USING STABLE ISOTOPES TO EXAMINE FORAGING ECOLOGY OF NEW YORK HARBOR COLONIAL WATERBIRDS

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ABSTRACT

New York Harbor has become an important breeding area for New York State's colonial waterbird community since their resurgence in the region in the 1970's. Current knowledge of these birds is generally limited to their breeding population sizes and nesting phenology. However, an understanding of foraging behavior is also critical to the conservation of these species. Stable isotope analysis is a valuable tool in the study of diet and foraging ecology of birds. Isotopic signatures observed in feathers reflect the bird's diet and foraging habitat at the time of feather formation. In this study, stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were measured in order to monitor diet, trophic position, and foraging habitat of colonial waterbirds nesting in New York Harbor. During the 2010 breeding season, feathers were collected from nestlings of six colonial waterbird species breeding on four islands within the New York Harbor. The species sampled included the Double-crested Cormorant, Great Black-backed Gull, Herring Gull, Great Egret, Black-crowned Night-Heron, and Glossy Ibis. Significant intra- and inter-specific variation in $\delta^{13}C$ and $\delta^{15}N$ was observed ($p<0.0001$), suggesting differences in foraging habitat (marine versus freshwater), variability of prey selection, and relative trophic position. Stable isotope analysis of feathers has proven to be a powerful and non-invasive tool for studying foraging ecology of colonial waterbirds in urban systems. The findings of this study can help guide resource managers in identifying and protecting important foraging habitat and prey base for these charismatic flagship species.

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INTRODUCTION

The New York-New Jersey Harbor Estuary, with an area of approximately 40,000 km^2, is home to 20 million people. However, it also provides a mosaic of urban habitat types for wildlife, ranging from open water, to fresh- and saltwater marsh, to uplands and the built environment. Small, abandoned islands in the harbor have become important breeding areas for many of New York State's colonial waterbirds since their resurgence in the region in the 1970's. Colonial waterbirds are species that tend to nest in large colonies and forage in aquatic systems. These birds are generally large, conspicuous species that constitute the charismatic megafauna of this urban estuary. Twelve colonial waterbird species are known to reproduce on these islands and forage in the surrounding wetlands and waterways to feed themselves and provision their young (Craig 2010; Elbin and Tsipoura 2010).

Current knowledge of these birds generally concerns their breeding population sizes and nesting phenology (Craig 2010). The Harbor Heron Conservation Plan of the New York-New Jersey Harbor Estuary Program calls for research to fill the information gap about foraging behavior of colonial waterbirds in this system (Elbin and Tsipoura 2010). Recent studies have employed citizen science observations of foraging birds (Tsipoura et al. 2010), and pellet and regurgitant analysis (Grubel and Waldman 2009), to elucidate resource use of focal species within the New York-New Jersey Harbor Estuary. While there are strengths to each of these approaches, both are observational studies that only encompass the diet and foraging habitat of the bird at the moment of observation (Barrett et al. 2007). This study used stable isotope analysis of feathers from nestling birds to elucidate foraging behavior of a suite of colonial waterbird species nesting in the

New York Harbor, focusing on six of the harbor's most numerically abundant colonial waterbird species, including three long-legged wading birds: Black-crowned Night-Heron (*Nycticorax nycticorax*), Great Egret (*Ardea alba*), Glossy Ibis (*Plegadis falcinellus*); and three seabirds: Double-crested Cormorant (*Phalacrocorax auritus*), Great Black-backed Gull (*Larus marinus*), and Herring Gull (*Larus argentatus*).

Stable isotope analysis is a valuable tool in the study of diet and foraging ecology of birds (Hobson and Clark 1992 a & b; Hobson 1999). Isotopic signatures observed in feathers (isotopically inert tissues) reflect the bird's entire diet and foraging habitat at the time of feather formation (Hobson and Clark 1992a). Stable isotope measurements therefore reflect resource use in a more comprehensive manner than behavioral observations or regurgitant and pellet analyses alone. With careful interpretation, isotopic signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can be used to monitor diet, relative trophic position, and foraging habitat of birds (Bond and Jones 2009). This study specifically inferred information about the type of diet items the parents used to feed their young, the relative trophic position of the prey items, and the habitat type (marine or freshwater) in which the parents primarily foraged. This approach, in combination with foraging behavior observations and diet studies, will improve the understanding of the foraging landscape used by colonial waterbird species in the harbor.

