0.062	0.000	0.177	0.000
EX	10	v.	**TO**	39	0.022	0.001	0.067	0.001
GB	9	v.	**TO**	39	0.020	0.004	0.062	0.004

This may reflect the reduction in sample size which reduced sample sizes in all regions except for TO to less than 10, but it also likely indicates that the geographic structuring of *Gm* in the Bahamas is being driven by the presence of groups of related individuals occurring in different regions, rather than geographic structure *per se*. A hierarchical AMOVA based on mtDNA data also indicated that the majority of mtDNA genetic variability was attributed to variation among groups within strata (Table 11).

Table 11. Analysis of molecular variance (AMOVA) results quantifying the partitioning of genetic variance for short-finned pilot whales (*Gm*) sampled in the Bahamas among geographic strata and encounter groups. Df is degrees of freedom, determined by sample size.

Source of variation	Df	Percentage of variation
Among strata	3	23.48
Among groups within strata	18	56.99
Within groups	48	19.53
Total	69	

Fitting Bayesian models to the genotype data in STRUCTURE detected significant genetic structure within the Bahamas with a highest mean log-likelihood and the statistic Δk when the samples were assigned to four groups (Figure 23). However, when related individuals were removed and the dataset restricted to unrelated individuals, STRUCTURE failed to detect definitive genetic groups, the most likely number of groups was ambiguous and assignment plots did not reveal any consistent structuring among Bahamas pilot whales (data not shown). This effect suggests that any structuring resolved from the unrestricted dataset is likely attributed to group effects rather than true geographical structuring.

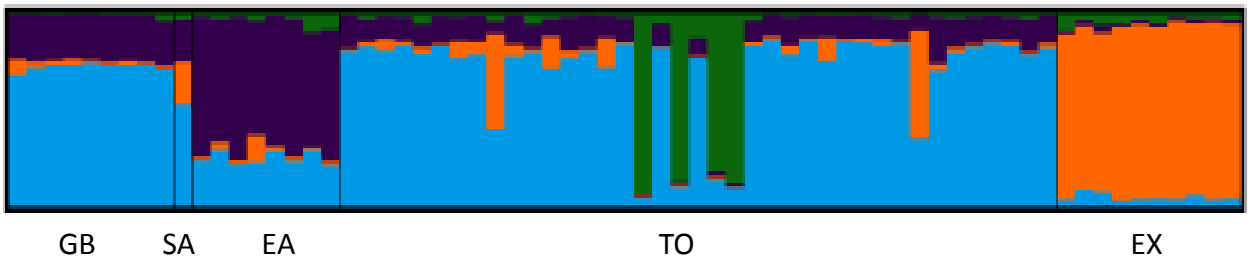


Figure 24. Bar plot showing the assignment of individual short-finned pilot whale (*Gm*) samples to genetic groups (by color) from the STRUCTURE model (k=4) fit to the unrestricted dataset. Sampling strata for each individual whale (vertical bar) are indicated by the two letter abbreviations on the horizontal axis: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

Average genetic relatedness among pairs of individuals was significantly higher between pairs sampled within the same stratum (t=-2.189, df=1359.7, P=0.0144). Of the 23 different *Gm* groups that were sampled, 16 groups were represented by multiple genotyped individuals. Pairwise genetic relatedness was significantly higher within encounter groups than between encounter groups across all strata (t=7.618, df=103.7, P<0.001; Figure 24). Based on congruence between results generated by KINGROUP and ML-RELATE, 24 pairs of individuals were identified as meeting the statistical criteria to be considered 'kin'. As expected, the majority of

these pairs were comprised of two individuals sampled within the same stratum with only 3 pairs of kin consisting of two individuals sampled in different strata within the Bahamas.

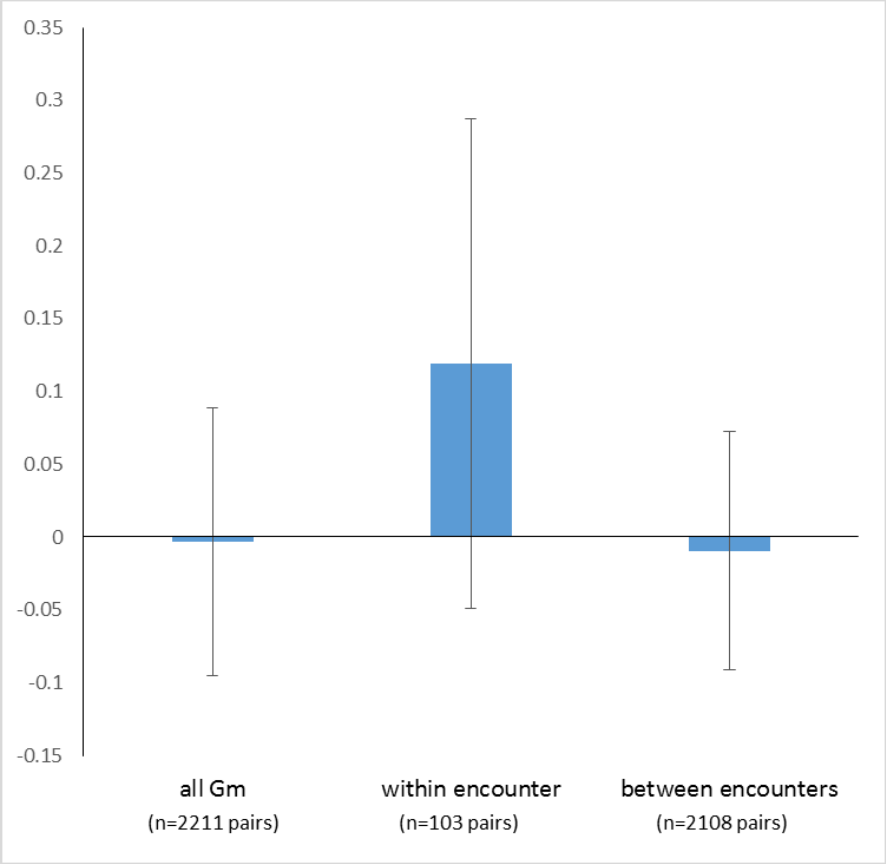


Figure 25. Mean (±sd) genetic relatedness among pairs of short-finned pilot whales (*Gm*), both sexes combined, biopsy sampled in the same encounter compared to those sampled across different encounters. 'nN pairs' indicates the number of pairwise comparisons, rather than the number of pairs of whales.

BLAINVILLE'S BEAKED WHALE (*Mesoplodon densirostris*)

Telemetry

A total of 12 tags were deployed on Blainville's beaked whales, resulting in 1442 location estimates (Table 4). These estimates were of moderate spatial resolution compared to other species, with an average error radius of 3.3km. Transmissions were received during tag durations up to 47 days, and deployment durations averaged 2-3 weeks (median = 19 days). Tags were distributed among adult females (*n*=7), adult males (*n*=4) and one sub-adult male. Movement tracks showed no evidence of sex differences in ranging patterns or extent (Figure 8). As with Cuvier's beaked whales, this species showed a remarkable level of small scale-site fidelity, with whales remaining within 100km of the tagging site for the duration of tag deployments (Figure 9). Movements were therefore only within strata, except for one whale that briefly moved between NE and TOTO before returning.

Blainville's beaked whales also displayed a distinct bimodality to diving behavior, which clearly delineated deeper foraging dives from surface activity (Figure 10). This species of beaked whale showed considerably less diurnal variation in near-surface non-foraging dive activity than observed in Cuvier's beaked whales. Daytime and night-time foraging dives exhibited a small but significant diurnal variation in depth, with deeper night-time foraging depths (depth median =1344 m, max = 1888 m; duration median = 47.6 mins, max = 64.7 mins) and shallower daytime foraging depths (depth median = 1056 m, max = 1568 m; duration median = 44.8 mins, max = 66.7 mins), which is the reverse of the pattern observed in the sperm whales and delphinids. As with Cuvier's beaked whales, this species spends only 20-30% of its time in target foraging strata. This species typically used habitat on canyon slope (Figure 8), but in areas where the benthos was shallow enough in middle of the canyon (e.g. TOTO) for this species to reach close to the sea floor their distribution spread over the entire width of the canyon. Because of the steep bathymetric gradients in these typical slope habitats, Argos location errors limited the precise determination of whether these whales were foraging above, close to, or on the sea floor, and prompted the large uncertainty shown by this species in Figure 12, but the evidence for diurnality in dive depths relative to bathymetric depths would suggest that they are not always feeding on the bottom, and are likely further off the bottom than Cuvier's beaked whales.

Because of this apparent foraging at least close to the benthos, the limited ranging patterns of individuals means that between-whale differences in diving may be driven by differences in bottom-depth between locations. Nonetheless, the adult males performed deeper dives on average than adult females, although the deepest dive was by an adult female (female depth median = 1056 m, max = 1888 m; male depth median = 1312 m, max = 1472 m). Similarly, adult males undertook slightly longer dives than the females (female duration median = 44.8 mins, max = 60.6 mins; male duration median = 46.5 mins, max = 66.7 mins).

Photo-identification

Movements

Extensive photo-identification data were collected for Blainville's beaked whales from 1991 – 2014 in all seven strata (Table 12). Using only high quality photographs (Q>1) of distinctively-marked individuals (D>0), a total of 321 individuals were photo-identified. Almost 50% of individuals were found in the SA stratum where this species has been the focus of shore-based studies since 1997, but more than 10 years of shore-based efforts have also occurred in the

TO (at AUTEC) and EA strata (see Figure 6 for encounter locations). Despite the longevity of this work, and sampling in all strata during ship surveys, very little movement between strata was documented; only 6 whales were photo-identified in more than one stratum, including 3 adult males, 1 adult female, and 2 sub-adult females, both of which became sexually mature between re-sightings. However, movements were limited in range to only adjacent strata, supporting telemetry findings of limited displacement for this species. *Md* exhibited the highest percentage of re-sightings compared to the other five species. Where long-term data exist (in SA, EA and TO), we found 36-45% of individuals photo-identified were re-sighted across multiple years, some over a decade. When combined with the telemetry results, we found that adult females in particular exhibited high long-term site fidelity to apparently very small localized areas, including on the AUTEC Weapons Range.

Table 12. Contingency table for Blainville's beaked whale photo-identification data collected from 1991 – 2014 in each strata in the Bahamas using high quality photographs (Q>1) of distinctively-marked individuals (D>0). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as limited movement between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	**GB**	**SA**	**EA**	**NE**	**TO**	**CU**	**EX**
GB	21 (0)	1	0	0	0	0	0
SA		145 (66)	3	1	0	0	0
EA			68 (25)	0	0	0	0
NE				13 (1)	0	0	0
TO					68 (28)	1	0
CU						7 (1)	0
EX							5 (0)

Social organization

Associations over time

The standardized lagged association rate (SLAR) calculated for adult females was higher than the null association rate for time periods up to approximately three years (Figure 25).

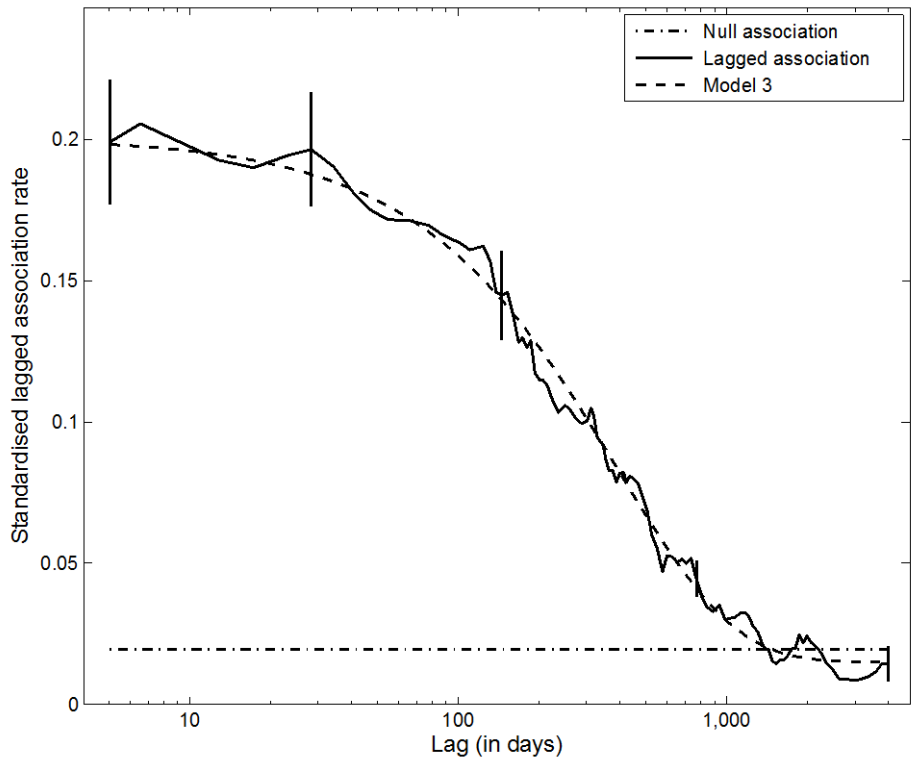


Figure 26. Standardized null and lagged association rates from photo-identification data for Blainville's beaked whale adult females using high quality photographs of distinctively-marked whales, showing the best-fit model, model 3, 'preferred companions and casual acquaintances' (Table 13). Vertical error bars represent temporal jackknife standard errors.

The best model for the SLAR for adult females was model 3: preferred companions and casual acquaintances, with virtually no support for the next best model, which had a ΔQAIC of 34 (Table 13).

Table 13. Model selection for the standardized null and lagged association rates of adult female Blainville's beaked whales. Association rates were calculated by the SOCPROG software (Whitehead 2008) using photo-identification data of high quality photographs (*Q*>0) of distinctively-marked individuals (*D*>0).

Model	QAIC	ΔQAIC	Comments
1. Preferred companions	3313	496	no support
2. Casual acquaintances	2854	37	no support
3. Preferred companions + casual acquaintances	**2817**	**0**	**best model**
4. Two levels of casual acquaintances	2851	34	no support

The SLAR calculated for the male associations with females was higher than the null association rate for time periods up to approximately one year (Figure 26), and the best model describing male associations with females, was again model 3 (preferred companions and casual acquaintances, Table 14).

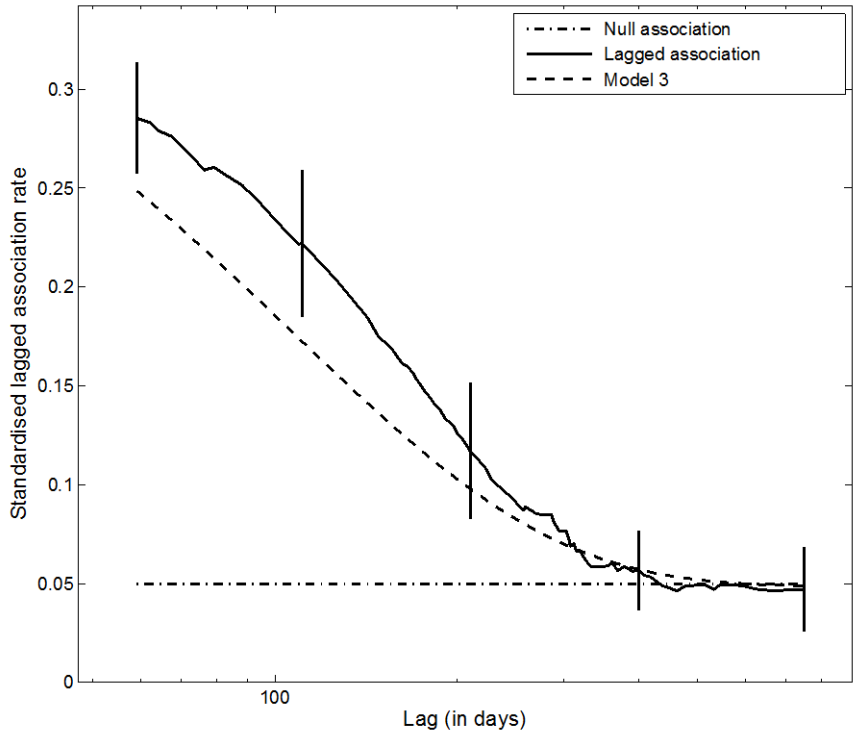


Figure 27. Standardized null and lagged association rates from photo-identification data for Blainville's beaked whale adult males associating with adult females, showing the best-fit model, model 3, 'preferred companions and casual acquaintances' (Table 14). Vertical error bars represent temporal jackknife standard errors. Only high quality photographs of distinctively-marked whales were included.

Table 14. Model selection for the standardized null and lagged association rates of adult male Blainville's beaked whales associating with adult females. Association rates were calculated by the SOCPROG software (Whitehead 2008) using photo-identification data of high quality photographs (Q>0) of distinctively-marked individuals (D>0).

Model	QAIC	ΔQAIC	Comments
1. Preferred companions	277	30	no support
2. Casual acquaintances	260	13	no support
3. Preferred companions + casual acquaintances	**247**	**0**	**best model**
4. Two levels of casual acquaintances	272	25	no support

Testing for non-random associations

The SLARs began to decline after a period of 100 days for the entire population (Figure 25), so a sampling period of 100 days was used for the preferred / avoidance tests, to look for associations between periods of 100 days. The number of random permutations was set at 10,000, as increasing this number did not affect the resulting *p*-values. The results for preferred and avoided associations were not different from random expectations for all except adult female associations with one another (Table 15). The SD of adult females' mean association index was significantly higher in the observed dataset than the randomly permuted data. Additionally, the proportion of non-zero association indices was significantly lower in the observed dataset than the random (having many more zero association indices than would be expected). These results suggest that adult female Blainville's beaked whales have both preferred associates and individuals they avoid among members of their own age/sex class, between periods of 100 days. Performing the same tests for a sampling period of a year produced very similar results.

Table 15. Permutation tests using association matrices and a mantel test for Blainville's beaked whale long-term preferred associations and avoidances, with a sampling period of 100 days, and 10,000 random permutations. Association rates were calculated by the SOCPROG software (Whitehead 2008) using photo-identification data of high quality photographs (Q>0) of distinctively-marked individuals (D>0). Adult females have both preferred and avoided associates.

	Long-term preferred associations? (standard deviation)			**Avoided associations? (proportion of non-zero)**		
Class	**Real**	**Random**	***p*-value**	**Real**	**Random**	***p*-value**
AM -> AF	0.0806	0.0801	0.4139	0.3333	0.3339	0.4718
AF -> AM	0.0806	0.0789	0.2990	0.3333	0.3319	0.5478
AF -> AF	0.0845	0.0684	<0.0001	0.3072	0.3620	0.0002

We found that females with dependent calves were much more likely to associate with other female–calf pairs, while females without dependents prefer to associate with one another (Figure 27). The mean association index of dyads in different reproductive classes was 0.0089 (SD 0.018), whereas it was twice as much, 0.0173 (SD 0.021) for animals in the same reproductive class (Mantel test: t=2.13, p = 0.01).

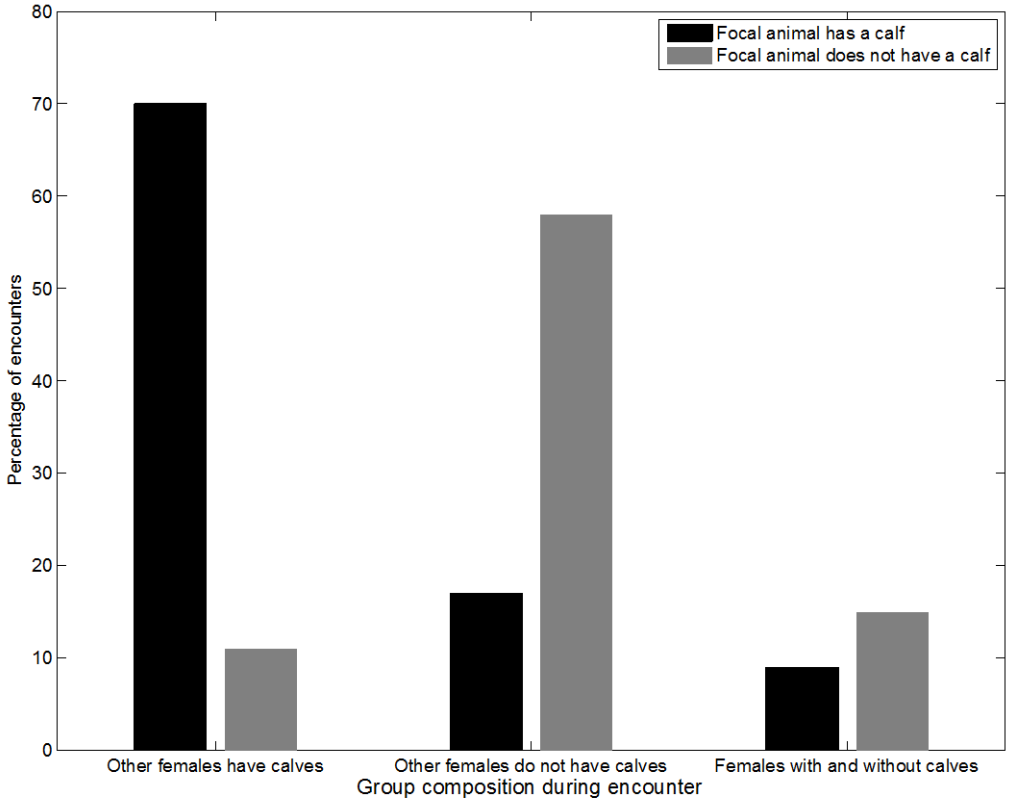


Figure 28. Frequency plot showing the group composition when the focal Blainville's beaked whale adult female is with and without a calf, in three different group compositions; groups which include only other females with calves, groups which include only other females without calves, and groups which include other females both with and without calves.