Carbon isotopic ratios in feathers are primarily indicative of the base of the food web in which the bird has recently foraged. More negative (smaller) $\delta^{13}C$ values can indicate a greater proportion of freshwater resource use, while less negative (larger) $\delta^{13}C$ values can indicate a greater proportion of marine resource use (Mizutani et al. 1990; Hobson and Clark 1992b; Bearhop et al. 1999; Bond and Jones 2009). Inclusion of C4 photosynthetic plant materials in the diet, such as products containing corn or sugar, can also create larger $\delta^{13}C$ values (Farquhar et al. 1989). Such values may indicate use of anthropogenic resources such as human food waste or intensive aquaculture (Hebert et al. 2009).

Nitrogen isotopic ratios increase with every trophic exchange, therefore $\delta^{15}N$ signatures in feathers are primarily indicative of the relative trophic position at which the bird has recently foraged (Hobson and Clark 1992b; Post 2002; Bond and Jones 2009). Higher $\delta^{15}N$ values indicate higher relative trophic position, and lower $\delta^{15}N$ values indicate lower relative trophic position. $\delta^{15}N$ values are also influenced by the $\delta^{15}N$ signature at the base of the food web, which can vary considerably among habitats with different sources of nitrogen and different ecosystem processes. Caution must be taken when interpreting $\delta^{15}N$ in terms of trophic position without prior knowledge of $\delta^{15}N$ signatures at the base of the food web (Post 2002). In this study, $\delta^{15}N$ signatures were compared among populations to infer relative, but not absolute, trophic position.

Feathers of nestling birds were used in this study because these tissues represent the local diet with which adult birds are provisioning their young. New York Harbor colonial waterbirds are generally migratory and can be long-lived, experiencing a multitude of habitats across their migratory range within their lifetimes. Depending on its time of formation, a feather from an adult bird may represent nutrients from a wide range of habitats beyond the breeding grounds. Feathers of nestling birds are therefore most suitable for answering questions about local foraging behavior and diet because they integrate only the resources that the adult bird has provided during the breeding season (Cherel et al. 2000).

Based on a general understanding of the foraging strategies of the focal species of this study, differences in isotopic signatures in species with differing foraging ecologies are to be expected. In general, ibis, egrets, and herons eat fish, crabs, amphibians, and aquatic invertebrates, cormorants eat primarily fish, and gulls eat a variety of items ranging from fish to human garbage (Pierotti and Good 1994; Good 1998; Hatch and Weseloh 1999; Davis and Kricher 2000; McCrimmon et al. 2001; Hothem et al. 2010). The stable isotope approach used in this study allows us to confirm assumed differences in foraging ecology among species. More significantly, the results of this study enhance the understanding of the specific habitat types and forage base that are most important in the diet of individual populations within this urban estuary. This information is critical to the conservation of these species and in determining which areas within the estuary should be prioritized for habitat protection or environmental remediation.

The objectives of this study were to examine the foraging ecology of a suite of colonial waterbird species nesting within New York Harbor, and to identify the key habitats and forage base that were particularly important to each individual population. The hypothesis tested was that colonial waterbird populations would exhibit both inter- and intra-specific variation in foraging behavior and habitat preference, observed through variation in stable isotope signatures, based on differences in their general foraging strategies and on habitat availability near their nesting locations. Identifying the key resources that are most important to these populations is instrumental in the conservation of colonial waterbirds in this urban system.

METHODS

Field Sites

Feather samples were collected at four locations (Figure 1): two in Lower New York Bay (Hoffman Island, Swinburne Island); one in the East River (South Brother Island); and one in Westchester County, New York (Muscoot Reservoir Island).

Hoffman and Swinburne islands are man-made islands located in Lower New York Bay off the east shore of Staten Island, New York (40.578716°N, 74.053752°W). Hoffman Island (approximately 4.5 hectares) and Swinburne Island (approximately 1.5 hectares) were constructed in the mid-1860s as quarantine islands for immigrants carrying contagious diseases. In 1961, all the buildings on Hoffman Island were razed, although many of the structures on Swinburne Island still stand. In 1972 the islands were entrusted to the federal government as part of the National Parks Service Gateway National Recreation Area (Seitz and Miller 1996). Public access is restricted. In 2010, nine species of colonial waterbirds nested on Hoffman Island: Black-crowned Night-Heron, Yellow-crowned Night-Heron, Great Egret, Snowy Egret, Glossy Ibis, Little Blue Heron, Double-crested Cormorant, Great Black-backed Gull, and Herring Gull. In 2010, four species of colonial waterbirds nested on Swinburne Island: Double-crested Cormorant, Great Black-backed Gull, Herring Gull, and Black-crowned Night-Heron (Craig 2010).

South Brother Island is a natural island in the East River situated between Riker's Island and the Bronx, New York (40.796110°N, 73.898060°W). This approximately three-hectare island has historically had only a single residential building, constructed in 1894. Since the destruction of this building by fire in 1909, the island has remained undeveloped (Seitz and Miller 1996). South Brother Island was acquired by New York City Department of Parks and Recreation in 2007. Public access is restricted. In 2010, eight species of colonial waterbirds nested on South Brother Island: Black-crowned Night-Heron, Yellow-crowned Night-Heron, Great Egret, Snowy Egret, Glossy Ibis, Double-crested Cormorant, Great Black-backed Gull, and Herring Gull (Craig 2010).

Muscoot Reservoir Island is a small island (less than 100 m^2) located in Muscoot Reservoir, 40 km north of New York Harbor, and directly north of the village of Katonah in Westchester County, New York (41.2694°N, 73.7070°W). Muscoot Reservoir is part of the Croton Reservoir system, which provides drinking water to New York City. In 2010, Double-crested Cormorants nested on Muscoot Reservoir Island (personal observation). This colony is monitored by the New York City Department of Environmental Protection.

Figure 1. Map of the New York-New Jersey Harbor and surrounding region. Feather samples were collected at Muscoot Reservoir and Hoffman, Swinburne, and South Brother islands.

Feather Collection

In June and July 2010, colonial waterbird nestlings of five species were captured by hand at nests on Hoffman, Swinburne, South Brother, and Muscoot Reservoir islands in coordination with permitted studies and banding programs conducted by New York City Audubon. Between one and 10 contour feathers per individual were collected while the nestlings were handled for banding. In addition, between June and September 2010, contour feathers were collected from all recently deceased colonial waterbird nestlings of known species identity encountered on each island. All feather samples were stored in individually labeled paper envelopes. A summary of the number of individuals sampled at each location can be found in Table 1.

Table 1. Summary of feather sampling. Feather samples were collected from colonial waterbird nestlings on islands in the New York-New Jersey Harbor Estuary and Muscoot Reservoir from June to September, 2010.

	South Brother Island	*Hoffman Island*	*Swinburne Island*	*Muscoot Reservoir*
Black-crowned Night-Heron	6	9	0	0
Glossy Ibis	0	13	0	0
Great Egret	20	15	0	0
Double-crested Cormorant	21	0	20	7
Great Black-backed Gull	0	20	0	0
Herring Gull	0	6	14	0

Stable Isotope Analysis

A one mg sample (± 0.1 mg) of each feather was encapsulated in tin and analyzed for $\delta^{13}C$ and $\delta^{15}N$ using an isotope ratio mass spectrometer with elemental analyzer (EA-IRMS) at Cornell University's Stable Isotope laboratory (COIL).