To investigate whether females with calves have preferred habitats, we created two symmetric matrices for all encounters in which there was an adult female present. One matrix detailed whether a calf was present or not in either encounter (1/0), and the other matrix had the distances between each encounter. The Mantel test did not reject the null hypothesis that there was no correlation between these two datasets (p=0.5, 10,000 permutations), suggesting that there is no general difference in habitat preference when a female is with or without a calf. If there had been preferred habitat when one was with a calf, the matrices would have correlated with shorter distances between sightings with calves.

Chemistry

In Figure 28 we provide results for nitrogen and carbon stable isotope ratios measured in the epidermal tissue of *Md* whales (both sex) where the individual whales are shown grouped by their primary designated strata. In particular, we compared δ15N and δ13C results for *Md* whales biopsied in each of the following six strata (CU, TO, GB, SA, NE, and EA).

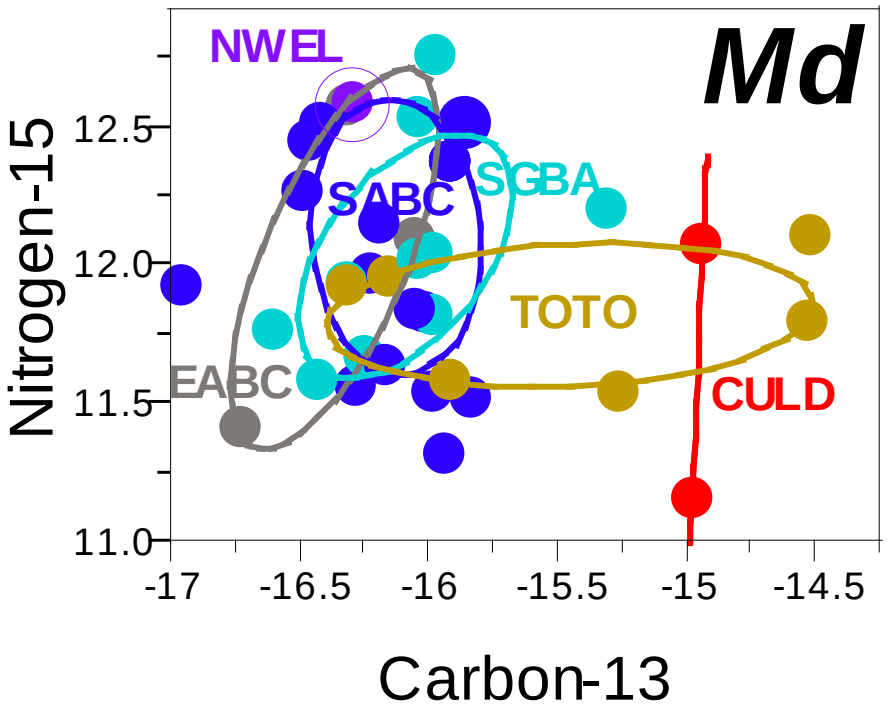


Figure 29. Differences in stable isotope ratios among Blainville's beaked whales (*Md*) of both sexes biopsy sampled in the northern Bahamas from 2007 – 2014 in the six color-coded strata indicated. Ovals represent the 50% probability density intervals of the distribution of isotopes within the regions indicated. Strata abbreviations: South Grand Bahama (SGBA); North Eleuthera (NWEL); East Abaco (EABC), South Abaco (SABC), Tongue of the Ocean (TOTO), and Cul de Sac (CULD).

First, of particular note, is the observation that mean δ15N values for each of the six strata depicted in Figure 28 are highly similar suggesting that the diets of this particular species are relatively uniform in composition across the entire study area. However, the range of δ15N values observed for *Md* (~11.2 to 12.7) greatly exceed analytical measurement errors ($\sigma = 0.3$) for this isotope which in turn implies that the diets of these whales are comprised of a mixed diet of two or more different prey items rather than being comprised of a single major food source. A possible exception to this mixed prey hypothesis are the *Md* whales biopsied at TO which exhibit a much narrower range of δ15N values than observed at the other locations suggesting a much simpler, less varied diet.

Moreover, whereas CU and TO strata animals are observed to be markedly different from the other four locations (most notably δ13C), we observe only very small offsets in SI values among *Md* whales biopsied further to the north (*i.e.*, outside of Tongue of the Ocean). The elevated δ13C values observed for the CU (and selected TO) whales appear to be the result of foraging entirely (or in part) within the CU region. We arrived at this conclusion based on the observation that all whales biopsied in the Cul de Sac regardless of species had elevated δ13C

values consistently greater than δ13C≥ -15.0. Thus, 13C values greater than this value will be interpreted as evidence of foraging either entirely (or part-time) within the CU region within the approximate two-month period leading up to the time the biopsy sample was acquired. Somewhat surprisingly, *Md* whales biopsied at GB, NE, SA, and EA exhibited very little difference in their SI ratios that in turn implies that their diets are mostly indistinguishable thus providing no direct evidence of site-fidelity within these four sub-strata based on SI results.

As a further test of the high degree of similarity of perceived diets of *Md* whales biopsied at the four Northwest Providence Channel locations relative to TO and CU strata whales, *Md* blubber dietary fatty acid results were subjected to a principal component analysis and no statistically significant separation was found among any of the six strata locations (data not presented). Thus, in contrast to the abundant photo-ID re-sight data for this species which clearly demonstrate that these whales exhibit a high degree of site-fidelity to the strata in which they are typically encountered, SI and dietary FA results both fail to provide any direct evidence of strong short-term site-fidelity for this species.

The most likely explanation why both SI and FA analyses failed to find differences among adjacent *Md* strata (especially among Northwest Providence Channel locations) is that the limited mix of specific prey seemingly consumed by this species migrate freely among these locations over the course of a season thus blurring out any location specific signals that might otherwise occur. In short, chemical tracers will only be successful at revealing site-specific foraging under the conditions that neither the whales (nor their primary prey) oscillate between the locations being studied.

Finally, in a separate analysis, the long-term foraging site-fidelity of *Md* whales were independently assessed by comparing the pattern of POPs (see list Appendix A, Table A2) measured in their outer-blubber biopsy tissues and comparing POP patterns among the six designated strata. Specifically, in Figure 29 we present the results of both a principal component and hierarchical cluster analysis of POP patterns measured in the blubber of all *Md* whales where the whales are shown grouped (color-coded) by their biopsy locations (strata). Very similar to what was described above for SIs and dietary FAs, we observe moderate-to-low separation among the six strata with the CU and TO groups of *Md* (Cluster A) again being different than the four Northwest Providence Channel strata animals (Clusters B-D). Thus, if we were to rely on chemical tracers alone to assess the site-fidelity of *Md* whales in the Bahamas (both seasonal and lifetime durations), we would erroneously conclude that this species exhibits low-to-moderate site-fidelity with the Northwest Providence Channel perhaps acting as a pseudo-boundary infrequently crossed during foraging bouts. Again, we speculate that our inability to detect differences in chemical tracers among strata for this species may simply be a reflection of large-scale prey movement among these locations for the specific prey consumed by these whales.

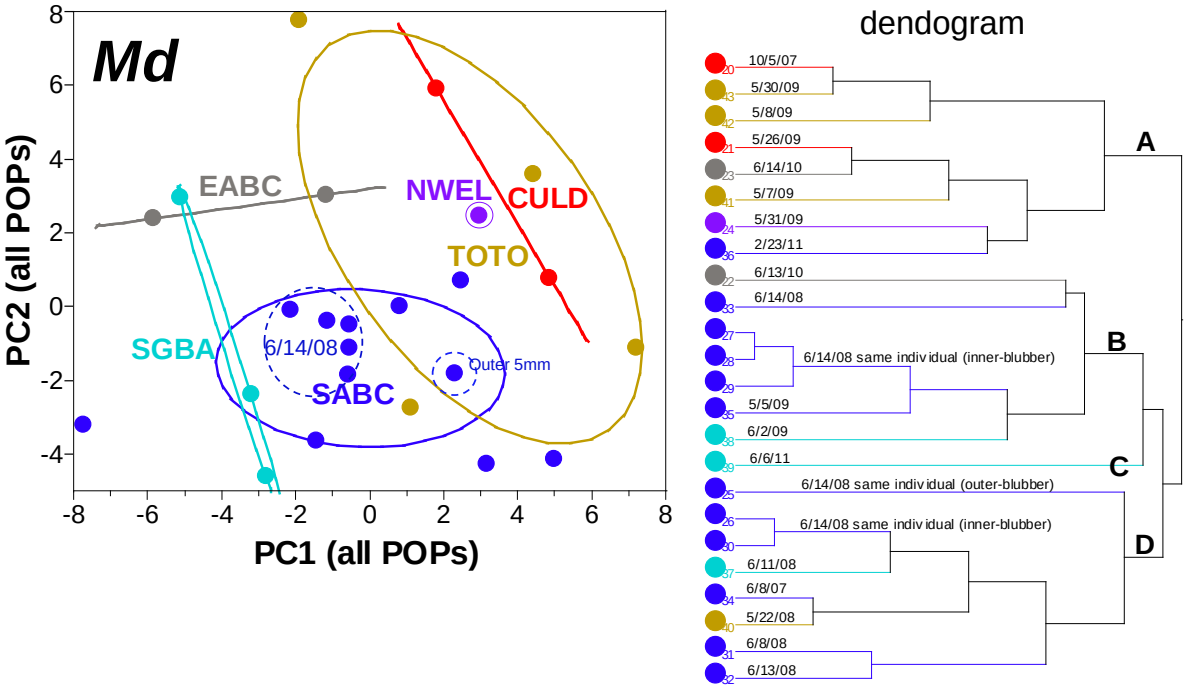


Figure 30. Principal Component and hierarchical cluster analysis of POP patterns measured in the epidermal tissues of Blainville's beaked whales (*Md*, males only) with whales grouped by their color-coded sampling strata. The dashed-line cluster of five SABC 6/14/08 animals represent a single individual where the 0-30 mm blubber was depth profiled in 5 mm increments. Ovals represent the 50% probability density intervals of the distribution of POPs within the strata indicated. Biopsy collection dates of each individual whale are indicated in the dendrogram plot where the letters A-D represent the four major clusters revealed as the result of the hierarchical cluster analysis. Strata abbreviations: South Grand Bahama (SGBA); North Eleuthera (NWEL); East Abaco (EABC), South Abaco (SABC), Tongue of the Ocean (TOTO), and Cul de Sac (CULD).

GERVAIS BEAKED WHALE (*Mesoplodon europaeus*)

Photo-identification

Movements

Photo-identification data were collected for Gervais' beaked whales from 2001 – 2012 but were limited due to the low number of sightings of this species (see Figure 6 for encounter locations). Using only high quality photographs (*Q*>1) of distinctively-marked individuals (*D*>0), a total of 47 individuals were photo-identified from four of the seven strata (Table 16). There were no movements between strata documented or re-sightings within strata over multiple years but this is not surprising given the low number of individuals photo-identified. It is noteworthy that despite the low sighting probability for *Me* in the Great Bahama Canyon and the lack of sightings at AUTEC, there have been multiple single stranding events of this species in TOTO (BMMRO unpublished data).

Table 16. Contingency table for Gervais' beaked whale photo-identification data collected from 2001 – 2012 in each strata in the Bahamas using high quality photographs (Q>1) of distinctively-marked individuals (D>0). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as the lack of movement between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	GB	SA	EA	NE	TO	CU	EX
GB	4 (0)	0	0	0	0	0	0
SA		0	0	0	0	0	0
EA			15 (0)	0	0	0	0
NE				0	0	0	0
TO					0	0	0
CU						11 (0)	0
EX							17 (0)

Chemistry

Unfortunately, very few Gervais' beaked whales were encountered and successfully biopsied during the course of this study thus greatly limiting our ability to employ chemical tracers as a tool to assess the foraging structure of this species in a manner similar to that described for *Md* and *Zc* beaked whales. Moreover, among the eleven *Me* beaked whale samples

biopsied and analyzed for their full suite of chemical tracers (see Appendix A - Table A1), almost all *Me* samples were collected at a single location (EA) with the exception of one animal biopsied in GB in 2011 and another in the CU in 2007. The mean $\pm$ SD nitrogen and carbon SI values obtained for the EA strata *Me* beaked whales were: (δ15N = 11.9 $\pm$ 0.3; δ13C = -16.5 $\pm$ 0.1). In contrast, the single *Me* beaked whale identified as part of the CU strata had a much higher carbon isotope ratio value (δ13C = -14.2) than the EA strata whales suggesting that this single CU strata whale likely foraged in the CU for much/all of the 2-3 month period prior to the time its biopsy sample was acquired. Although the δ15N value for this single CU strata *Me* sample (δ15N = 11.6) was comparable to the EA strata whales (initially implying similar diets), when the dietary FA profile of this single CU strata whale was compared to the EA strata *Me* beaked whales using principal component analysis (data not shown), we observed a large difference in dietary FA profiles between the two strata suggesting that prey preferences likely differ substantially between these two relatively distant (non-adjacent) locations. In addition, POP pattern results for this species (data not shown) also revealed that the CU strata whale had a substantially different POP composition than the EA strata *Me* whales. Thus, despite the very small n-number of samples analyzed, all of these results begin to hint at the possibility that the foraging structure of Bahamas *Me* beaked whales may be somewhat similar to the other two Bahamas beaked whale species (*Md* and *Zc*), specifically by demonstrating some level of both short-term and long-term foraging site fidelity. Clearly, additional *Me* biopsy samples will need to be collected throughout the entirety of the Bahamas study area and analyzed for their chemical tracers before their foraging structure can be more fully evaluated using chemical tracers.

To assess the potential differences in the diets of these three beaked whale species (not including *Gm, Pe, Pm*) we also subjected the dietary FA profile data for the beaked whales to a Multidimensional Scaling Analysis (Figure 30) and applied the ANOSIM algorithm to compute the pair-wise significant difference levels between species. Whereas the difference in FA profiles of *Md* and *Zc* were found to be statistically significantly different (p<0.001), *Me* whales were found to be only marginally different from *Md* (p<0.15) and statistically indistinguishable from *Zc* (p=0.43). Thus, when the SI and dietary FA results of Figures 14, 15 and 30 are evaluated both separately and in combination, we conclude that the preferred prey of the six cetacean species studied are likely largely dissimilar with the possible exception of *Me* and *Zc* which exhibit rather similar dietary FA profiles. However, despite the similarity in dietary FA profiles between these two species, we do observe that the mean 13C stable isotope value for *Me* (δ13C =-16.5) is statistically significantly lower than *Zc* (δ13C =-15.9; p<0.01), perhaps suggesting some small degree of niche separation between these two. However this could be largely because the *Me* whales were sampled in a more offshore/pelagic environment off EA compared to most of the *Zc* samples.

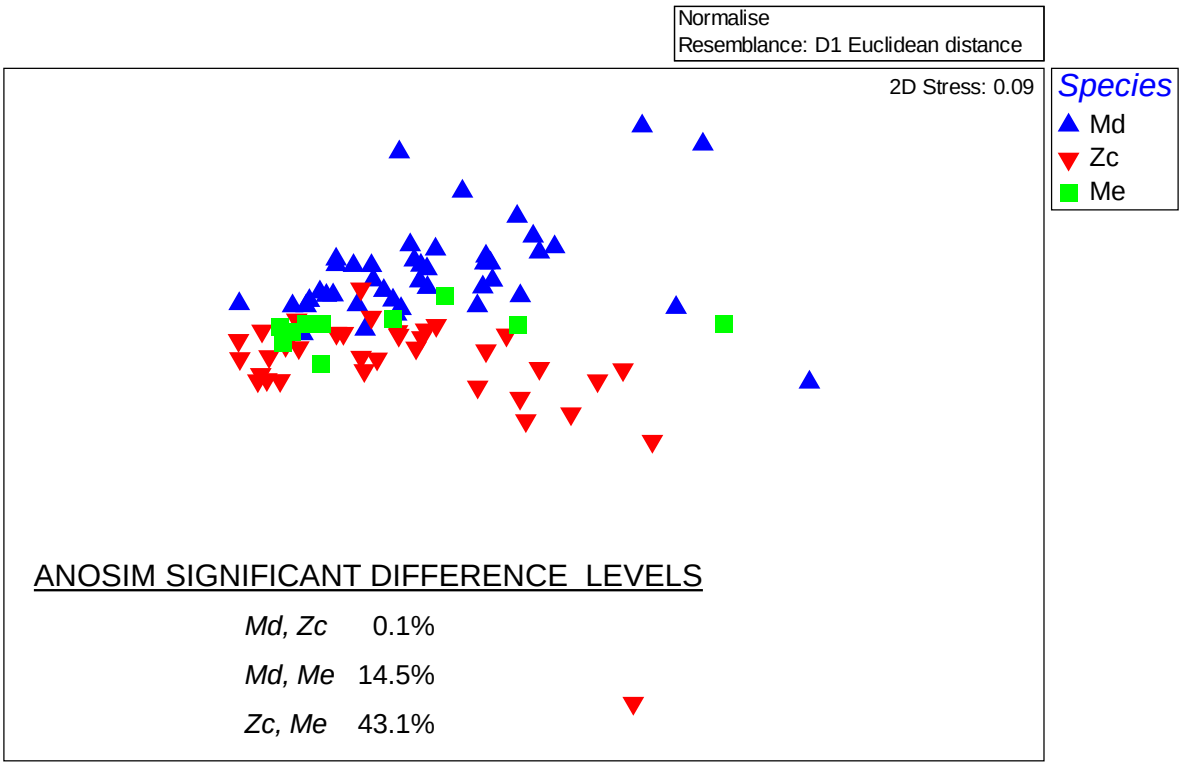


Figure 31. Differences in the pattern of dietary fatty acids among Blainville's (*Md*, blue triangles), Cuvier's (*Zc*, red triangles), and Gervais' (*Me*, green squares) beaked whales of both sex revealed using Multidimensional Scaling Analysis with differences between the 3 pairs of species statistically evaluated using the Analysis of Similarity algorithm.

Integration of the mean telemetry foraging dive depth data provided in Figure 12 with measured blubber FA compositions for the five Bahamas cetacean species in which LIMPET tags have been successfully deployed (*Pe*, *Gm*, *Pm*, *Md*, and *Zc*) reveal that specific FAs (or FA ratios) appear to change systematically with mean foraging depth. At present, we have no LIMPET dive-depth data for Gervais' beaked whales in which to compare to our existing blubber FA results for this species, but as will be shown below, it is now possible to predict the mean foraging dive depths of *Me* beaked whales from their blubber FA compositions. Other published research studies have also shown that specific FAs, most notably polyunsaturated fatty acids, branched-chain FAs, monounsaturated, and odd-chain FAs, generally decrease in composition with depth in the marine environment providing some support for our preliminary findings here but these studies generally focused on much lower trophic organisms such as teleost fish and particular organic matter (*e.g.*, Lewis 1967, Jones *et al.* 2008, Saito *et al.* 1996). The most robust fatty acid-foraging dive depth model obtained in this particular study is shown in Figure 31 wherein we observe a strong linear relationship between the FA ratios [C15:0/C17:1n8] measured in the blubber tissues of *Pe*, *Gm*, *Pm*, *Md*, and *Zc* and their tag-determined mean foraging dive depths (Figure 12). This somewhat unexpected yet highly useful result thus in theory provides us with an indirect analytical method to predict the mean foraging depth of any individual Bahamas whale via biopsy sampling. Using this model, the overall mean

foraging depth for the eleven Gervais' beaked whales biopsied in this study is predicted from their [C15:0/C17:1n8] ratios to be 1080m (SD = 140m). Thus, among all six DOD-priority cetacean species collected and analyzed as part of this study, our limited data for this species indicates that the foraging structures of *Me* beaked whales are, as expected, most similar to the other two species of beaked whales as evidenced by their more similar SI and dietary FA signatures (Figures 14, 15 and 30) as well as their more similar mean foraging dive depths (Figure 31) compared to sperm whales and the two delphinids, *Pe* and *Gm*.

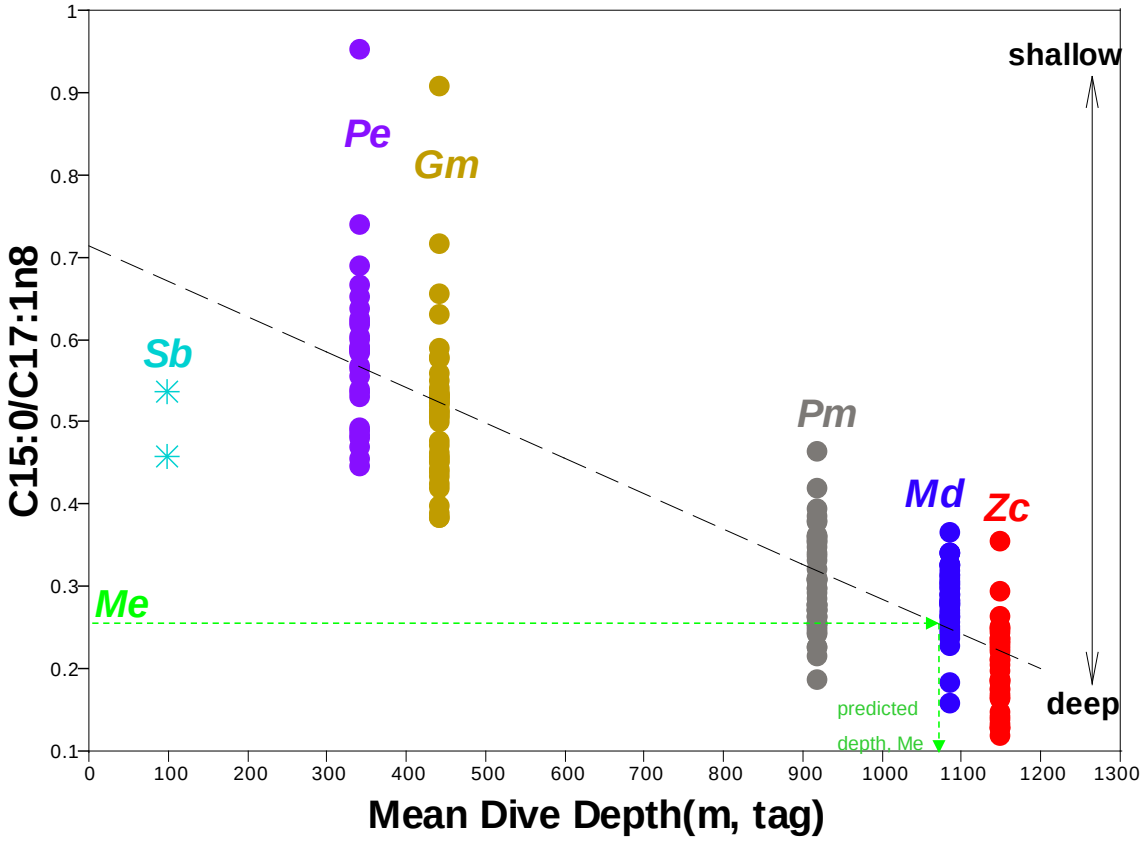


Figure 32. Relationship between the fatty acid ratio [C15:0/C17:1n8] and mean foraging dive depth (m) for the five cetacean species (*Pe*, *Gm*, *Pm*, *Md*, and *Zc*) for which LIMPET dive depth recorders were successfully deployed. The mean foraging depth of the nine Gervais whales biopsy sampled and measured for fatty acids was predicted from this FA-depth relationship to be 1080m. Data for two individual rough-toothed dolphin (*Sb*) samples are also shown plotted but are used here primarily as a test of the robustness of the FA-depth to other cetacean species in the Bahamas. Species abbreviations: short-finned pilot whale (*Gm*, in gold); Blainville's beaked whale (*Md*, in blue); Gervais' beaked whale (*Me*, in green); melon-headed whale (*Pe*, in purple); sperm whale (*Pm*, in grey); Cuvier's beaked whale (*Zc*, in red); and rough-toothed dolphin (*Sb*, in teal).

CUVIER'S BEAKED WHALE (*Ziphius cavirostris*)

Telemetry

Seven tags were deployed on Cuvier's beaked whales, resulting in 594 location estimates (Table 4). These estimates were imprecise compared to other species, with an average error radius of 5.6 km owing to long dives and infrequent surfacing (see Figure 10). Tag longevity was good: transmissions were received during tag durations up to 92 days, and deployment durations averaged 3-4 weeks (median = 26 days). Tags were distributed among adult females (*n*=3) and adult males (*n*=4). Movement tracks showed no evidence of sex differences in ranging patterns or extent (Figure 8, see male and female tracks overlaid at top left of *Zc* plot). This species showed a remarkable level of small scale-site fidelity, with whales remaining within 100 km of the tagging site (Figure 9), even for durations of up to 13 weeks. Movements were only within strata, except for one whale that moved to an adjacent strata (TOTO to Cul de Sac).

Cuvier's beaked whales displayed a distinct bimodality to diving behavior, which clearly delineated deeper foraging dives from surface activity (Figure 10). There was also a distinct diurnal variation in near-surface non-foraging dive activity, however daytime (depth median =1120 m, max = 1888 m; duration median = 65.1 mins, max = 103.5 mins) and night-time (depth median = 1120 m, max = 1600 m; duration median = 65.0 mins, max = 100.8 mins) foraging dives were relatively consistent (Figure 10). Although relatively large Argos location errors prevented the precise identification of foraging habitat relative to bottom depths, it is clear that Cuvier's beaked whales forage closest to the benthos of all the species in our sample (Figure 12) and their foraging dive depths in some areas were likely constrained by local bottom depths producing the wide variation in foraging dive depths seen in Figure 10. Overall this species spends only 20-30% of its time in its foraging strata (Figure 11). This species typically used both canyon slopes (Figure 8), and/or lower relief topography in the middle of the canyon (e.g. NW Providence Channel) where water depths were shallow enough that this species could dive close to the sea floor (Figure 12).

The limited ranging patterns of individuals means that between-whale differences in diving may be driven by differences in bottom-depth between locations. Nonetheless, the deepest dives recorded in this study were by adult males (female depth median =1088 m, max = 1408 m; male depth median = 1200 m, max = 1888 m) but the longest dives were by females (female duration median = 70.4 mins, max = 103.5 mins; male duration median = 62.5 mins, max = 92.2 mins).

Photo-identification

Movements

Photo-identification data were collected for Cuvier's beaked whales from 1993 – 2014 in all seven strata (Table 17). Using only high quality photographs (*Q*>1) of distinctively-marked individuals (*D*>0), a total of 89 individuals were photo-identified, although 30% of these whales were from a single stratum (EA). We found limited movements between strata but these were notably different to *Md* movement patterns. An adult female *Zc* showed site fidelity to one stratum (SA) over three years, and live-stranded in SA during an atypical stranding on March 15th, 2000 caused by a Navy sonar exercise (Balcomb and Claridge 2001). This whale was pushed off the beach by rescuers and was later re-sighted in 2009 in an adjacent stratum (NE), a relatively short distance (75 km) away. Movements were also found for two adult male *Zc*; over

a time period of 3 years, one male was photo-identified in SA and NE while the other male moved into the Great Bahama Canyon from outside (EX, at least 300 km away). There was a small number of multi-year re-sightings, involving adult males and females, one of which spanned across 13 years. *Zc* movement patterns appear to be more expansive in the longer term than *Md*, with perhaps long-term site fidelity to two adjacent strata.

Table 17. Contingency table for Cuvier's beaked whale photo-identification data collected from 1993 – 2014 in each strata in the Bahamas using high quality photographs (*Q*>1) of distinctively-marked individuals (*D*>0). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as limited movement between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	**GB**	**SA**	**EA**	**NE**	**TO**	**CU**	**EX**
GB	16 (2)	0	0	0	0	0	0
SA		17 (2)	0	2	0	0	0
EA			29 (1)	0	0	0	0
NE				5 (0)	0	0	0
TO					7 (0)	0	1
CU						17 (0)	0
EX							1 (0)

Chemistry

Analogous to the chemical tracer results described above for *Md* whales, the short-term and long-term foraging structures of Cuvier's beaked whales were studied by measuring the relative distribution of each of the three chemical tracers (SIs, FAs, POPs) among the five designated strata identified for this species (specifically CU, NA, GB, NE, and EA). A plot depicting differences in stable isotope ratios measured among the five *Zc* strata is shown in Figure 32. Unlike *Md* whales that exhibited relatively small differences in SIs among locations, *Zc* whales within each of the five strata displayed a relatively high degree of intra-strata similarity in SI values but differ substantially between most strata. We interpret this finding as an indication that *Zc* beaked whales display a relatively high degree of short-term foraging site fidelity with short-term foraging seemingly occurring primarily within the confines of a single stratum. Further evidence of short-term foraging site-fidelity of *Zc* to individual strata is also provided by the dietary FA data obtained for this species wherein principal component analysis

of the pattern of dietary FAs measured in these whales (data not shown) also exhibit a high degree of intra-strata similarity yet reveals large differences in FA profiles among *Zc* strata.

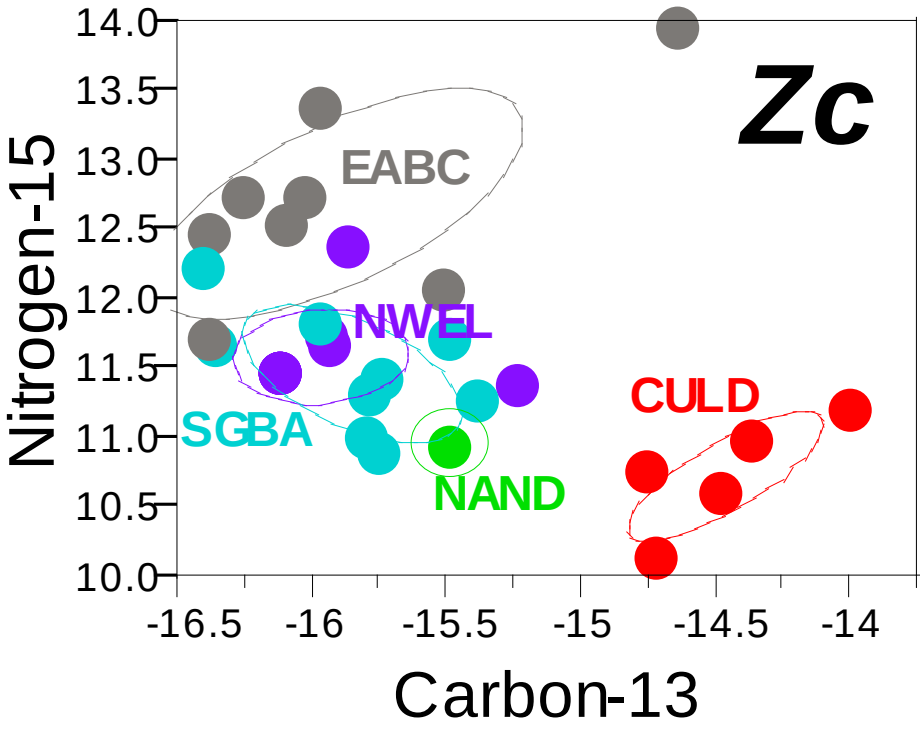
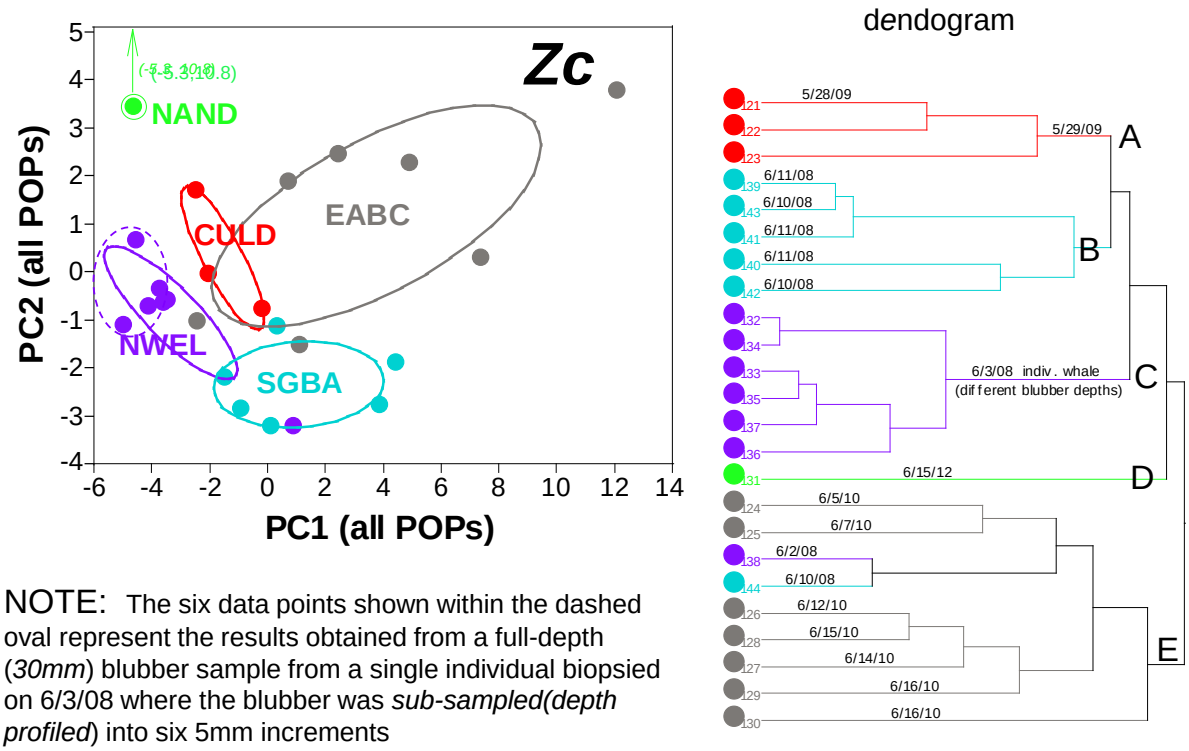


Figure 33. Differences in stable isotope ratios among Cuvier's beaked whales (*Zc*) of both sexes biopsy sampled in the five color-coded locations indicated. Ovals represent the 50% probability density intervals of the distribution of isotopes within the regions indicated. Strata abbreviations: South Grand Bahama (SGBA); North Eleuthera (NWEL); East Abaco (EABC); North Andros/South Berry Is. (NAND); and Cul de Sac (CULD).

In Figure 33 we demonstrate how the patterns of POPs measured in the epidermal tissues of *Zc* beaked whales (males only) differ among individuals and among the five designated strata. Specifically, we present the results of both a principal component and hierarchical cluster analysis of POP patterns measured in the blubber of all *Zc* whales where the whales are again shown grouped by their biopsy locations (strata). Similar to *Zc* SI and FA results, POP contaminant patterns are observed to be largely different when comparing among the five strata, which in turn provides support for the assertion that Bahamas *Zc* beaked whales, in addition to exhibiting evidence of short-term site-fidelity, also exhibit relatively strong long-term foraging site fidelity over their lifetimes. These results are qualitatively consistent with both the photo-ID re-sight data provided for this species (Table 17) and the satellite tag displacement results shown in Figures 8 and 9 connoting limited foraging ranges for this species.



NOTE: The six data points shown within the dashed oval represent the results obtained from a full-depth (*30mm*) blubber sample from a single individual biopsied on 6/3/08 where the blubber was *sub-sampled(depth profiled*) into six 5mm increments

Figure 34. Principal Component and hierarchical cluster analysis of POP patterns measured in the epidermal tissues of Cuvier's beaked whales (*Zc*, males only) with whales grouped by their five color-coded sampling locations. Ovals represent the 50% probability density intervals of the distribution of POPs within the regions indicated. Strata abbreviations: South Grand Bahama (SGBA); North Eleuthera (NWEL); East Abaco (EABC); North Andros/South Berry Is. (NAND); and Cul de Sac (CULD). Biopsy collection dates of each individual whale are indicated in the dendrogram plot. Letters A-E represent the five major clusters revealed as the result of the hierarchical cluster analysis.

SPERM WHALE (*Physeter macrocephalus*)

Telemetry

A total of 27 tags were deployed on sperm whales, more than any other species, resulting in 1449 location estimates (Table 4). These estimates were moderately precise compared to other species, with an average error radius of 3.3 km. The slow surface logging behavior of this species might be expected to allow frequent tag transmissions, but the dorsal hump of the these adult female and sub-adult males was relatively small (compared to large adult males) and therefore likely did not clear the water surface often to allow frequent activation of the tag's saltwater switch. Tag longevity was surprisingly low, perhaps because tags were removed during social body contact: transmissions were received during tag durations up to 19 days, but deployment durations were more typically 1-2 weeks (median = 10 days). Tags were distributed among adult females (n=10), sub-adult males (n=10) and whales of unknown gender (n=7) that were likely either adult females or smaller sub-adult males. Movement tracks showed a general pattern of area partitioning between adult females and sub-adult males, with the females in our sample using a consistent range within NW Providence Channel (GB strata) compared to the males that ranged more widely within TOTO and beyond (Figure 8). Three whales, two of which were sub-adult males (one unconfirmed), moved beyond the Great Bahama Canyon into the subtropical North Atlantic east of the study area (Figure 34). The extent of displacement away from the tagging site was therefore greater for these young males than for the adult females (Figure 9).

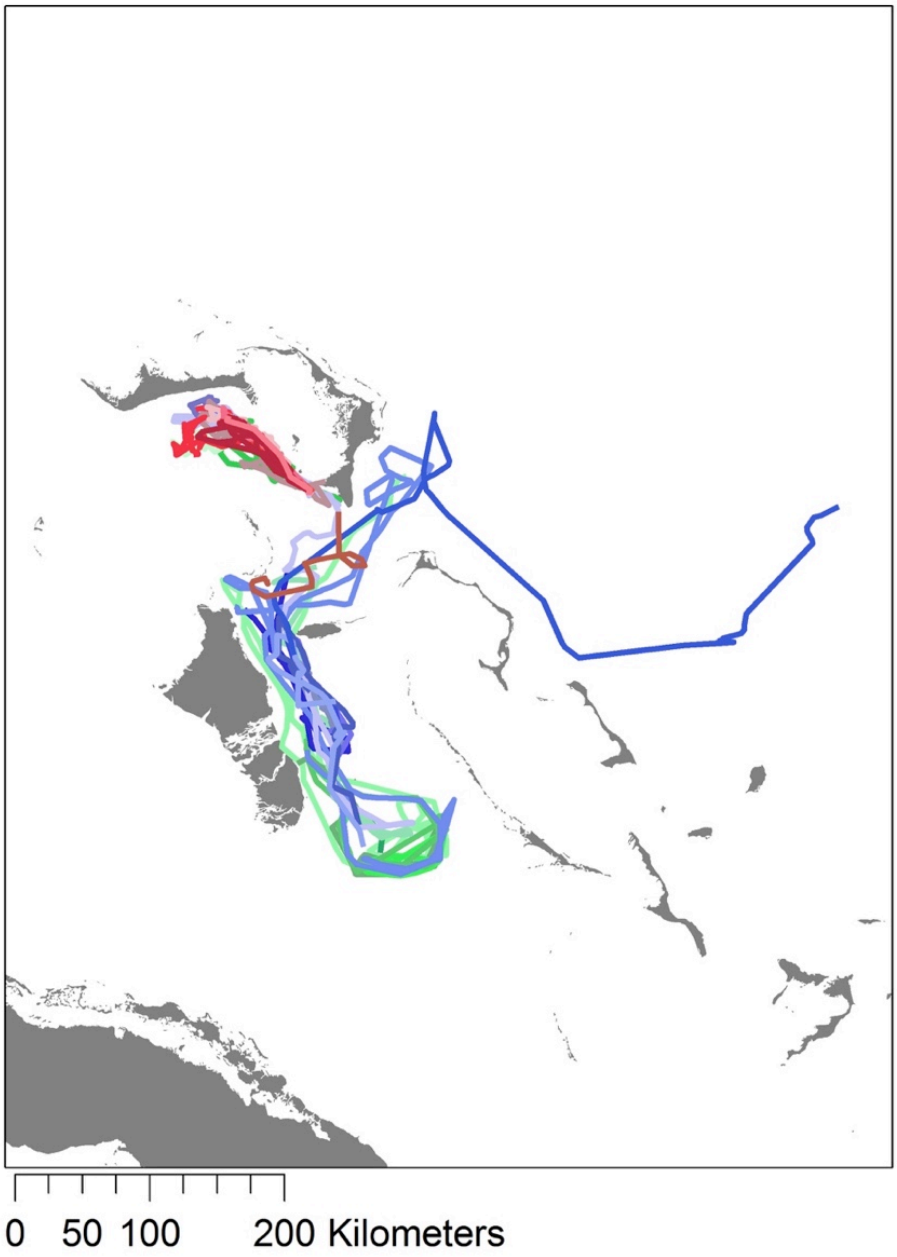


Figure 35. Movement tracks of sperm whales (*n*=27) showing movements generally within the Great Bahama Canyon, but three whales (two sub-adult males, one unconfirmed gender) ranged out of the canyon and to the east. Tracks represent the maximum likelihood fit of a continuous-time correlated random walk model (Johnson *et al.* 2008) to location estimates from the Argos satellite system; colors reflect gender of tagged whales (red = females, blue = males, green = unknown) with shading to identify individual tracks.

Sperm whales displayed a distinct bimodality to diving behavior, which clearly delineated deeper foraging dives from surface activity (Figure 10). There was evidence of modest diurnal variation in dive depth and vertical habitat occupancy, with daytime dives that were typically deeper than night dives (median day dives = 920 m, max = 1344 m; median night dives = 888 m, max = 1216 m). However, daytime dives were only marginally longer in duration (day median = 47.8 mins, max = 62.1 mins; night median = 47.5 mins, max = 60.2 mins), and sperm whales therefore spent approximately 50% of their time within foraging strata both day and night (Figure 11). Activity was typically concentrated over canyon slopes (Figure 8), although sub-adult males ranging widely within the Tongue of the Ocean showed less affinity for slope habitats. Because of the steep bathymetric gradients in these typical sperm whale habitats, Argos location errors limited the precise determination of whether these whales were foraging above, close to, or on the sea floor, and prompted the large uncertainty shown by this species in Figure 7, but the evidence for diurnality in dive depths relative to bathymetric depths would suggest that they are not always feeding on the bottom.