Statistical Analysis

Single-factor MANOVA and post-hoc ANOVA with Tukey-Kramer HSD were used to determine statistically significant variation in $\delta^{13}C$ and $\delta^{15}N$ signatures using a factor of nesting location or species depending on the analysis. Additionally, a MANOVA of $\delta^{13}C$ and $\delta^{15}N$ was conducted using mortality as the single factor to confirm that isotope signatures did not differ significantly with mortality. The $\delta^{13}C$ and $\delta^{15}N$ signatures of feathers collected from live versus dead nestlings were not found to differ significantly ($p=0.6227$). Therefore, the data were analyzed regardless of mortality for all subsequent analyses.

RESULTS

Intra-specific Variation Among Colonies

Cormorants

As anticipated, $\delta^{13}C$ signatures were found to vary significantly among the three cormorant breeding colonies sampled in this study ($p < 0.0001$; Fig. 2). Cormorants from Muscoot Reservoir Island, located in a purely freshwater environment, had the lowest average $\delta^{13}C$ values (mean ± SD of -27.52 ± 0.85 ‰) indicative of freshwater resource use. Cormorants from Swinburne Island, located in the tidal Lower New York Bay and coastal Atlantic Ocean, had the highest average $\delta^{13}C$ values (-16.95 ± 1.78 ‰) indicative of marine resource use. Cormorants from South Brother Island, located in the tidal East River near freshwater tributaries, exhibited intermediate $\delta^{13}C$ values (-20.53 ± 3.83 ‰). Cormorants from South Brother Island also exhibited the largest standard deviation (3.83 ‰) and range (12.65 ‰) in $\delta^{13}C$ values, indicating a larger range and variety of foraging habitat use in birds from this location. No significant differences in $\delta^{15}N$ were observed among cormorant colonies.