Sperm whales are extremely sexually dimorphic, but large fully-grown males have not been seen in this study area. Consequently, within this sample consisting of similarly-sized adult females and sub-adult males there was little evidence for sex differences in average dive depths (Figure 19; females depth median = 904 m, males depth median = 888 mm). However, there was more variability within sub-adult males, likely reflecting size differences (see discussion), and sub-adult males also performed the deepest dives (females depth max = 1056 m, males depth max = 1344 m). There was also evidence of the sub-adult males performing longer dives (females duration median = 45.0 mins, max = 58.2 mins; males duration median = 49.4 mins, max = 61.6 mins).

Photo-identification

Movements

Extensive photo-identification data were collected for sperm whales from 1992 – 2014 in all but one strata (Table 18). Using only high quality photographs (Q>1) of distinctively-marked individuals (D>0), a total of 184 individuals were photo-identified but over 80% of individuals were found in the SA stratum (see Figure 6 for encounter locations). Movements were found between *Pm* identified in SA to all but one other stratum where photo-identification data were collected, including one stratum outside the canyon (EX). However, the majority of movements were undertaken by adult females and only between SA and a single, adjacent stratum, GB, and primarily only individuals that were genetically-sexed as males moved beyond adjacent strata. Re-sightings across multiple years were found in three strata but at variable levels (2% in GB, 12% in TO, 39% in SA), which may partially reflect the varying amount of field effort in each with GB having the least and SA the most. Perhaps of greater significance though is that individuals genetically-sexed in SA and TO were predominantly females and males, respectively, so the difference in the percentage of whales re-sighted within either of these strata likely represents a sex-based difference in residency pattern. Overall, the photo-identification results suggest long-term site fidelity of adult females to two adjacent strata GB and SA, and possible shorter-term site fidelity of males (later determined to be sub-adult, see section below regarding size measurements) to TO, including AUTEC. We also found support for the telemetry results suggesting that these sub-adult males are ranging outside the canyon while adult females show more limited ranging patterns.

Table 18. Contingency table for sperm whale photo-identification data collected from 1992 – 2014 in each strata in the Bahamas using high quality photographs (*Q*>1) of distinctively-marked individuals (*D*>0). The total number of photo-IDs in a single stratum with the number of multi-year re-sightings in parentheses are shown as well as all movements between strata. Strata are: Grand Bahama (GB), South Abaco (SA), East Abaco (EA), North Eleuthera (NE), Tongue of the Ocean (TO), Cul de Sac (CU), Exuma (EX).

Strata	GB	SA	EA	NE	TO	CU	EX
GB	12 (2)	10	0	0	0	0	0
SA		155 (61)	0	1	4	0	1
EA			3 (0)	0	0	0	0
NE				2 (0)	0	0	0
TO					25 (3)	0	0
CU						0	0
EX							3 (0)

Association analyses

The filtered dataset of animals with high quality photographs (Q>1) and distinctively-marked flukes (D>0), comprised 22 years of photo-identification data from 1992-2014, resulting in 79 individual whales Seven social units were identified from the association analysis (Table 19), where a unit was defined as pairs of whales that were associated across two separate years (Gero *et al.* 2014; Whitehead *et al.* 1991).

Table 19. Sperm whale social unit names and membership compositions, where % known males and females are genetically sexed individuals using tissue samples collected from whales using remote biopsy sampling or opportunistic collection of sloughed skin. Units are defined as pairs of whales that association across years, based on photo-identification data, using high quality photographs (*Q*>0) of distinctively-marked individuals (*D*>0).

Unit	# whales	% known females	% known males	# years at least one member identified
A	8	0	0	4
B	4	0	0	4
C	3	33	0	4
D	5	0	60	7
E	19	53	11	15
F	8	13	0	7
G	19	21	5	13

The cophenetic correlation coefficient for the dendrogram (Figure 35) was 0.918 and the modularity Q-value 0.702, indicating the population is modular and the dendrogram provides a good representation of the associations. Most of the units identified contained a small number of "potential members" (Gero *et al.* 2014), which are individuals that were only associated with other unit members only once (in contrast to other members that associated at least twice across years) but are believed to be members of the unit. Constraints of photographing all animals in a unit in a single day were likely the cause of these members only having been seen associated once.

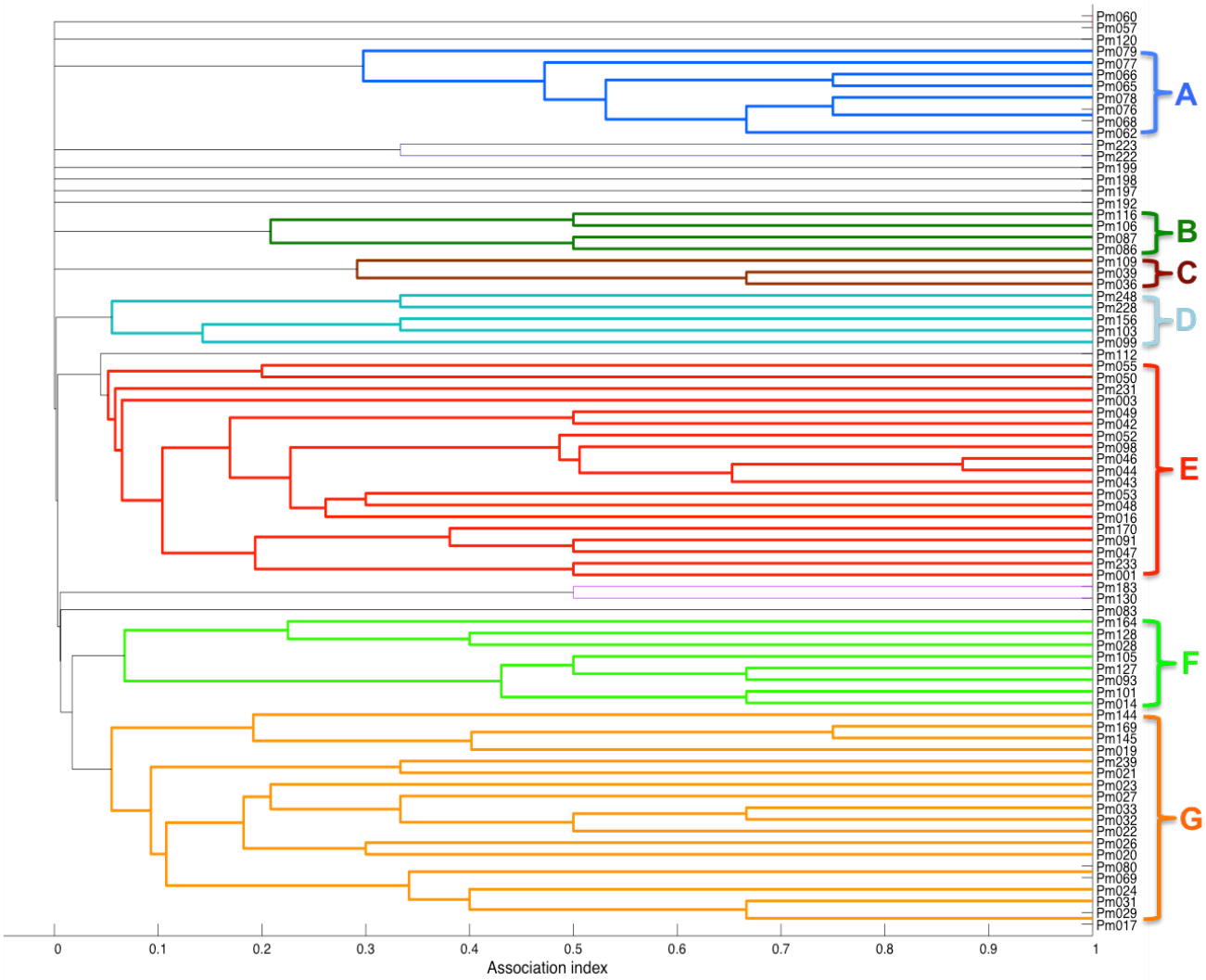


Figure 36. Dendrogram showing the association index between all sperm whales from photo-identification data using only high quality photographs (*Q*>1) and distinctively marked individuals (*D*>0). The seven sperm whale social units A-G (pairs of whales seen associating in more than one year) are shown in different colors.

Unit D appears to be a bachelor unit (see section on size measurements using click recordings obtained from two of the males in this this unit). Units E and G, the biggest units,

included related individuals (see genetic results below). The overall mean association index within units was 0.19 (sd=0.16), and 0.00 (sd=0.01) between units. The social network diagram of all seven units (Figure 36) shows stronger associations within units (thicker lines connecting nodes) than between. The placement of the unconnected units, A, B and C, do not represent association distance.

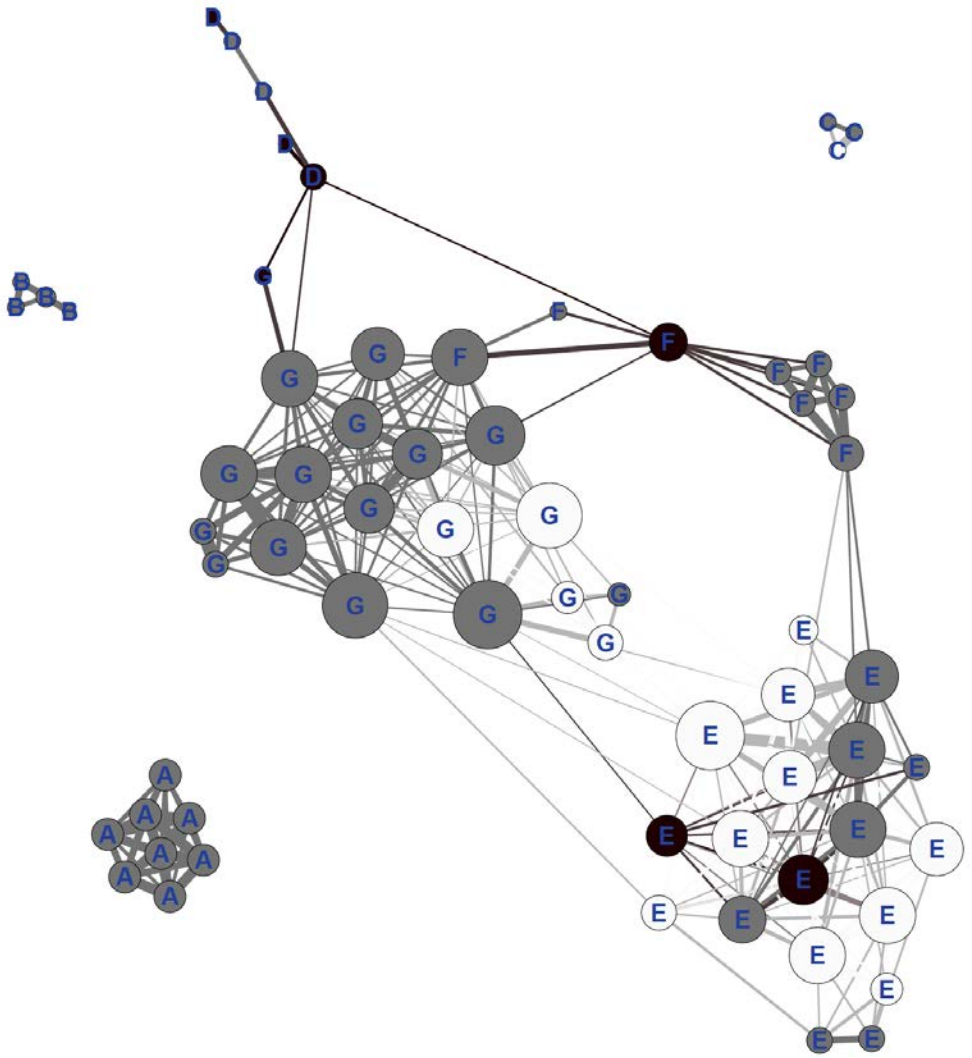


Figure 37. Individual-level social network of seven sperm whale social units (letters A-G) from photo-identification data, using only high quality photographs (*Q*>1) and distinctively marked individuals (*D*>0) seen in more than one year. Black circles (or nodes) represent males, white nodes are females, and grey are individuals of unknown sex. Edge thickness between nodes is based on a simple-ratio index of associations of individuals. Nodes are sized according to the number of their connected nodes. The distance to the unconnected units is not proportional to any associations. Plotted using Gephi 0.8.2beta (https://www.gephi.org) and a Force Atlas 2 layout algorithm (details: http://bit.ly/1kmVfe5), where linked nodes attract each other and non-linked nodes are pushed apart.

Chemistry

Similar to the chemical tracer results described for the five other Bahamas cetacean species, the short-term and long-term foraging structures of *Pm* whales were also studied by measuring the relative distribution of each of the three chemical tracers (SIs, FAs, POPs) among the six designated strata identified for this species (specifically EA, GB, SA, TO, NA, and NE). Plots depicting differences in epidermis SI ratios and blubber POP patterns measured among the six *Pm* strata are shown in Figures 37 and 38, respectively. Similar to Blainville's beaked whales, SI ratios (as well as dietary fatty acids - data not shown) are observed to differ very little among strata for Bahamas *Pm* whales despite clear evidence from the satellite tagging, photo-ID re-sight, and genetics data that *Pm* whales (most notably adult females) exhibit both strong short-term and strong long-term foraging site fidelity within the Bahamas study area. The failure of SIs, dietary FAs, and POPs to reveal differences among *Pm* strata (thus conveying short-/long-term site fidelity for this species) is most likely due to a combination of the poorer sample quality (low lipid) for the biopsies obtained for *Pm* and may possibly also reflect large-scale movement of their specific preferred prey throughout the entire Bahamas study area.

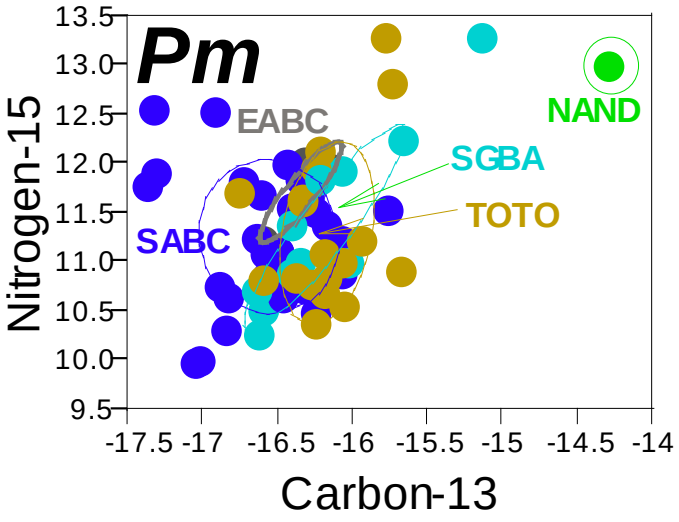
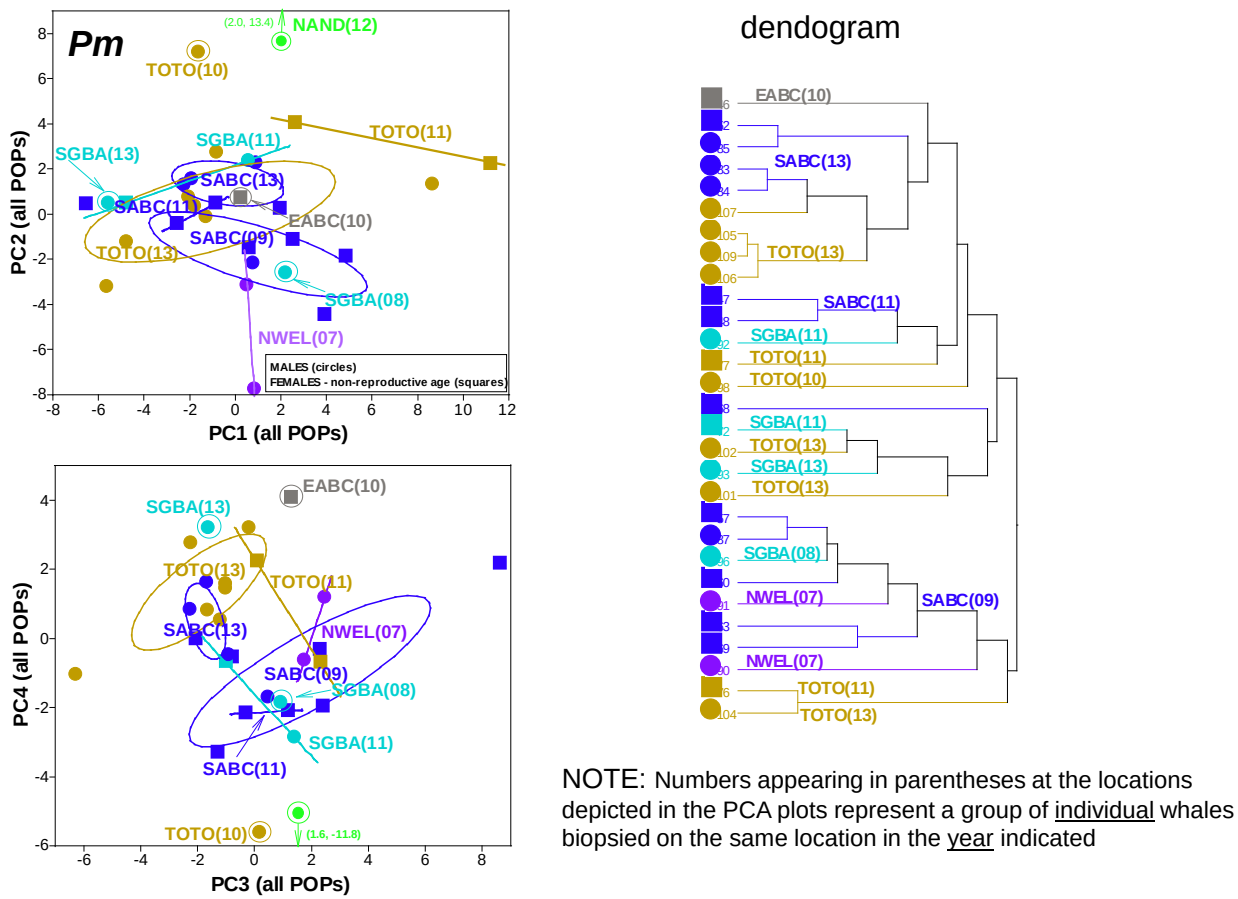


Figure 38. Differences in stable isotope ratios among sperm whales (*Pm*) of both sexes biopsy sampled in the five color-coded locations indicated. Ovals represent the 50% probability density intervals of the distribution of isotopes within the strata indicated. Strata abbreviations: Tongue of the Ocean (TOTO); South Grand Bahama (SGBA); East Abaco (EABC); North Andros/South Berry Is. (NAND); and South Abaco (SABC).



NOTE: Numbers appearing in parentheses at the locations depicted in the PCA plots represent a group of individual whales biopsied on the same location in the year indicated

Figure 39. Principal Component and hierarchical cluster analysis of POP patterns measured in the epidermal tissues of sperm whales (*Pm*, males and non-reproductive females) with whales grouped by their six color-coded sampling locations. Ovals represent the 50% probability density intervals of the distribution of POPs within the strata indicated. Strata abbreviations: Tongue of the Ocean (TOTO); South Grand Bahama (SGBA); East Abaco (EABC); Northwest Eleuthera (NWEL); North Andros/South Berry Is. (NAND); and South Abaco (SABC).

The population structure of *Pm* were further appraised by comparing SI ratios measured among *Pm* encounter groups rather than comparing among strata as described above. Differences in SI ratios among the thirteen different *Pm* encounter groups biopsied in this study are presented in Figure 39. Similar to what was observed for short-finned pilot whales, the most remarkable feature of these data is the high degree of similarity in SI ratios that is observed among *Pm* individuals within the individual encounter groups.

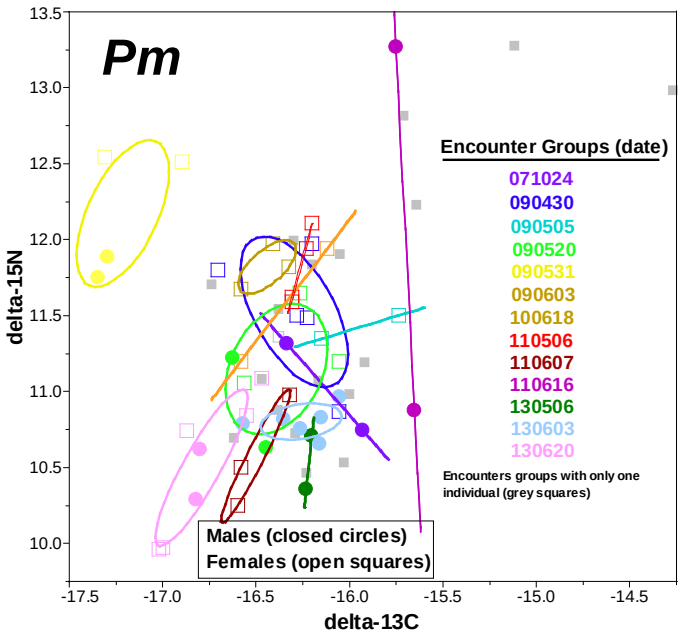


Figure 40. Differences in epidermal stable isotope ratios among encounter groups of sperm whales (*Pm*) of both sexes biopsied on the dates indicated (YYmmDD). Ovals represent the 50% probability density intervals of the distribution of isotopes within the encounter groups depicted. Colors reflect whales sampled during the same encounter.

Genetics

Genetic diversity and differentiation in sperm whales

One hundred and fifty-seven tissue samples were collected from sperm whales in the Bahamas, including skin/blubber biopsies (*n*=106), sloughed skin samples (*n*=48), one stranding and two fecal samples. All samples were genotyped at 18 loci (mean = 17.05 ± 2.00 loci), 17 of which were found to be polymorphic for Bahamas sperm whales. Two samples failed to yield DNA of sufficient quality/quantity to generate a reliable genotype. A genotyping error rate of 0.51% was empirically estimated from independent replicate genotyping of 19 samples.

Comparing multilocus genotypes, we identified 96 unique genotypes from Bahamas samples, and 39 whales that were represented by multiple samples. Samples were collected between 2002 and 2014, and 16 whales were sampled three or more times, with replicate samples being collected up to 11 years apart. Fifteen individuals were sampled by both biopsy and the collection of sloughed skin. Two individuals were sampled twice, but in different strata. These two samples provide direct evidence of males moving between strata and identified males sampled 6yr and 1yr apart that moved from either SA to GB or TO.

After removing duplicate samples and those genotyped at <10 loci, the final Bahamas *Pm* dataset comprised 95 unique individual genotypes. No significant deviations from Hardy-Weinberg equilibrium were found across all strata. While no locus pairs were found to be in linkage disequilibrium (LD) across all strata, samples representing two strata were in linkage disequilibrium. SA was in LD for 16 pairs of loci and exhibited significant heterozygote deficit at Eva1 and SW13. EA also exhibited a significant heterozygote deficit at Texvet5. Such deficits

are not unusual in small populations where samples may represent a number of related individuals.

Three unique mtDNA haplotypes were identified based on nucleotide differences across 398bp of the control region. All three haplotypes have been previously described from *Pm* samples collected in both the eastern tropical Pacific and the North Atlantic (Engelhaupt *et al.* 2009, Mesnick *et al.* 2011). Nucleotide and haplotype diversity were low, consistent with published data for this species (Table 20).

Table 20. Sperm whale mitochondrial haplotype diversity (h), frequency (n) and nucleotide diversity (pi) within each of the sampled strata in the Bahamas. Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

	n	**pi**	**H**	**Pm_a**	**Pm_b**	**Pm_c**
EA	5	0	0			5
EX	3	0.003 ±0.003	1.0 ± 0.272	1	1	1
NE	1	0	1			1
SA	45	0.001 ± 0.001	0.246 ± 0.081	3	3	39
GB	7	0.001 ± 0.001	0.286 ± 0.196	1		6
TO	33	0.002 ± 0.001	0.549 ± 0.054	12	2	19
Genbank accession				DQ512921	DQ512922	DQ512923

Global tests of genetic differentiation revealed significant genetic divergence among strata for both mtDNA mtDNA (F_{ST} = 0.121, *P* =0.015; Phi_{ST} = 0.143, *P* =0.013) and nuDNA (F_{ST} = 0.022, F'_{ST} = 0.075, *P* < 0.01) datasets, indicating the presence of significant genetic structure within *Pm* in the Bahamas. Using mtDNA sequence data, the only significant pairwise comparison was between SA and TO (Table 21). Based on nuDNA genotype data, significant genetic differentiation was found between EA and both SA (F_{ST} = 0.019, *P*=0.04) and GB (F_{ST} = 0.049, *P*=0.01), as well as between SA and TO (F_{ST} = 0.013, *P*<0.001).

Table 21. Sperm whale genetic divergence among strata within the Bahamas estimated from mtDNA sequence data. Conventional FST below diagonal, PhiST above diagonal. (p<0.001 indicated by **). Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

	EA	**EX**	**NE**	**SA**	**GB**	**TO**
EA		0.496	0.000	-0.046	-0.055	0.195
EX	0.423		-0.332	0.412	0.146	-0.139
NE	0.000	-0.500		-0.818	-1.000	-0.245
SA	-0.055	0.371	-0.841		-0.072	0.201**
GB	-0.055	0.178	-1.000	-0.066		0.050
TO	0.172	-0.070	-0.295	0.170**	0.041	

Restricting the dataset by removing genotypes of 11 individuals that were estimated to be genetic kin marginally decreased both global estimates of genetic divergence (F_{ST} = 0.010, F'_{ST} = 0.034, *P*= 0.005). Restricting the dataset by removing genetic relatives rendered the difference between EA and SA not statistically significant, but all others remained similar in magnitude and statistical significance (Table 22). Restricting the dataset further to include only adult female sperm whales supported the significant genetic divergence between both SA and GB when compared to TO (SA-TO, F_{ST} = 0.035, F'_{ST} = 0.119, *P*<0.01; GB-TO F_{ST} = 0.061, F'_{ST} = 0.202, *P*< 0.01).

Table 22. Genetic divergence (pairwise divergence metrics, F_{ST} and F'_{ST}) among strata within the Bahamas estimated from sperm whale nuclear genotypes with genetic kin removed (sample sizes in parentheses). Statistical significance (p.val) based on 5000 permutations of the original dataset (*p*<0.05 indicated by *). Geographic strata denoted as: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

Strata pair	**F_{ST}**	**F_{ST} p.val**	**F'_{ST}**	**F'_{ST} p.val**
EA (6) v. EX (3)	0.036	0.086	0.112	0.086
EA (6) v. SA (38)	0.017	0.068	0.053	0.070
EA (6) v. GB (5)	0.039	0.034*	0.123	0.034*
EA (6) v. TO (31)	0.016	0.058	0.052	0.066
EX (3) v. SA (38)	0.002	0.424	0.005	0.423
EX (3) v. GB (5)	-0.027	0.839	-0.092	0.839
EX (3) v. TO (31)	-0.011	0.742	-0.040	0.736
SA (38) v. GB (5)	0.009	0.207	0.029	0.203
SA (38) v. TO (31)	0.011	0.002*	0.038	0.002*
GB (5) v. TO (31)	0.002	0.407	0.006	0.409

STRUCTURE indicated that genotyped sperm whales in the Bahamas most likely represent 3 or 4 genetic groups. The best fit model based on both highest mean log-likelihood and the statistic Δk was 4 groups for the unrestricted dataset, and 3 groups when related individuals were removed, however concordance between genetic groups and geographic strata in which individuals were biopsied was equivocal (Figure 40). Analysis of a dataset restricted just to females, which have been demonstrated to show more site fidelity than males supported the pairwise tests of genetic differentiation suggesting significant genetic divergence between SA and GB females and those sampled in TO (Figure 41).

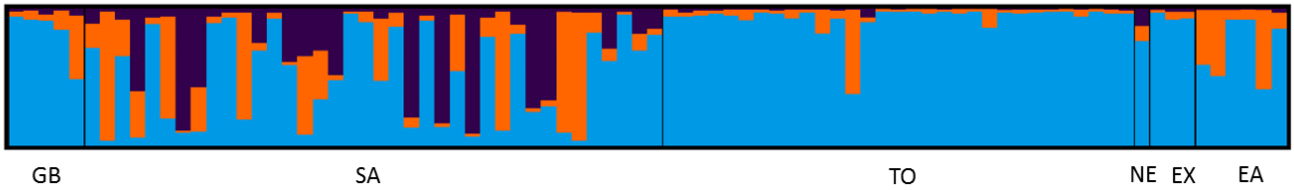


Figure 41. Bar plot showing the assignment of all individual sperm whale (*Pm*) skin samples to genetic groups (by color) from the STRUCTURE model (k=3) fit to the unrestricted dataset. Sampling strata for each individual whale (vertical bar) are indicated by the two letter abbreviations on the horizontal axis: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

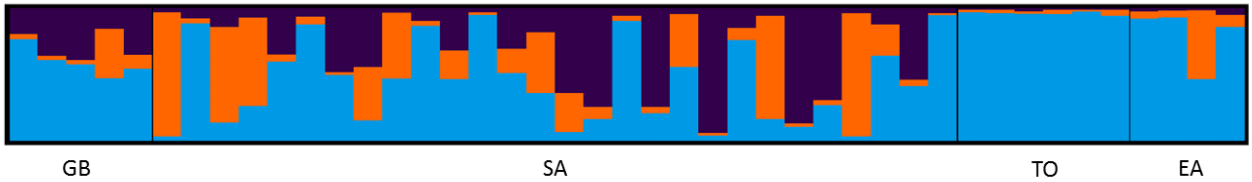


Figure 42. Bar plot showing the assignment of individual female sperm whale skin samples to genetic groups (by color) from the STRUCTURE model (k=3). Sampling strata for each individual whale (vertical bar) are indicated by the two letter abbreviations on the horizontal axis: East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

Average genetic relatedness among pairs of sperm whales overall was 0.033 (sd = 0.083). Within regions, genetic relatedness was highest among Pm sampled in GB. Of the 55 sampled sperm whale groups, we genotyped an average of 1.82 (sd = 1.48) whales/group. Twenty-three groups were represented by multiple (≥2) genotypes (Table 23), and of those only three groups were comprised of multiple haplotypes. Of the two encounter groups represented by more than five sampled individuals, all biopsied whales were found to have haplotype Pm_c. Based on congruence between direct hypothesis testing in KINGROUP and 95% CI for estimated genetic relationship in ML-RELATE, 40 pairs of Pm kin were identified, 82.5% (*n*=33) of which were composed of two whales sampled in the same stratum. Fifteen of these identified pairs of kin were identified as putative parent-offspring pairs with statistical support from both analytical approaches.

Table 23. Numbers of sperm whales genotyped per encounter group within each stratum; East Abaco (EA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), Tongue of the Ocean (TO).

SERDP strata	# genotypes	# sampled groups	# groups n>1	average genotypes/group
EA	6	3	2	2
EX	3	2	1	1.5
NE	1	1	0	1
SA	50	25	11	2
GB	7	6	1	1.167
TO	33	18	8	1.833

A Mantel test comparing pairwise genetic relatedness coefficient (r) with pairwise association index revealed a significant correlation between relatedness and persistence of association among sperm whales (R=0.179, *P*<0.0001; Figure 42).

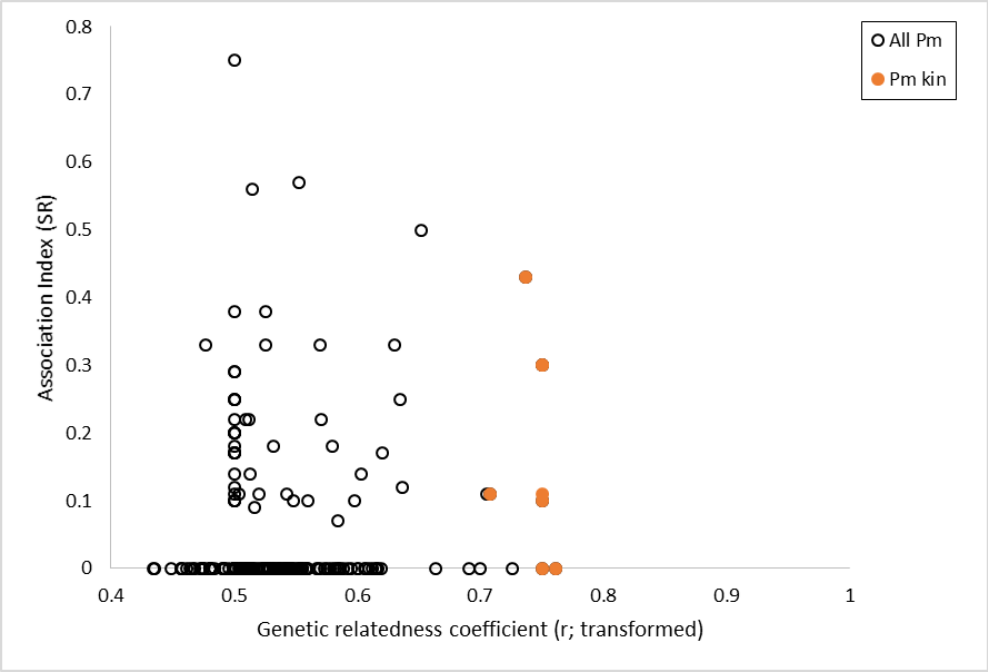


Figure 43. Rates of association as quantified by the simple ratio index based on photographic re-sightings among pairs of sperm whales plotted against genetic relatedness for the same pair. Photo-identification data included only high quality photographs of distinctive whales (*i.e.*, nick in tail flukes). Pairs of whales identified as putative kin based on congruence between ML-RELATE and Kingroup likelihood models are indicated with closed orange symbols.

Furthermore, the relatedness of individual *Pm* is significantly greater among those whales within social units suggesting a genetic basis for strong associations among Bahamas sperm whales (t=3.86, df=85, *P*=0.0002; Figure 43). Across all surveyed areas, we examined a subset of data restricted to those individuals identified as adult females or sub-adult males. Genetic relatedness among adult females was significantly greater than between adult females and sub-adult males (F-F: *n*=153 pairwise comparisons; mean=0.062 ± 0.121; F-M mean=0.046 ± 0.077; t=3.61, df=197, *P*<0.004). However, relatedness among sub-adult males (*n*=21 males, 210 pairwise comparisons; mean=0.046 ± 0.077) did not differ significantly from the level of relatedness among adult females (t=-1.45, df=240, *P*<0.15).

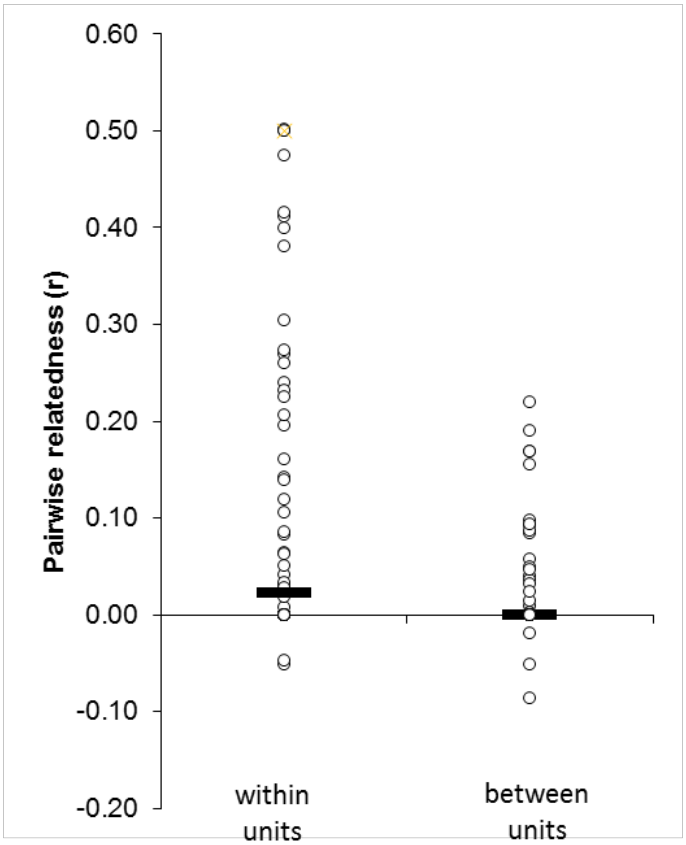


Figure 44. A plot of the range of pairwise coefficients of genetic relatedness (r) among sperm whales within (median=0.023) and between (median=0.000) social units as defined by pairs of whales that associate across years. Horizontal bars indicate median r for each class.

Acoustics

Size measurements

Size measurements ranged from 8.3 – 15.7 m for all whales measured (Figure 44); 9.2 – 15.5 m for males and 8.3 – 13.0 m for females. The size estimates for females in this study were larger than previously reported; Nishiwaki *et al.* (1963) reported female sperm whales become sexually mature at a length of 8.6 m, and around 9 years old, and physically mature at around

11.0 m. Physical maturity for male sperm whales has been reported between 15.5 and 15.9 m (Gaskin and Cawthorn 1973), whereas sexual maturity is estimated to be between 9.5 – 13.8 m (Gaskin 1970; Nishiwaki *et al.* 1963). This implies that the majority of the males measured in this study have not yet reached physical maturity, but are pubescent. One male was recorded across one year (Pm103) and grew 0.8 m during this time.

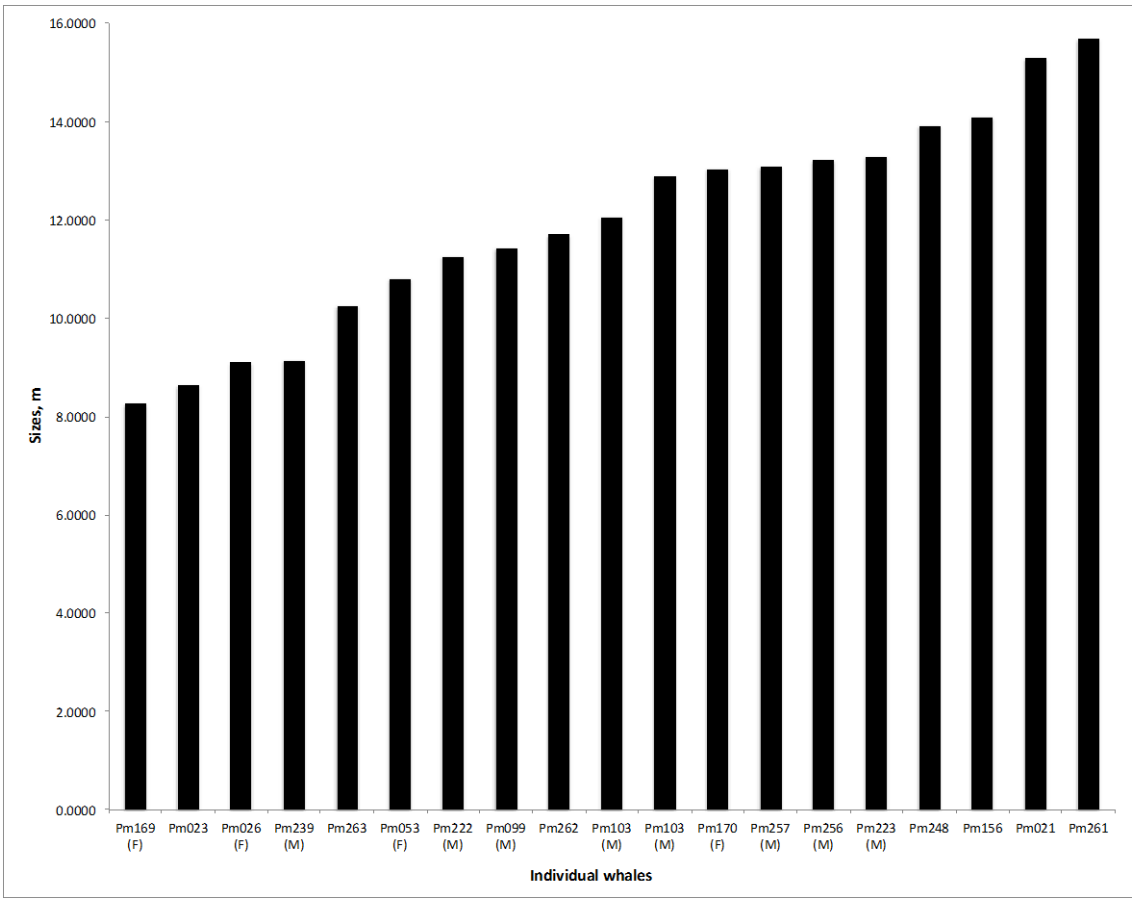


Figure 45. Plot showing length estimates of sperm whales, in ascending size order, calculated from acoustic recordings of each individuals' clicks. Genetically-determined sex, shown in brackets, was from tissue samples collected from whales using remote biopsy sampling or opportunistic collection of sloughed skin.

Codas

Codas were recorded during five encounters with sperm whales, three of which were with the same social unit, F. The remaining recordings were not from whales assigned to units. In total, sixty-three different codas were identified, the majority of codas were recorded from Unit F, and the most common codas produced were those containing a total of 7 or 9 clicks (Figure 45).