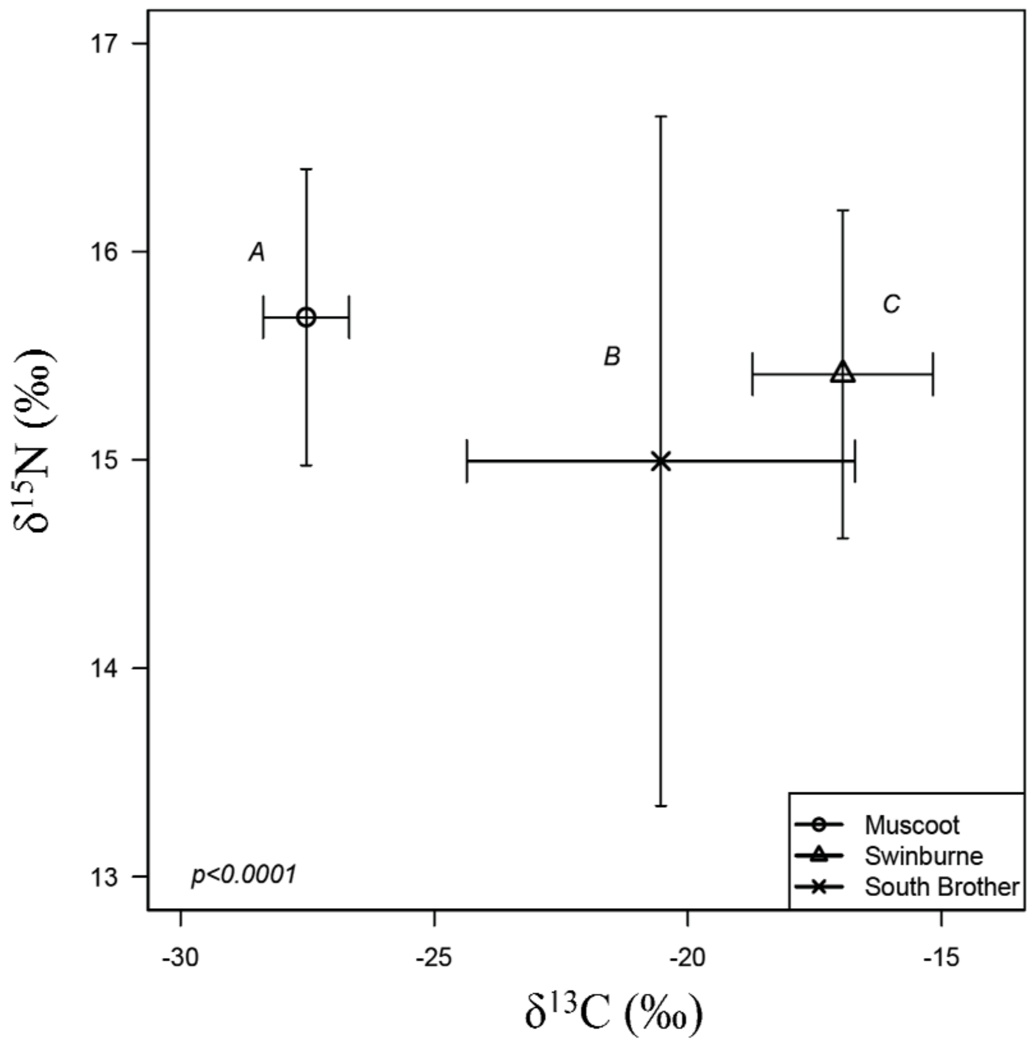

Figure 2. Cormorants across the New York-New Jersey Harbor Estuary. Mean ± SD $\delta^{13}C$ versus $\delta^{15}N$ among breeding colonies of cormorants in 2010 (Muscoot Reservoir Island, Swinburne Island, and South Brother Island). $\delta^{13}C$ varied significantly over time ($p<0.0001$). Different letters signify statistically significant differences among colonies according to Tukey-Kramer HSD.

Long-legged Wading Birds

No significant differences in isotopic signatures were observed among colonies of Great Egrets or Black-crowned Night-Herons (the only long-legged wading birds sampled at multiple locations). However, wading birds nesting on South Brother Island tended to have greater ranges in $\delta^{13}C$ than conspecifics nesting on Hoffman Island. Great Egret $\delta^{13}C$ values had a range of 11.66 ‰ on South Brother Island in comparison to a range of 5.75 ‰ on Hoffman Island. Black-crowned Night-Herons exhibit smaller differences in $\delta^{13}C$ range: 8.67 ‰ on South Brother Island and 6.32 ‰ on Hoffman Island.

Inter-specific Variation

To determine inter-specific variation in foraging behavior at a single nesting colony, variation in $\delta^{13}C$ and $\delta^{15}N$ was analyzed among species nesting on Hoffman and Swinburne islands combined, as these two nesting islands exist in very close proximity and therefore have the same available surrounding foraging habitat. Significant variation in both $\delta^{13}C$ and $\delta^{15}N$ was observed using a MANOVA with species as the single factor ($p<0.0001$; Fig. 3).