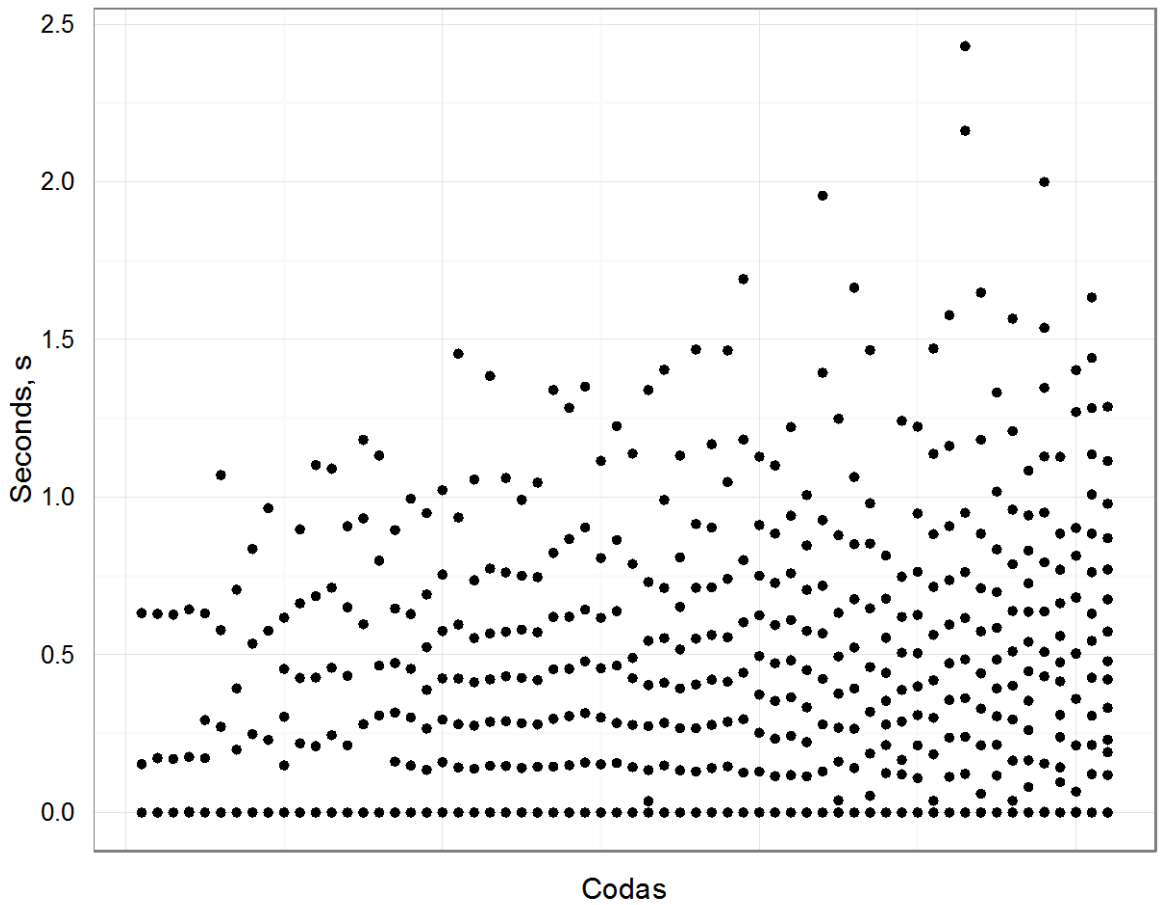


Figure 46. Rhythm plot of 63 sperm whale codas, encompassing 12 variations in the number of clicks per coda, ranging from 3 to 14, recorded during five encounters, three of which were with unit F. Coda clicks are plotted vertically at the time they are produced, in seconds, starting at 0, with time increasing on the y-axis.

Clangs

Slow clicks or clangs are a unique signal usually associated with adult male sperm whales Gordon 1987). We found clangs in recordings from three separate encounters; the first with unit G, the second in the presence of a genetically-sexed male (field observations suggest this animal is a sub-adult), and the third in the presence of a confirmed sub-adult male (genetically sexed and measured 12.89m). Clangs have previously been suggested to serve a communicative function, including a possible acoustic display for female competition or for competition of aggregations of prey (Madsen *et al.* 2002). Notably, a young male sperm whale in Dominica began producing clangs concurrent with dispersing from its natal group (Gero *et al.* 2013). This may be the case for at least one of these sub-adult males as it has been sighted in our study area for over a decade.

Persistent organic pollutant concentrations in whales and prey

Summed concentrations of five classes of persistent organic pollutants (POPs) measured in the blubber of the six species of odontocetes collected from various strata in the Bahamas are reported in Table 24.

Table 24. Concentrations (mean +/- SD in ng/g, lipid weight) of summed polybrominated biphenyls (ΣPCBs), summed DDTs (ΣDDTs), summed chlrodanes (ΣCHLRs), summed hexochlorocyclohexanes (ΣHCHs), summed polybrominated diphenyl ethers (ΣPBDEs) measured in the blubber of six species of odontocetes sampled in the Bahamas. Strata and substrata abbreviations: East Abaco (EA), North Andros (NA), Exuma (EX), North Eleuthera (NE), South Abaco (SA), Grand Bahama (GB), and Tongue of the Ocean (TO). "LOQ" means below lower limit of quantitation for all analytes.

			ng/g, lipid weight				
Species	**Strata**	**Sex**	**ΣPCBs**	**ΣDDTs**	**ΣCHLRs**	**ΣHCHs**	**ΣPBDEs**
Short-finned	EA	F (n=4)	15,000 ± 14,000	8800 ± 9100	1800 ± 1700	8.9 ± 7.5	730 ± 600
pilot whale	EA	M (n=4)	23,000 ± 11,000	23,000 ± 12,000	3000 ± 1300	5.8 ± 2.3	850 ± 260
	NA	F (n=8)	600 ± 3300	3800 ± 2500	1000 ± 700	5.6 ± 3.1	500 ± 220
	NA	M (n=13)	8900 ± 4100	7700 ± 4500	1400 ± 730	3.7 ± 1.7	620 ± 230
	GB	F (n=5)	5000 ± 2700	4100 ± 2700	680 ± 560	2.6 ± 2.4	210 ± 140
	GB	M (n=1)	15,000	15,000	2000	14.0	480
	TO	F (n=5)	5800 ± 4300	4700 ± 4000	870 ± 850	2.5 ± 0.9	420 ± 290
	TO	M (n=6)	3800 ± 1900	1800 ± 870	390 ± 230	4.2 ± 6.4	310 ± 200
	GB	F (n=1)	4500	3100	930	12.0	350
	GB	M (n=3)	10,000 ± 4000	9800 ± 4900	2300 ± 1000	16 ± 7.3	570 ± 270
Blainville's	CU	M (n=2)	19,000 ± 11,000	24,000 ± 18,000	3100 ± 1700	19 ± 16	1000 ± 390
beaked whale							
	EA	F (n=1)	4200	2600	560	6.3	220
	EA	M (n=2)	27,000 ± 7100	35,000 ± 14,000	3000 ± 350	17 ± 6.4	550 ± 35
	NE	M (n=1)	18,000	22,000	2600	22.0	370
	SA	F (n=9)	5800 ± 1700	4200 ± 1800	720 ± 280	6.7 ± 3.5	220 ± 75
	SA	M (n=9)	11,000 ± 4600	12,000 ± 5100	1400 ± 630	4.3 ± 3.9	230 ± 170
	GB	F (n=7)	4300 ± 970	3100 ± 960	530 ± 150	5.7 ± 6.3	220 ± 52
	GB	M (n=3)	16,000 ± 4400	16,000 ± 7200	2100 ± 760	11 ± 13	460 ± 220
	TO	F (n=2)	7100 ± 2700	6700 ± 2900	990 ± 300	12 ± 0	300 ± 160
	TO	M (n=4)	18,000 ± 11,000	22,000 ± 18,000	2700 ± 1500	20 ± 18	720 ± 460

Table 24 cont. Concentrations (mean +/- SD in ng/g, lipid weight of summed polybrominated biphenyls (ΣPCBs), summed DDTs (ΣDDTs), summed chlrodanes (ΣCHLRs), summed hexochlorocyclohexanes (ΣHCHs), summed polybrominated diphenyl ethers (ΣPBDEs) measured in the blubber of six species of odontocetes sampled in the Bahamas.

			ng/g, lipid weight				
Species	**Strata**	**Sex**	**ΣPCBs**	**ΣDDTs**	**ΣCHLRs**	**ΣHCHs**	**ΣPBDEs**
Gervais' beaked whale	CU	M (n=1)	7600	8100	1100	0.0	130
	EA	F (n=4)	5700 ± 2200	5500 ± 2600	1000 ± 590	9.4 ± 7.4	250 ± 57
	EA	M (n=5)	9500 ± 5800	9200 ± 5500	1900 ± 1100	12 ± 5.1	470 ± 260
Melon-headed whale	EA	M (n=1)	26,000	19,000	5800	10.0	1800
	NA	F (n=1)	9200	7100	1400	6.9	900
	NA	M (n=4)	19,000 ± 2400	23,000 ± 9600	2900 ± 740	18 ± 6.9	1500 ± 330
	GB	F (n=1)	11,000	7800	1800	8.1	1200
	GB	M (n=10)	17,000 ± 6100	14,000 ± 6600	2700 ± 680	16 ± 24	1500 ± 350
	TO	F (n=6)	9600 ± 7100	7700 ± 7300	2000 ± 1400	10 ± 7.5	880 ± 620
	TO	M (n=6)	14,000 ± 3800	15,000 ± 4400	2500 ± 700	15 ± 7.0	1300 ± 330
Sperm whale	EA	F (n=3)	7800 ± 5400	6600 ± 6400	1500 ± 1300	11 ± 4.8	350 ± 240
	NA	M (n=1)	5700	1400	93	30	130
	NE	M (n=2)	4700 ± 4700	6900 ± 7200	700 ± 710	6.0 ± 8.5	71 ± 69
	SA	F (n=21)	4000 ± 1800	3800 ± 2800	660 ± 370	2.8 ± 4.4	140 ± 82
	SA	M (n=4)	3900 ± 840	3800 ± 680	650 ± 110	0.7 ± 0.6	220 ± 67
			839	683	112	0.5	67
	GB	F (n=4)	4700 ± 3600	3800 ± 3300	500 ± 280	4.6 ± 3.4	160 ± 88
	GB	M (n=3)	5900 ± 3100	6000 ± 1500	720 ± 250	1.6 ± 1.4	240 ± 170
	TO	F (n=2)	6800 ± 4200	7500 ± 6400	1700 ± 1300	5.2 ± 6.2	180 ± 92
	TO	M (n=8)	5300 ± 3100	5900 ± 4000	890 ± 660	2.5 ± 2.1	250 ± 96
Cuvier's beaked whale	CU	F (n=2)	7500 ± 1300	8100 ± 4100	830 ± 380	< LOQ	230 ± 160
	CU	M (n=3)	13,000 ± 580	18,000 ± 1000	1500 ± 170	8.0 ± 7.2	370 ± 110
	EA	F (n=1)	4600	2900	600	4.1	120
	EA	M (n=7)	17,000 ± 9900	21,000 ± 15,000	2400 ± 1200	11 ± 6.2	370 ± 98
	NA	F (n=1)	7900	6800	1200	5.1	360
	NA	M (n=1)	20000	17000	1700	6.6	310
	NE	F (n=3)	12,000 ± 7900	19,000 ± 17,000	1600 ± 1100	6.5 ± 5.7	190 ± 76
	NE	M (n=4)	24,000 ± 2200	33,000 ± 1700	3000 ± 170	9.8 ± 9.1	230 ± 110
	GB	F (n=3)	7100 ± 1900	9200 ± 3500	1000 ± 150	2.1 ± 3.7	260 ± 120
	GB	M (n=4)	17,000 ± 3500	23,000 ± 7500	2200 ± 340	1.3 ± 3.5	360 ± 160

Regardless of species or sampling strata, the rank order of the POPs were ΣDDTs ≈ ΣPCBs > ΣCHLRs > ΣPBDEs >> ΣHCHs. At each sampling region, males generally had elevated summed concentrations of PCBs, DDTs, CHLRs and PBDEs compared to females except sperm whales from SA and TO. For the SA and TO sperm whales, the levels were comparable or slightly elevated in females compared to males and may indicate sampling of higher proportions of sub-adult males and/or higher proportions of sub-adult females in these two strata compared to the proportions of sampled from the other areas. The highest mean concentrations of ΣPCBs (27,000 ng/g, l.w.), ΣDDTs (35,000 ng/g, lipid weight (l.w.)), ΣCHLRs (3100 ng/g, l.w.) and ΣHCHs (20 ng/g, l.w.) were determined in male Blainville's beaked whales from various collection strata. The highest mean ΣPBDE values were measured in male melon-headed whales sampled in NA and GB (mean value at both sites 1500 ng/g, l.w.).

Elevated concentrations of PBDEs are most frequently measured in environmental samples collected in urban marine waters, especially those areas near municipal sewage treatment plants and landfills (Shaw and Kannan 2009) but the particular sources of these compounds in the NA and GB regions are not known. The concentrations of POPs measured in the current study are comparable to or slightly higher than those reported recently in blubber of Blainville's beaked whales, Cuvier's beaked whales, melon-headed whales and sperm whales that stranded in the Pacific Islands from 1997 through 2011 (Bachman *et al.* 2014).

Assessing differences in contaminant levels based on sampling region for each species was not attempted because information on age or age class of each whale was not known for all animals sampled in this study. Moreover, for whales in which these data were available, too few samples were available to make statistical comparisons. In addition to sex, age and age class information, data on other biological and physiological parameters (*e.g.*, reproductive status, birth order, nutritional status) would also be helpful in interpreting the POPs data as previous studies have shown these factors to influence blubber POPs concentrations in cetaceans (Aguilar *et al.* 1999, Ross *et al.* 2000, Wells *et al.* 2005, Ylitalo *et al.* 2001).

A number of biological and physiological effects (*e.g.*, immune suppression, reproductive impairment, carcinoma) have been associated with high tissue levels of POPs in marine mammals (Beckmen *et al.* 2003, Lahvis *et al.* 1995, Ross *et al.* 1995, Subramanian *et al.* 1987, Ylitalo *et al.* 2005). We compared the ΣPCB value for each Bahamian whale to a blubber ΣPCB threshold concentration (17,000 ng/g, lipid) that is based on a number of studies that measured various toxicological endpoints (*e.g.*, thyroid hormone concentrations) together with ΣPCB concentrations (Kannan *et al.* 2000). Approximately 16% (34 out of 209) of the whales sampled in the current study had ΣPCB concentrations that exceeded this threshold value, indicating that some whales are exposed to PCB levels that may adversely affect their health. In addition to PCBs, these animals may also have been exposed to other classes of chemical contaminants (*e.g.*, polycyclic aromatic hydrocarbons, xenoestrogens) that could also compromise their health.

Concentrations of ΣPCBs, ΣDDTs, ΣCHLRs, ΣHCHs and ΣPBDEs measured in putative prey of whales from The Bahamas are shown in Table 25.

Table 25. Concentrations (ng/g, lipid weight) of summed polybrominated biphenyls (ΣPCBs), summed DDTs (ΣDDTs), summed chlrodanes (ΣCHLRs), summed hexochlorocyclohexanes (ΣHCHs), summed polybrominated diphenyl ethers (ΣPBDEs) measured in potential prey of six species of odontocetes sampled in the Bahamas. Strata and substrata abbreviations: North Andros (NA), South Abaco (SA), Tongue of the Ocean (TO). "LOQ" means below lower limit of quantitation for all analytes.

		ng/g, lipid weight				
Species	**Strata**	**ΣPCBs**	**ΣDDTs**	**ΣCHLRs**	**ΣHCHs**	**ΣPBDEs**
Cephalopod?	SA	1800	62	16	< LOQ	94
Jellyfish?	SA	13,000	270	< LOQ	< LOQ	390
Dragonfish(sp?)	SA	4100	240	72	61	120
Dragonfish(*barbled*)	NA	7100	2200	900	< LOQ	290
Hatchetfish	SA	1000	28	4.5	< LOQ	50
Glass squid	TO	36,000	140	38	57	870
Glass squid	TO	40,000	130	33	62	990
Glass squid	TO	34,000	160	48	51	890
Cockeyed squid	SA	530	47	14	11	39
Teleost fish (unknown species)	SA	260	5.0	5.8	1.8	14

PCBs were the most abundant POPs measured in the prey with levels ranging from 260 – 40,000 ng/g, l.w. In most cases, the concentrations of the other POPs were at least an order of magnitude lower than the ΣPCBs measured in the same sample. Glass squid from TOTO had the highest levels of ΣPCBs, ΣHCHs and ΣPBDEs whereas dragonfish from SA and NA had the highest concentrations of ΣDDTs and ΣCHLRs.

Discussion

Population structure and ranging patterns

This study was very successful in using satellite telemetry to describe the movement and behavior of five-species of deep-diving whales that occur sympatrically within the Great Bahama Canyon. Ranging patterns varied among species, with a general trend in site fidelity between apparently nomadic short-finned pilot whales at one extreme and apparently site-faithful beaked whales at the other. For pilot whales, tag durations of up to 42 days documented rapid and widespread movements across strata throughout the Great Bahama Canyon, but also revealed long-range movements of five individuals (in two different groups) into Gulf Stream waters off the coast of Florida. One tagged whale ranged as far north as 32º N, off the coast of South Carolina (Figure 18). Together with a low re-sighting rate from individual photo-identification (<1% of individuals), these data suggest a range that extends well beyond the Bahamas. Movement data further support a general lack of geographic differentiation among genotyped individuals and genetic data that suggest that the structuring of *Gm* in the Bahamas is being driven by the presence of groups of related individuals occurring in different regions, rather than geographic structure *per se*. These data fill a critical data gap in existing knowledge of population structure for short-finned pilot whales and suggest that existing stock assessments that consider the western North Atlantic stock to be separate from pilot whales in the wider Caribbean may require revision.

The movements of melon-headed whales were also relatively expansive within the canyon, again across strata, but they did not displace as rapidly from the tagging site as pilot whales. However, the distinctly seasonal pattern to their encounters in this study area (April – September) and the anomalous signatures of persistent organic pollutants measured in blubber biopsies, compared to the other species, suggest they may be seasonal migrants into the study area from elsewhere.

Although sperm whales exhibited expansive movements across strata within the Great Bahama Canyon, and out of the canyon to the east, multiple lines of evidence supported sex-based habitat partitioning. Genetically-sexed sub-adult males had larger ranging patterns than adult females, but the majority of these young males were tracked within TOTO while adult female groups and their calves rarely used this area but had a consistent range within NW Providence Channel (GB and SA strata). Photo-identification data have documented between-year re-sightings of both females and sub-adult males within these respective areas, and females in particular appear to be highly site faithful. Genetic analysis from biopsied individuals revealed that the level of relatedness among these young males was comparable to relatedness among adult females from this region. However, on average sub-adult males appear to be more closely related to one another than to adult females within the study area, suggesting these males may be immigrants from neighboring areas.

The Bahamas are an important area to address sperm whale stock structure in the Northwest Atlantic as they lie between the Gulf of Mexico where unique mtDNA haplotypes have been found, and other areas in the North Atlantic where multiple haplotypes have been identified (Engelhaupt *et al.* 2009). Both molecular genetic datasets (mtDNA and nuDNA) clearly indicate significant genetic structuring among sperm whales sampled in the Bahamas. In particular, individuals sampled in the waters of Tongue of the Ocean appear to be genetically differentiated from those sampled off Abaco and Grand Bahama. However, samples from adjacent regions are needed to characterize patterns of male-mediated gene flow between the

Bahamas and the Northwest Atlantic. The few acoustic codas recorded so far in the Bahamas do not yet enable us to describe a repertoire for this region. However, as the dataset of recordings increases, it may be possible to compare units codas with other results obtained during this study. For example, in other regions, diet differences have been found between clans [units sharing the same repertoire of codas (Rendell and Whitehead 2003)], using SI analysis (Marcoux *et al.* 2007).

Compared to the other species, telemetry data showed that both Blainville's and Cuvier's beaked whales exhibit a high level of site-fidelity on a very small-scale. Satellite telemetry for both species showed limited dispersion from the tagging site of <100 km, typically within strata, during tag durations up to 47 days and 92 days, respectively. This is supported by photo-identification analysis for Blainville's beaked whales, which has documented high site fidelity of adult females to local sampling strata across multiple years, while some adult males roamed between adjacent areas. Schorr *et al.* (2010) found similar high levels of site fidelity for this species off the island of Hawai'i. In contrast, our photo-identification data suggest Cuvier's beaked whale movement patterns are more expansive in the longer term, with fewer photographic re-sightings (albeit constrained by low sighting probability). For example, one *Zc* male moved into the Great Bahama Canyon from outside (at least 300 km away) over a time period of 3 years. Nonetheless, longer-term site fidelity has been documented photographically for some individuals, and telemetry results and POP concentrations support relatively strong foraging site fidelity over both the short-term and over their lifetimes. Our results suggest that beaked whales, particularly, Blainville's beaked whales, may be vulnerable to repeated disturbances (*e.g.*, on the weapons range at AUTEC) due to their limited ranging patterns. Furthermore, recent genetic analyses (Phil Morin, NOAA / Southwest Fisheries Science Center (SWFSC) unpublished data) suggest a higher degree of relatedness of Blainville's beaked whale individuals sampled within than between strata within our study area and strong evidence of population structure between TO (the strata in which AUTEC lies) and all other strata. This indicates significant population structure and suggests that the subpopulation at AUTEC may need to be considered a separate conservation unit.

Social organization

Our results characterize diverse patterns of social organization among odontocete species in the Bahamas. We describe a range of social structures for sympatric species including long-term matrilineal associations of *Gm*, social units constructed around related adult females of *Pm*, the unique harem-like organization of *Md*, to the fission-fusion social structure of *Pe.* Molecular genetic studies of long-finned pilot whales (*Globicephala melas)* in several regions indicated natal group philopatry and suggested matrilineal structure within groups (Amos *et al*. 1993, Fullard *et al*. 2000, Oremus *et al*. 2009). Mahaffy *et al*. (2015) recently described long-term social fidelity in the congeneric short-finned pilot whales (*Gm*) in Hawaii using a photographic mark-recapture approach. Our findings from the Bahamas provide further support for long-term stable social groupings consisting of related individuals. We found a high degree of kinship (parent, sibling*)* within *Gm* encounter groups, and with only one exception, all individuals within each encounter group had identical matrilineal mtDNA haplotypes. Furthermore, data from chemical tracers indicate that related *Gm* whales forage together in similar areas on somewhat similar prey and some of these kinship-based foraging associations may remain intact over very long periods of time (perhaps even lifetimes).

Our sperm whale study supports studies in other regions that suggest that social units defined by *Pm* individuals that preferentially associate with one another are often comprised of related females and offspring (see review in Gero *et al.* 2015). Unlike *Gm*, sub-adult male sperm whales tend to disperse from these natal units and travel considerable distances to higher latitudes (Best 1979; Gaskin 1970; Whitehead 2003, Gero *et al.* 2015). Genetic data, chemical tracers and association analyses from sperm whales provide multiple lines of evidence that clearly indicate that *Pm* encountered in the Bahamas tend to associate more frequently with individuals to whom they are related. These data also suggest a degree of kinship among adult females, particularly within social units, and indicate that the sub-adult males within the area, though related to one another, do not appear to be closely related to the adult females within the study area. Unlike Dominica where sperm whales have been found to largely comprise a single mtDNA haplotype (Gero *et al*. 2008, Gero *et al*. 2014), here we identified three mtDNA haplotypes and found that, while rare, some encounter groups contained individuals with different haplotypes. Among sperm whales, sex differences in the degree of genetic differentiation across ocean basins have been largely attributed to female philopatry. However, patterns of within-group relatedness from different regions have been shown to vary. For example, sperm whales from Dominica constitute pure matrilines (Gero *et al.* 2008), but this is the only geographical region where this appears to be true. In contrast, studies of over 150 sperm whale groups around the world have found assemblages comprised of mixed matrilines (Mesnick 2001). Future analyses of our *Pm* genetic data will help to address whether or not matrilines are pure or mixed in the Bahamas.

The only beaked whale species for which we were able to conduct social structure analyses was Blainville's beaked whale (*Md*) due to data limitations for *Me* and *Zc*. Previous studies of *Md* within the Bahamas and the Hawaiian Islands described small harem-like social units consisting of a single adult male with several reproductive females and their young, despite having relatively fluid social structure overall (Claridge 2006, McSweeney *et al.* 2007). In this study, we learned that males remained with the same harem-like unit for up to a year and rarely returned to the same group. Associations among adult females persist on average for three years, and are driven by reproductive state. Unlike sperm whales, alloparental care has not been observed in *Md*, but females' choice of associates is likely driven by similar needs with respect to increased foraging demands and risk of predation.

The pattern of association for melon-headed whales in the Bahamas generally supports the fission-fusion society described for other populations of *Pe* (Jefferson and Barros, 1997). However, results from both association analyses and POPs suggest some underlying structure in *Pe* social organization in the Bahamas. We found two primary clusters of animals with higher association indices among individuals within clusters than between. Recent analyses of past stranding specimens from Japan with respect to life history by Amano *et al.* (2014) suggests that females show philopatry to a group, whereas males may move between groups. Here, we found similar POP concentrations among males within encounters, suggesting that males may form long-term bonds, perhaps analogous to the bonds between male bottlenose dolphins (Scott *et al.* 1990). It would be interesting to learn whether or not these males are closely related genetically as is the case with bottlenose dolphins in the Bahamas (Parsons *et al.* 2003a).

Overall, we found evidence of long-term and/or complex social structure in all species for which we had sufficient data (4/6 species) raising concern for anthropogenic activities that could disrupt key individuals within social units, thereby potentially negatively impacting an entire social unit. For example, detrimental effects of removal of post-reproductive female African

elephants (*Loxodonta africana*) have been found to manifest in the demographics of the entire herd (Moss 2001). In cetaceans, studies of fish-eating killer whales suggest that the adaptive benefits of post-reproductive females within stable social units (pods) include increased survival of their adult male offspring (Foster *et al.* 2012) and leadership of groups during collective foraging (Brent *et al.* 2015). Social covariates are therefore important to consider when developing models to predict impacts of disturbance at the population level, and when possible, their effect on model outcome should be tested.

Foraging habitat and behavior

Diving

Inference from tag-derived dive data collected from this study provides unprecedented insight into how these sympatric deep-diving odontocete species partition their three-dimensional habitat within the Great Bahama Canyon. To our knowledge ours is the first bio-logging effort to describe distribution of subsurface activity in melon-headed whales, but for other species these descriptions are congruent with published accounts of diving activities from other study areas. The dive patterns of short-finned pilot whales we recorded were very similar to the short-duration deep daytime and shallow night-time foraging dives exhibited by this species in the Canary Islands (Aguilar de Soto *et al.* 2008), with our maximum dive depth (984 m) being very similar to that reported by Aguilar de Soto *et al.* (1019 m). Deep peaks of presumed sperm whale foraging activity that we observed (~800-900 m) were comparable to diving and foraging behavior of adult female and sub-adult male sperm whales in the Gulf of Mexico, Western Atlantic Ocean, and Mediterranean Sea (*i.e.*, similar to the demographic mixture tagged in our study, Watwood *et al.* 2006).

Similarly, our average presumed foraging in the 1000-1400 m range by Blainville's beaked whales and around 1100-1200 m by Cuvier's beaked whales overlap with the foraging dive depths reported from Hawaii, the Canary Islands and Ligurian Sea (Baird *et al.* 2006, Tyack *et al.* 2006). In contrast, Schorr *et al.* (2014) reported a maximum dive depth (2992 m) off southern California for Cuvier's beaked whales that considerably exceeded our maximum recorded dive of 1888 m; but our dataset showed consistency with the mean duration and mean of dive depth maxima reported by Schorr *et al.* (2014). Our analyses suggest that Cuvier's beaked whale foraging dives ranged close to the benthos in the areas where tagged animals occurred within our study area, thus we hypothesize that these whales may have the capacity to dive to deeper depths when not constrained by the relatively shallow bottom depths in our study area.

Foraging strategies

The allometric scaling of oxygen utilization relative to the isometric scaling of oxygen storage capacity has been hypothesized as an important factor in determining cetacean breath-hold diving capacity and diving, allowing species with larger body masses to dive for longer periods (Noren and Williams 2000, Halsey *et al.* 2006, Micerta *et al.* 2013). Longer dive durations are also expected to increase the ratio of bottom time to commuting time, allowing larger whales to more efficiently access deeper foraging niches (Georges *et al.* 2000, Costa and Gales 2003). By comparing the vertical foraging ranges across species in our study we find some significant departures from this expectation. Notably, both tagged beaked whale species have maximum dive depths and durations that exceed even those of the much larger sperm whales (dive maximums: *Md* 1888 m and 67 mins; *Zc* 1888 m and 104 mins; compared to 1344

m and 62 mins for larger sperm whales). These relatively long and deep foraging dives likely exceeded aerobic dive limits for the smaller beaked whales and were followed by recovery periods of shallow non-foraging dives (*e.g.*, Tyack *et al.* 2006), which contrasted with relatively continuous bouts of deep-diving exhibited by both delphinid species and sperm whales. This difference in dive strategy enabled beaked whales to access upper bathypelagic foraging niches despite their relatively small sizes, but at the cost of significantly reduced dive efficiency (<30% of total time spent in target foraging strata). This further demonstrates the large energetic and time investment per foraging dive in the beaked whales and suggests that these species may be particularly vulnerable to disturbance, as any disruption to normal behavior could constrain foraging opportunities that are already physiologically limited. Bioenergetics models also support this hypothesis of vulnerability, suggesting that beaked whales require relatively high-quality habitat in order to meet their high-energy requirements, and that regular displacement from preferred feeding habitats could potentially impact survival and reproduction through compromised body condition (New *et al.* 2013).

Nonetheless, body size does appear to explain some of our findings. The frequent night-time diving of melon-headed whales is similar to that of short-finned pilot whales, both spending >60% of their time in foraging strata at night. However, the larger pilot whales (adult length reaching 5.5 m in females and 7.2 m in males; Jefferson *et al.* 2011) were capable of much deeper and longer dives than the smaller melon-headed whales (<3 m maximum length; Jefferson *et al.* 2011). This helps to explain the lack of dives below surface waters in the daytime by melon-headed whales – they likely could not dive deep or long enough to access diurnally migrating prey when they were at greater daytime depths. In contrast, pilot whales conducted infrequent but much deeper foraging dives in the daytime.

We see a similar effect within species when comparing individuals of varying sizes. Although there were not clear differences in the median depth or median duration of dives between adult male pilot whales and a presumed adult female, the maximum depth and duration were notably deeper and longer for the adult males (Figure 19). For sperm whales, length estimates from acoustic analyses were available for four of our tagged whales, ranging from 11.3 m to 15.5 m for males, and one estimate of 13.0 m for an adult female. This suggests that we likely tagged males that were both smaller and larger than adult females, helping to explain the greater variability in measured diving behavior by sub-adult males. Previous work has suggested that buoyancy influences swimming decisions in sperm whales and that these whales benefit by obtaining neutral buoyancy at depth (Miller *et al.* 2004b). So, it could be that differences in body size and condition between these sperm whales results in different depth ranges in which they are neutrally buoyant, in addition to greater diving capacity possible due to larger body size. Even the deep-diving beaked whales appear to have some dive similarities and differences between sexes that may be explained by size. Of all our study species these are the least sexually-dimorphic in body size: *Zc* has been recorded to reach 8.5 m long in females and 9.8 m in males (Jefferson *et al*. 2011); *Md* has been recorded to 4.7 m long and has not been reported to be sexually dimorphic (Jefferson *et al.* 2011), but our field observations suggest males are likely slightly longer and have greater mass (BMMRO, unpublished data). It is clear that for both species, both males and females are capable of extremely deep (>1250 m) and long dives (>1 hr), with generally similar diving abilities that match their similar body sizes. However, the deepest dives recorded by both species were from adult males, with males performing deeper dives on average in both species, perhaps indicative of subtle sex differences in body size and diving capabilities for both.

Inferring diet differences

Species differences in diurnal patterns of diving (Figure 19), and diving relative to the available bathymetric depth (Figure 12), provide insight about foraging differences and diet. The beaked whales (*Zc* and *Md*) appear to forage closest to the benthos, and are the least diurnal of the species tagged. Of these, *Zc* appears most likely to feed on or close to the benthos, with *Md* possibly feeding slightly higher in the water column. Although no direct dive data were recorded from the third species of beaked whale, *Me*, inference gleaned from the ratio of blubber FAs that appear to change systematically with foraging depths across species estimated the overall average foraging depth for *Me* whales biopsied in this study to be 1080 m; similar to both the other beaked whale species (Figure 31). The other three species undertook shallower dives (typically <1000 m for *Pm*, and <500 for *Gm* and *Pe*) that showed distinct diurnality – *Pm* and *Gm* have deeper and longer daytime dives than night dives, presumably responding to the diurnal vertical migration of their prey in the water column. The nighttime-only diving of *Pe* is an extreme extension of this adaptation – they appear to wait to feed only at night when their prey are in the accessible within their dive depth range, and likely can't dive deep enough during the day to reach prey layers. Notably, all the species vary in their use of foraging habitat (Figs, 10, 12, 19) suggesting diet differences.

This is supported by chemical analyses of skin and blubber biopsies. There was evidence of separation between all six species in nitrogen and carbon SI results (Figure 14), with the two delphinid species (*Gm* and *Pe*) apparently feeding at a much lower mean trophic level ($\delta 15N_{mean}$~10.3) than any of the three beaked whale species ($\delta 15N_{mean}$~11.8). Conversely, sperm whales appear to be feeding at trophic levels intermediate between that of the delphinids and the beaked whales ($\delta 15N_{mean}$~11.3). The rather large differences observed in δ15N values between these three groups (delphinids, sperm, and beaked whales) suggests that the diets of these groups are very different from one another which is qualitatively consistent with the differences in their mean foraging dive depths. Similarly, we observed that the dietary FA profile data (see Appendix A, Table A2) generally separate into the same three distinct groupings (Figure 15). Although there appears to be a high degree of overlap among the three beaked whale species, there is some separation in dietary FAs. On the whole, we therefore conclude that, in additional to maintaining a moderately high degree of niche separation by foraging at different depths (Figure 12, 19), the six species also maintain an additional degree of niche separation by selecting differing prey items even when two or more of these species are geographically co-located.

Conclusions and Implications for Future Research

The results presented in this report provide new information on the behavioral ecology of six taxonomically diverse, Department of Defense priority species (melon-headed whales *Peponocephala electra, Pe*, short-finned pilot whales, *Globicephala macrorhynchus, Gm*; three species of beaked whales (Blainville's, *Mesoplodon densirostris, Md*; Gervais', *Mesoplodon europaeus, Me*; Cuvier's, *Ziphius cavirostris, Zc*) and the sperm whale, *Physeter macrocephalus, Pm*). All six species occur sympatrically in the Bahamas, including but not limited to the U.S. Navy's AUTEC Weapons Range, making them potentially vulnerable to disturbance from Navy activities. Using a multi-disciplinary approach that included integration of data generated through photo-identification, molecular genetics and chemical tracers from tissue biopsies, satellite telemetry and acoustic recordings collected for individual whales, we were able to describe the population structure and movement patterns, social organization, foraging behavior and habitat of these species for which limited data were available. In this section, we describe the study conclusions and recommend future research directions. We also provide suggestions for DoD and other resource managers to aid in the development of future management directives for each species, primarily to mitigate impacts at AUTEC.

Melon-headed whales are a highly mobile species that appear to be seasonally migratory based on their anomalous pollutant signatures and temporal occurrence in the Bahamas. However, re-sightings across multiple years of over a third of individuals photo-identified at AUTEC suggest site fidelity and vulnerability to repeated disturbance. As such, ongoing monitoring is required to assess and identify population-level impacts from repeated disturbance that may occur at this site. Further research is needed to fill remaining data gaps in our understanding of *Pe* population ecology. Specifically, a population genetics study is warranted to help identify and define the population using the waters around AUTEC and should be conducted concurrently with efforts to estimate *Pe* abundance at AUTEC to provide baseline information for monitoring the status of this population. Perhaps of greater concern for *Pe* in the Bahamas are impacts from other anthropogenic activities including health effects and identification of potential input sources of high levels of persistent organic pollutants should be a research priority.

Short-finned pilot whales were the only species tracked from the Bahamas into U.S. waters. Together with a very low re-sighting rate over multiple years from photo-identifications within the Bahamas (<0.01% of individuals), these data suggest a range that extends well beyond the Bahamas and that these whales are likely part of a stock recognized in the U.S. Although this species appears to occur regularly in the Tongue of the Ocean, we believe that groups of related individuals are using the area on a transient or irregular basis. To fully address the management needs of *Gm* in the Bahamas and off the U.S. southeast coast, additional work is needed to compare genetic data and photo-identifications between the two regions. In the interim, estimates of Navy "takes" of the *Gm* stock off the U.S. southeast coast likely need to include takes that occur at AUTEC due to the documented exchange of individuals between regions.

Blainville's beaked whales exhibit a high level of site-fidelity on a very small scale (tag movements <100 km). This was supported by photo-identification analysis for *Md*, which documented site fidelity across years of adult females to small geographic areas, including the AUTEC Weapons Range. Recent population genetic studies revealed a distinct subpopulation in

TOTO, with their distribution including the AUTEC range suggesting a potential need for this unique subpopulation to be considered a separate conservation unit. Despite their relatively small body size, *Md* in the Bahamas are accessing upper bathypelagic foraging niches at depth, but at the cost of significantly reduced dive efficiency (<30% of total time spent in these deep target foraging strata) because they are physiologically constrained by necessary recovery periods. This suggests likely fitness consequences associated with decreased foraging success if disturbed by anthropogenic activities. In combination, these data indicate that Blainville's beaked whales are vulnerable to repeated disturbances due to their limited ranging patterns and foraging requirements. This is likely to be particularly true for reproductive females with high energetic demands, perhaps explaining differences in the reported reproductive success at AUTEC Weapons Range compared to southwest Abaco. Research gaps remain to test this hypothesis, including the need for further investigation into the foraging ecology and body condition of *Md* at AUTEC to parameterize the PCoD model to better understand the energetic cost of disturbance at the individual and population levels.

Gervais' beaked whales are not evenly distributed throughout the canyon, and may not be as abundant as the other two beaked whale species known from the Bahamas. *Me* have never been sighted on AUTEC Weapons Range although occasional single animal strandings have occurred nearby and they have been sighted in the Cul de Sac to the south of the range. Due to the low number of sightings of this species during our study, large data gaps still exist in our knowledge about their behavioral ecology. Future research efforts should strive to fill these data gaps with a directed population ecology study of this species in order to assess their vulnerability.

Cuvier's beaked whales are the most common species in atypical strandings associated with navy sonar globally, suggesting particular vulnerability of *Zc* to anthropogenic noise. Although *Zc* occur in Tongue of the Ocean, and are regularly seen north and south of the AUTEC Weapons Range, this species is rarely seen at AUTEC. We found limited displacement of less than 100 km during 3-month tag deployments. Furthermore, re-sightings across multiple years for some individuals, and chemical tracers that suggest long-term site fidelity of *Zc* to small geographic areas. However, recent studies have suggested some gene flow throughout the northern Bahamas indicating that this species may have larger ranging patterns than *Md*. *Zc* are extreme divers, feeding at or close to the bottom, and like the other beaked whales *Zc* also face physiological constraints due to this foraging strategy. Therefore as with *Md*, Cuvier's beaked whales in the Bahamas should be considered vulnerable to disturbance. Future work in the Bahamas should focus on developing a longitudinal dataset for *Zc* in TOTO and surrounding waters of sufficient resolution to allow monitoring of potential impacts.

Sperm whales exhibited sex-based habitat partitioning. Genetically-confirmed sub-adult males had larger ranging patterns than adult females, but the majority of these young males occurred solitarily or in bachelor groups, and were tracked primarily using Tongue of the Ocean, including the AUTEC Weapons Range. In contrast, groups comprised of adult females and calves rarely used the AUTEC area. Photo-identification data documented multi-year re-sightings of individuals of both age/sex classes. Sub-adult males may be vulnerable to repeated disturbance by sonar exposure at AUTEC during an important period of growth in their early lives. Genetic analysis revealed that bachelor males were more closely related to one another than to adult females, suggesting these males may be immigrating from outside the canyon and, as such, may represent significant contributions to gene flow throughout the wider Caribbean. To assess the population consequences of disturbance at AUTEC, further research is required to

assess behavioral responses to sonar exposure and link these responses to life functions (*e.g.*, individual condition and growth). Further work is needed to identify the stock identity of whales using TOTO to evaluate and monitor any population consequences of disturbance. To address this need, the sperm whale photo-identification catalogue and acoustic recordings of codas compiled during this project will be shared with collaborators in the North Atlantic to document potential movements of bachelor males and elucidate the population structure in the wider region.

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Appendices

Appendix A – Supporting data

Table A1. Field ID, sex, collection location (strata), and collection date of Blainville's, Cuvier's, Gervais', melon-headed, short-finned pilot, and sperm whale biopsy samples collected for this study and successfully analyzed for one or more of the following chemical tracers (stable isotopes, fatty acids and/or persistent organic pollutants).

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
Blainville's Beaked Whales				
1	071005_Md1a	M	CU	10/5/2007
2	090526_Md1a	M	CU	5/26/2009
3	100613_Md6ac	F	EA	6/13/2010
4	100613_Md4ac	M	EA	6/13/2010
5	100614_Md1ac	M	EA	6/14/2010
6	080611_Md3a	F	GB	6/11/2008
7	080611_Md2a	F	GB	6/11/2008
8	080611_Msp2a	F	GB	6/11/2008
9	080611_Msp3a	F	GB	6/11/2008
10	080611_Msp1a	F	GB	6/11/2008
11	080611_Md1a	M	GB	6/11/2008
12	090602_Md2a	F	GB	6/2/2009
13	090602_Md1a	M	GB	6/2/2009
14	110606_Md1a	F	GB	6/6/2011
15	110606_Md2a	M	GB	6/6/2011
16	090531_Md1a	M	NE	31/05/2009
17	070608_Md1c	M	SA	08/06/2007
18	070611_Md1b	F	SA	11/06/2007
19	080608_Md2a	F	SA	08/06/2008
20	080608_Md1a	M	SA	08/06/2008
21	080613_Md1a	M	SA	13/06/2008
22	080614_Md2a	F	SA	14/06/2008
23	080614_Md5a	F	SA	14/06/2008
24	080614_Md6a	F	SA	14/06/2008
25	080614_Md1a (0-5mm depth)	M	SA	14/06/2008
26	080614_Md1a (5-10mm depth)	M	SA	14/06/2008
27	080614_Md1a (10-15mm depth)	M	SA	6/14/2008
28	080614_Md1a (15-20mm depth)	M	SA	6/14/2008
29	080614_Md1a (20-25mm depth)	M	SA	6/14/2008
30	080614_Md1a (25-30mm depth)	M	SA	6/14/2008
31	080614_Md3a	M	SA	6/14/2008
32	090505_Md1a	M	SA	5/5/2009
33	110223_Md4a	F	SA	2/23/2011
34	110223_Md3a	M	SA	2/23/2011
35	110605_Md1a	F	SA	6/5/2011
36	110626_Md1a	F	SA	6/26/2011
37	110626_Md2a	F	SA	6/26/2011
38	080522_Md1a	F	TO	5/22/2008
39	080522_Md2a	M	TO	5/22/2008
40	090507_Md1a	M	TO	5/7/2009
41	090508_Md2a	F	TO	5/8/2009
42	090508_Md1a	M	TO	5/8/2009
43	090530_Md1a	M	TO	5/30/2009

Table A1. cont.