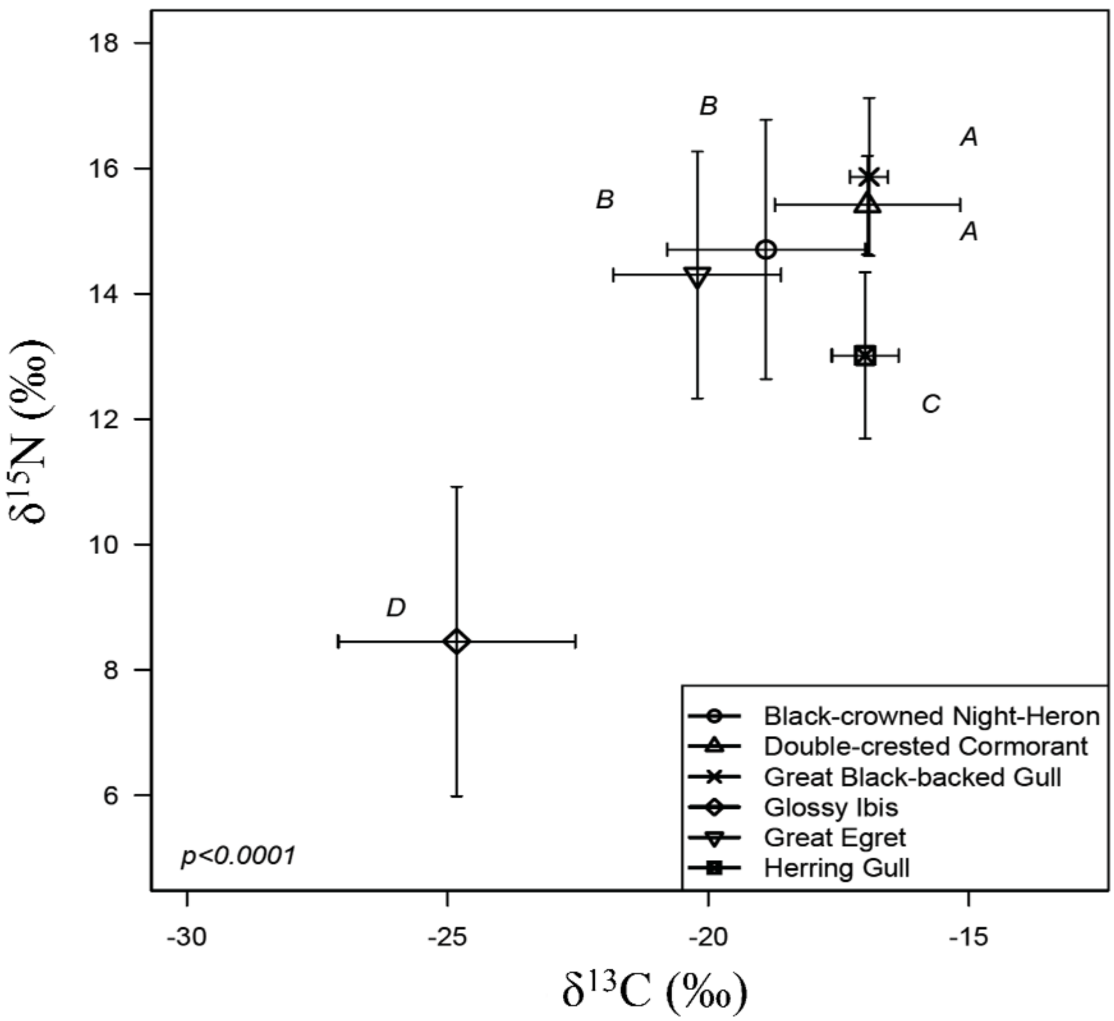

Figure 3. Colonial waterbird species on Hoffman & Swinburne islands. Mean ± SD $\delta^{13}C$ versus $\delta^{15}N$ among species on Hoffman & Swinburne islands combined. Both $\delta^{13}C$ and $\delta^{15}N$ varied significantly among species ($p<0.0001$). Different letters signify statistically significant differences among species according to Tukey-Kramer HSD.

Great Egret and Black-crowned Night-Heron isotopic signatures were not statistically different from one another. Double-crested Cormorants and Great Black-backed Gulls also were not statistically different from one another. Isotopic signatures of both Herring Gulls and Glossy Ibis were individually distinct from all other species nesting on Hoffman and Swinburne Islands in 2010.

DISCUSSION

The results of this study elucidate foraging behaviors of a suite of colonial waterbird species nesting within New York Harbor. These data allow us to identify key habitat types and forage base that are particularly important to individual populations. Both intra- and inter-specific variation in foraging behavior were examined in order to make observations of foraging behaviors on both the population and breeding colony scales.