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
Cuvier's Beaked Whales				
44	071005_Zc1a	F	CU	05/10/2007
45	090528_Zc2a	F	CU	28/05/2009
46	090528_Zc1a	M	CU	28/05/2009
47	090529_Zc1a	M	CU	29/05/2009
48	090529_Zc2a	M	CU	29/05/2009
49	100605_Zc1ac	M	EA	05/06/2010
50	100607_Zc1ac	M	EA	07/06/2010
51	100612_Zc1ac	M	EA	12/06/2010
52	100614_Zc2ac	M	EA	14/06/2010
53	100615_Zc1ac	F	EA	15/06/2010
54	100615_Zc3ac	M	EA	15/06/2010
55	100616_Zc1ac	M	EA	16/06/2010
56	100616_Zc3ac	M	EA	16/06/2010
57	080610_Zc5a	M	GB	10/06/2008
58	080610_Zc2a	M	GB	10/06/2008
59	080610_Zc3a	M	GB	10/06/2008
60	080611_Zc6a	F	GB	11/06/2008
61	080611_Zc5a	F	GB	11/06/2008
62	080611_Zc1a	F	GB	11/06/2008
63	080611_Zc4a	M	GB	11/06/2008
64	080611_Zc3a	M	GB	11/06/2008
65	080611_Zc7a	M	GB	11/06/2008
66	130614_Zc1a	M	GB	14/06/2013
67	110613_Zc2a	F	NA	13/06/2011
68	120615_Zc1b	M	NA	15/06/2012
69	080602_Zc1a	M	NE	02/06/2008
70	080603_Zc1a	F	NE	03/06/2008
71	080603_Zc2a (0-5mm depth)	M	NE	03/06/2008
72	080603_Zc2a (5-10mm depth)	M	NE	03/06/2008
73	080603_Zc2a (10-15mm depth)	M	NE	03/06/2008
74	080603_Zc2a (15-20mm depth)	M	NE	03/06/2008
75	080603_Zc2a (20-25mm depth)	M	NE	03/06/2008
76	080603_Zc2a (25-30mm depth)	M	NE	03/06/2008
77	090506_Zc1a	F	NE	06/05/2009
78	090506_Zc2a	F	NE	06/05/2009
Gervais' Beaked Whales				
79	071004_Me1a	M	CU	10/4/2007
80	100604_Me3ac	F	EA	6/4/2010
81	100604_Me2ac	M	EA	6/4/2010
82	100604_Me4ac	M	EA	6/4/2010
83	100606_Me2ac	F	EA	6/6/2010
84	100606_Me4ac	F	EA	6/6/2010
85	100606_Me1ac	M	EA	6/6/2010
86	100606_Me3ac	M	EA	6/6/2010
87	100617_Me2ac	F	EA	6/17/2010
88	100617_Me1ac	M	EA	6/17/2010
89	100902_Me1a[*]	M	EA	9/2/2010

Table A1. cont.

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
Melon-headed Whales				
90	100614_Pe2a	M	EA	6/14/2010
91	120609_Pe5b	F	GB	6/9/2012
92	120609_Pe3b	M	GB	6/9/2012
93	120609_Pe4b	M	GB	6/9/2012
94	120609_Pe6b	M	GB	6/9/2012
95	130613_Pe1b	M	GB	6/13/2013
96	130613_Pe2b	M	GB	6/13/2013
97	130613_Pe5b	M	GB	6/13/2013
98	130613_Pe6b	M	GB	6/13/2013
99	130613_Pe7b	M	GB	6/13/2013
100	130614_Pe2b	M	GB	6/14/2013
101	130614_Pe3b	M	GB	6/14/2013
102	110615_Pe5a	F	NA	6/15/2010
103	110615_Pe2a	M	NA	6/15/2010
104	110615_Pe3a	M	NA	6/15/2010
105	110615_Pe4a	M	NA	6/15/2010
106	120708_Pe2b	M	NA	7/8/2012
107	100505_Pe2a	F	TO	5/5/2010
108	100505_Pe1a	M	TO	5/5/2010
109	100505_Pe3a	M	TO	5/5/2010
110	100506_Pe2a	F	TO	5/6/2010
111	100506_Pe1a	M	TO	5/6/2010
112	130501-01_Pe1b	F	TO	5/1/2013
113	130501-01_Pe2b	F	TO	5/1/2013
114	130501-01_Pe3b	M	TO	5/1/2013
115	130501-01_Pe4b	M	TO	5/1/2013
116	130506-02_Pe1b	F	TO	5/6/2013
117	130506-02_Pe2b	F	TO	5/6/2013
118	140427_Pe1b	M	TO	4/27/2014
Short-finned Pilot Whales				
119	100608_Gm2a	F	EA	6/8/2010
120	100608_Gm3a	F	EA	6/8/2010
121	100608_Gm4a	F	EA	6/8/2010
122	100608_Gm5a	F	EA	6/8/2010
123	100608_Gm1a	M	EA	6/8/2010
124	100608_Gm6a	M	EA	6/8/2010
125	100608_Gm7a	M	EA	6/8/2010
126	100608_Gm8a	M	EA	6/8/2010
127	090602_Gm1a	F	GB	6/2/2009
128	090602_Gm2a	F	GB	6/2/2009
129	090602_Gm4a	F	GB	6/2/2009
130	090602_Gm5a	F	GB	6/2/2009
131	090602_Gm6a	F	GB	6/2/2009
132	090602_Gm3a	M	GB	6/2/2009
133	110430_Gm4a	F	NA	4/30/2011
134	110430_Gm5a	F	NA	4/30/2011
135	110430_Gm1a	M	NA	4/30/2011

Table A1. cont.

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
136	110430_Gm2a	M	NA	4/30/2011
137	110430_Gm3a	M	NA	4/30/2011
138	120615_Gm3b	F	NA	6/15/2012
139	120615_Gm4b	F	NA	6/15/2012
140	120615_Gm1b	M	NA	6/15/2012
141	120615_Gm2b	M	NA	6/15/2012
142	120615_Gm5b	M	NA	6/15/2012
143	120615_Gm6b	M	NA	6/15/2012
144	120615_Gm7b	M	NA	6/15/2012
145	140424_Gm5b	F	NA	4/24/2014
146	140424_Gm6b	F	NA	4/24/2014
147	140424_Gm7b	F	NA	4/24/2014
148	140424_Gm8b	F	NA	4/24/2014
149	140424_Gm1b	M	NA	4/24/2014
150	140424_Gm2b	M	NA	4/24/2014
151	140424_Gm3b	M	NA	4/24/2014
152	140424_Gm4b	M	NA	4/24/2014
153	140424_Gm9b	M	NA	4/24/2014
154	110504_Gm1a	F	TO	5/4/2011
155	110504_Gm2a	F	TO	5/4/2011
156	130506_Gm1b	F	TO	5/6/2013
157	130506_Gm2b	F	TO	5/6/2013
158	130506_Gm4b	F	TO	5/6/2013
159	130506_Gm3b	M	TO	5/6/2013
160	130506_Gm5b	M	TO	5/6/2013
161	130506_Gm6b	M	TO	5/6/2013
162	130506_Gm7b	M	TO	5/6/2013
163	130506_Gm8b	M	TO	5/6/2013
164	140426_Gm1b	M	TO	4/26/2014
165	100412_Gm3a*	U	GB	4/12/2010
166	100412_Gm1a*	F	GB	4/12/2010
167	100412_Gm2a*	M	GB	4/12/2010
168	100412_Gm4a*	M	GB	4/12/2010
169	100412_Gm5a*	M	GB	4/12/2010
Sperm Whales				
170	100617_Pm2a	F	EA	6/17/2010
171	100618_Pm1a	F	EA	6/18/2010
172	100618_Pm2a	F	EA	6/18/2010
173	071020_Pm2a	M	GB	10/20/2007
174	071021_Pm1a	M	GB	10/21/2007
175	080610_Pm1a	M	GB	6/10/2008
176	090601_Pm1a	F	GB	6/1/2009
177	110606_Pm1a	F	GB	6/6/2011
178	110607_Pm1a	F	GB	6/7/2011
179	110607_Pm2a	F	GB	6/7/2011
180	110607_Pm3a	F	GB	6/7/2011
181	110608_Pm1a	M	GB	6/8/2011
182	120606_Pm1b	F	GB	6/6/2012

Table A1. cont.

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
183	130617_Pm1b	M	GB	6/17/2013
184	120613_Pm1b	M	NA	6/13/2012
185	071024_Pm1a	M	NE	10/24/2007
186	071024_Pm2a	M	NE	10/24/2007
187	090430_Pm1a	F	SA	4/30/2009
188	090430_Pm2a	F	SA	4/30/2009
189	090430_Pm3a	F	SA	4/30/2009
190	090430_Pm4a	F	SA	4/30/2009
191	090430_Pm5a	F	SA	4/30/2009
192	090430_Pm6a	F	SA	4/30/2009
193	090505_Pm1a	F	SA	5/5/2009
194	090505_Pm2a	F	SA	5/5/2009
195	090520_Pm1a	F	SA	5/20/2009
196	090520_Pm2a	F	SA	5/20/2009
197	090520_Pm4a	F	SA	5/20/2009
198	090520_Pm5a	M	SA	5/20/2009
199	090520_Pm6a	M	SA	5/20/2009
200	090531_Pm1a	F	SA	5/31/2009
201	090531_Pm2a	F	SA	5/31/2009
202	090531_Pm3a	M	SA	5/31/2009
203	090531_Pm4a	M	SA	5/31/2009
204	090603_Pm1a	F	SA	6/3/2009
205	090603_Pm2a	F	SA	6/3/2009
206	090603_Pm3a	F	SA	6/3/2009
207	110206_Pm1a	F	SA	2/6/2011
208	110219_Pm1a	F	SA	2/19/2011
209	110626_Pm1a	M	SA	6/26/2011
210	130515_Pm1b	M	SA	5/15/2013
211	130620_Pm1b	F	SA	6/20/2013
212	130620_Pm3b	F	SA	6/20/2013
213	130620_Pm5b	F	SA	6/20/2013
214	130620_Pm6b	F	SA	6/20/2013
215	130620_Pm7b	F	SA	6/20/2013
216	130620_Pm2b	M	SA	6/20/2013
217	130620_Pm4b	M	SA	6/20/2013
218	080525_Pm1a	M	TO	5/25/2008
219	100505_Pm1a	M	TO	5/5/2010
220	110504_Pm1a	M	TO	5/4/2011
221	110505_Pm1a	F	TO	5/5/2011
222	110506_Pm10a	F	TO	5/6/2011
223	110506_Pm11a	F	TO	5/6/2011
224	110506_Pm12a	F	TO	5/6/2011
225	110506_Pm1a	F	TO	5/6/2011
226	110616_Pm1a	M	TO	6/16/2011
227	110616_Pm3a	M	TO	6/16/2011
228	130504-01_Pm1b	M	TO	5/4/2013
229	130506-01_Pm1b	M	TO	5/6/2013
230	130506-01_Pm2b	M	TO	5/6/2013
231	130603_Pm1b	M	TO	6/3/2013

Table A1. cont.

Sample#	Field ID	Sex[a]	Collection location[b] (strata)	Collection date
232	130603_Pm2b	M	TO	6/3/2013
233	130603_Pm3b	M	TO	6/3/2013
234	130603_Pm4b	M	TO	6/3/2013
235	130603_Pm5b	M	TO	6/3/2013
236	130603_Pm6b	M	TO	6/3/2013
Rough-toothed Dolphins[c]				
237	130501_Sb01a	U	TO	5/1/2013
238	130501_Sb02a	U	TO	5/1/2013
Opportunistic Prey Samples[d]				
239	Prey Fragment (11 May 2011)	Cephalopod?	SA	5/11/2011
240	Prey Fragment (17 May 2011)	Jellyfish?	SA	5/17/2011
241	Hatchet Fish (21 May 2011)	*S. diaphana* (hatchet fish)	SA	5/21/2011
242	Prey 1a 110613	*M. niger* (barbled dragonfish)	NA	6/13/2011
243	Unknown FECAL Prey 16 July 2011	*P. margarita* (dragonfish)	SA	7/16/2011
244	2013_SQUID_67 (tentacle)	*Magalocranchia sp* (glass squid)	TO	11/2/2013
245	2013_SQUID_68 (tentacle)	*Magalocranchia sp* (glass squid)	TO	11/2/2013
246	2013_SQUID_69 (tentacle)	*Magalocranchia sp* (glass squid)	TO	11/2/2013
247	140506_ Unidentified fish (whole-body)	unidentified teleost fish	SA	5/6/2014
248	140617_SQUID (partial mantle + tentacle)	*H. hoylei* (cockeyed squid)	SA	6/17/2014

[a] The sexes of all animals were genetically determined (M=Male; F=Female; U=Unknown).

[b] Location/Strata Abbreviations: CU (Cul deSac); TO (TOTO/AUTEC); NA (N.Andros/S. Berry Is.); GB (South Grand Bahama Is); NE (N. Eleuthera Is.); SA (S. Abaco Is.); EA (E. Abaco Is.).

[c] Rough-toothed Dolphin samples were collected opportunistically and were used solely to test the efficacy of the FA-depth model described herein.

[d] Presumed prey samples (*fragments, fecal remains, and whole-bodies*) collected opportunistically and analyzed for all three chemical tracers.

[*] Field IDs with an asterix indicate the sample was collected from a stranded animal.

Table A2. List of analytes[a] (SIs, FAs, POPs) used to study the foraging structure and differential prey preferences of each of the six Bahamas DOD-priority species using chemical tracers.

DIETARY FATTY ACIDS[b] *(wt% composition basis)*	**STABLE ISOTOPE RATIOS** (*per mille* , ‰)	**INDIVIDUAL PCB CONGENERS**[c] *(wt% composition basis)*		**POP RATIOS**[c] *(concentrations - unitless)*
C18:2n6	δ13C	PCB 052	PCB 170	ΣPCBs / ΣPOPs
C18:3n3	δ15N	PCB 066	PCB 171	ΣDDTs / ΣPOPs
C18:4n3		PCB 070	PCB 177	ΣCHLRs / ΣPOPs
C20:1n9		PCB 074	PCB 180	ΣHCHs / ΣPOPs
C20:2n6		PCB 083	PCB 183	ΣPBDEs / ΣPOPs
C20:3n6		PCB 087	PCB 187	HCB / ΣPOPs
C20:4n6		PCB 095	PCB 191	mirex / ΣPOPs
C20:3n3		PCB 099	PCB 194	dieldrin/ ΣPOPs
C20:4n3		PCB 101	PCB 195	a-chlor / ΣCHLRs
C20:5n3		PCB 105	PCB 199	c-nona / ΣCHLRs
C22:1n11		PCB 110	PCB 206	g-chlor / ΣCHLRs
C22:2n6		PCB 118	PCB 208	nona-3 / ΣCHLRs
C22:6n3		PCB 128	PCB 209	t-nonachlor / ΣCHLRs
		PCB 138		o,p'-DDD /ΣDDTs
		PCB 149		o,p'-DDE / ΣDDTs
		PCB 151		o,p'-DDT / ΣDDTs
		PCB 153		p,p'-DDD /ΣDDTs
		PCB 156		p,p'-DDE / ΣDDTs
		PCB 158		p,p'-DDT / ΣDDTs

[a] The IUPAC and/or common names of each of these abbreviated compounds can be found listed in Sloan *et al.* 2006.

[b] The subset of 13 fatty acids believed to be primarily dietary in origin among the 83 total individual fatty acids measured.

[c] The subset of 32 individual PCB congeners and 19 constructed POP ratios used in the "All POPs" models to assess long-term site-fidelity and foraging structure.

Table A3. References, annealing temperatures and multiplex sets for microsatellite loci used to genotype pilot and sperm whales. "Rt" denotes a reverse primer that has been amended to include a tail to reduce allelic stutter.

SPECIES	LOCUS	REFERENCE	PCR MULTIPLEX	ANNEALING TEMPERATURE	ABI CO-LOADING
Physeter macrocephalus	Eva5	Valsecchi & Amos (1996)	Pm-I	58^0	Pm-A
Physeter macrocephalus	Eva37	Valsecchi & Amos (1996)	Pm-I	58^0	Pm-A
Physeter macrocephalus	Eva1	Valsecchi & Amos (1996)	Pm-I	58^0	Pm-A
Physeter macrocephalus	199/200	Amos et al (1993)	-----	45^0	Pm-A
Physeter macrocephalus	Dde70	Coughlan et al (2006)	Pm-II	61^0	Pm-B
Physeter macrocephalus	Texvet5	Rooney et al (1999)	Pm-II	61^0	Pm-B
Physeter macrocephalus	SW10 (Rt)	Richard et al (1996)	Pm-III	56^0	Pm-C
Physeter macrocephalus	D22	Shinohara et al (1997)	Pm-III	56^0	Pm-C
Physeter macrocephalus	D17 (Rt)	Buchanan et al (1996)	Pm-III	56^0	Pm-C
Physeter macrocephalus	SW13	Richard et al (1996)	Pm-IV	55^0	Pm-D
Physeter macrocephalus	SW19	Richard et al (1996)	-----	55^0	Pm-D
Physeter macrocephalus	Fcb14	Buchanan et al (1996)	Pm-IV	55^0	Pm-D
Physeter macrocephalus	GATA028	Palsboll et al (1997)	Pm-IV	55^0	Pm-D
Physeter macrocephalus	Fcb1	Buchanan et al (1996)	Pm-IV	55^0	Pm-D
Physeter macrocephalus	D08	Shinohara et al 1997	-----	53^0	Pm-E
Physeter macrocephalus	Eva104	Valsecchi & Amos (1996)	Pm-V	53^0	Pm-E
Physeter macrocephalus	MK6	Kruetzen et al (2001)	Pm-V	53^0	Pm-E
Physeter macrocephalus	GATA417	Palsboll et al (1997)	Pm-V	53^0	Pm-E
Globicephala macrorhynchus	EV94 (Rt)	Valsecchi & Amos (1996)	Gm-I	62^0	Gm-A
Globicephala macrorhynchus	MK5 (Rt)	Kruetzen et al (2001)	Gm-I	62^0	Gm-A
Globicephala macrorhynchus	PPho131	Rosel et al (1999)	Gm-I	62^0	Gm-A
Globicephala macrorhynchus	Ttr63 (Rt)	Rosel et al (2005)	Gm-I	62^0	Gm-A
Globicephala macrorhynchus	KWM12a (Rt)	Hoelzel et al 1998	Gm-II	61^0	Gm-B
Globicephala macrorhynchus	MK9 (Rt)	Kruetzen et al (2001)	Gm-II	61^0	Gm-B
Globicephala macrorhynchus	Ttr04 (Rt)	Rosel et al (2005)	Gm-II	61^0	Gm-B
Globicephala macrorhynchus	Ttr11 (Rt)	Rosel et al (2005)	Gm-II	61^0	Gm-B
Globicephala macrorhynchus	Ttr19 (Rt)	Rosel et al (2005)	Gm-II	61^0	Gm-B
Globicephala macrorhynchus	PPho130 (Rt)	Rosel et al (1999)	Gm-III	49^0	Gm-C
Globicephala macrorhynchus	415416 (Rt)	Amos et al (1993)	Gm-III	49^0	Gm-C
Globicephala macrorhynchus	464465 (Rt)	Amos et al (1993)	Gm-III	49^0	Gm-C
Globicephala macrorhynchus	468469 (Rt)	Amos et al (1993)	-----	45^0	Gm-C
Globicephala macrorhynchus	MK8 (Rt)	Kruetzen et al (2001)	Gm-IV	52^0	Gm-D
Globicephala macrorhynchus	199200 (Rt)	Amos et al (1993)	Gm-IV	52^0	Gm-D
Globicephala macrorhynchus	409470 (Rt)	Amos et al (1993)	Gm-IV	52^0	Gm-D
Globicephala macrorhynchus	417418 (Rt)	Amos et al (1993)	Gm-IV	52^0	Gm-D
Globicephala macrorhynchus	EV14 (Rt)	Valsecchi & Amos (1996)	Gm-V	59^0	Gm-E
Globicephala macrorhynchus	EV37 (Rt)	Valsecchi & Amos (1996)	Gm-V	59^0	Gm-E
Globicephala macrorhynchus	Ttr34 (Rt)	Rosel et al (2005)	Gm-V	59^0	Gm-E
Globicephala macrorhynchus	Ttr48 (Rt)	Rosel et al (2005)	Gm-V	59^0	Gm-E
Globicephala macrorhynchus	FF6 (Rt)	Rosel et al (2005)	-----	57^0	Gm-E

Appendix B – List of scientific publications

In preparation:

Use of time-at-temperature data to describe dive behavior in five species of sympatric deep-diving toothed whales

Allometric scaling and vertical habitat ranges in deep-diving toothed-whales of the northern Bahamas

Small scale site fidelity and population structuring of Blainville's & Cuvier's beaked whales increases risk from local disturbance

Planned:

Population identity of short-finned pilot whales in the Bahamas: an extension of the western North Atlantic Stock beyond U.S. waters?

Population structuring & abundance of sperm whales in the Bahamas

Blainville's beaked whale social structure

Social structure, relatedness and kinship of odontocetes in the Bahamas (*Pm, Md, Gm*)

POP levels of odontocete cetaceans in the Bahamas

Abstracts submitted:

Submitted to 21st Biennial Conference on the Biology of Marine Mammals (December 13-18, 2015):

Allometric scaling and vertical habitat ranges in deep-diving toothed-whales of the northern Bahamas

Stable groups and roaming residence: Characterizing residency and group stability among Caribbean pilot whales (*Globicephala macrorhynchus*)

Bachelor sperm whales (*Physeter macrocephalus*) in the Bahamas: insights from a multi-disciplinary study

Fine-scale population structure and high site fidelity increase vulnerability of Blainville's beaked whales on a navy range in the Bahamas