Intra-specific Variation Among Colonies

Double-crested Cormorants exhibited significant variation in isotopic signatures across the breeding colonies at which they were sampled ($p<0.0001$; Fig. 2). As predicted, the predominant foraging habitats represented in the isotopic signatures reflected the available habitat types in the vicinity of each colony. Cormorants from Muscoot Reservoir Island had isotopic signatures indicative of a predominantly freshwater diet (relatively low $\delta^{13}C$ values). Birds nesting at this colony were most likely foraging at Muscoot Reservoir and the surrounding reservoir and river system. Cormorants from Swinburne Island had isotopic signatures indicative of a predominantly marine diet (relatively high $\delta^{13}C$ values), and were most likely foraging within Lower New York Harbor and the surrounding coastal Atlantic Ocean. Cormorants from South Brother Island exhibited a greater range in $\delta^{13}C$ signatures than observed at the other two colony locations (nearly twice the range observed in Swinburne Island cormorants, and nearly six times the range observed in Muscoot Reservoir Island cormorants), indicating that a wider range of foraging habitats contributed to the diet of these birds. This observation reflects the diverse nature of foraging habitat availability near South Brother Island, located in the tidal East River surrounded by its freshwater tributaries. The area surrounding South Brother Island is also highly developed, and cormorants nesting at this location may forage at greater distances from the island to meet their metabolic needs. The resulting increased foraging distance would also explain the greater range of foraging habitats exhibited in the isotopic signatures of cormorants from the South Brother Island colony. These data provide a valuable perspective on intra-specific variation in foraging behavior of cormorants within the New York-New Jersey Harbor Estuary system.

Interestingly, no significant intra-specific differences were observed in isotopic signatures of Great Egrets or Black-crowned Night-Herons (both nesting on Hoffman and South Brother islands). As long-legged wading birds, the foraging strategies of these two species may also require them to forage at greater distances from their colony sites, exposing them to a larger range of potential foraging habitat types. While long-legged wading bird species appear to be foraging in similar habitat types regardless of nesting colony location, the range in $\delta^{13}C$ signatures was greater in birds from South Brother Island than from Hoffman Island, as observed in cormorants. These results indicate that long-legged wading birds, as well as cormorants, nesting at South Brother Island may be foraging in a wider range of habitats, and potentially at a greater foraging distance, than conspecifics nesting on Hoffman Island.

Inter-specific Variation

As anticipated, a significant inter-specific variation in foraging behavior of species nesting on Hoffman Island was observed ($p<0.0001$; Fig. 3). The species sampled on this island represent a wide range of foraging strategies and the significant variation in both $\delta^{13}C$ and $\delta^{15}N$ reflect those differences.

Glossy Ibis tend to forage by probing for invertebrates in shallow water, fields, and marshes (Davis and Kricher 2000). Based on the significantly lower $\delta^{13}C$ values observed in this species, it can be concluded that freshwater foraging habitat is the most important habitat type for this population during chick rearing. Glossy Ibis also exhibited significantly lower average $\delta^{15}N$ values, which may indicate a difference in source nitrogen in ibis foraging habitats, but most likely also indicates that ibis were foraging at a lower relative trophic position than other species nesting on Hoffman Island. As ibis primarily consume low trophic position prey, this observation supports the general understanding of ibis foraging ecology.

Great Egrets and Black-crowned Night-Herons exhibited no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values. These species may therefore share similar forage base and range of foraging habitats within the New York-New Jersey Harbor Estuary. Based on average $\delta^{13}C$ values observed for both of these species, these long-legged wading birds are expected to forage in a mix of both freshwater and marine environments.

Double-crested Cormorants are diving birds that prey on a wide variety of fish. Cormorants at Swinburne Island exhibited relatively high $\delta^{13}C$ values indicating a large proportion of marine resource use at this location. Interestingly, the Great Black-backed Gulls observed on adjacent Hoffman Island (an island on which cormorants also nest) exhibited $\delta^{13}C$ and $\delta^{15}N$ values very similar to those observed in cormorants. The general understanding of the foraging strategies of these two species does not explain this phenomenon; gulls tend to be more generalist scavengers and cormorants are piscivorous, diving predators. Great Black-backed Gulls, however, have been known to exhibit predatory behavior (Good 1998), and were observed during this study predating cormorant nests when cormorant colonies were disturbed. However, if cormorant nest contents (nestlings or eggs) were the main component of Great Black-backed Gull diet, higher $\delta^{15}N$ values would be expected in gulls than in cormorants. As this is not the case, the similarity between cormorant and Great Black-backed Gull isotopic signatures is hypothesized to be due to a combination of gulls predating early-stage cormorant nests, and scavenging for food scraps in the understory beneath the cormorant colony. Regardless of the specific scavenging or predatory behavior, the data suggest that cormorant-related diet items may be the most important food source for Great Black-backed Gulls nesting on Hoffman Island.

Herring Gulls also exhibited relatively high $\delta^{13}C$ values, although significantly lower $\delta^{15}N$ values than observed in the Great Black-backed Gulls. Herring Gull isotopic signatures did not overlap with cormorant signatures as observed in the Great Black-backed Gull, although Herring Gulls have also been observed predating cormorant nests. Anthropogenic resource use, including scavenging of human food waste, could lead to high $\delta^{13}C$ values due to the consumption of C4 photosynthetic plant materials such as corn- and sugar-based foods. Such resource use would also lead to lower $\delta^{15}N$ values due to the low relative trophic position of these diet items. Herring Gull isotopic signatures, therefore, may be explained by either the scavenging of lower trophic position fish from the marine environment, or anthropogenic resource use. Further analysis of these feathers using EA-IRMS to measure $\delta^{34}S$ would determine which interpretation is most likely.

Sulfur isotopic ratios in feathers are primarily indicative of the type of aquatic habitat (freshwater versus marine) in which the bird has recently foraged. While $\delta^{13}C$ can also indicate freshwater or marine resource use, several other factors independent of salinity can influence these signatures. $\delta^{34}S$ could serve as a more straightforward indicator of freshwater versus marine resource use in this case.

Implications for Conservation

Government action to conserve New York Harbor colonial waterbirds has generally focused on protecting critical breeding habitats (Elbin and Tsipoura 2010). The results of this study indicate that, even within a single mixed-species breeding colony, different colonial waterbird species encounter and rely upon very different foraging habitats while provisioning their young. Management efforts must consider population-specific foraging behavior to effectively conserve New York Harbor's colonial waterbirds.

Waterbirds have high metabolic needs and are top-level consumers in the food web. As top predators in aquatic systems, colonial waterbirds have the potential to encounter biomagnified concentrations of contaminants in their diet, and birds foraging at higher trophic positions may be at relatively greater risk (Burger and Gochfeld 2004). Double-crested Cormorants, Great Black-backed Gulls, Great Egrets and Black-crowned Night-Herons exhibited the highest average $\delta^{15}N$ values in the New York Harbor colonial waterbird community, potentially indicating higher relative trophic position. These birds may therefore be at greater risk concerning exposure to environmental contaminants.

An understanding of foraging behavior, including the knowledge of which areas and resources are most important to species of conservation concern, is critical to the conservation of colonial waterbirds in the New York-New Jersey Harbor Estuary. Stable isotope analysis of feathers is a powerful and non-invasive tool for studying foraging ecology of colonial waterbirds in urban systems. Combining results from this study with foraging behavior observations and diet studies will improve the understanding of the foraging landscape used by different waterbird species in the harbor, and will help guide resource managers in the protection of important foraging habitat for these charismatic flagship species.

Future Directions

To complement these findings of the important foraging habitat types used by colonial waterbirds in New York Harbor, the next step in this line of research will be to determine the relative importance of specific diet items to the overall diet of birds at different focal colonies. Stable isotope analyses (comparable to those presented in this study) will be conducted on common diet items found in cormorant regurgitant, collected from Swinburne and South Brother islands in collaboration with a study conducted by Grubel and Waldman (2009). Using a stable isotope mixing model (including novel information on tissue fractionation rates in cormorants; Craig et al. In preparation), the relative importance of these diet items in the overall diet of cormorants at these nesting colonies will be determined (Bond and Jones 2009). These analyses will add a greater level of detail to the understanding of the foraging landscape used by colonial waterbirds in this system.

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