AVIAN CONSERVATION
& ECOLOGY

VOLUME 18, ISSUE 2, ARTICLE 1

Smith, O. A., and E. C. Craig. 2023. Effects of Atlantic butterfish (*Peprilus triacanthus*) in diets of Common Terns (*Sterna hirundo*): a case study of climate change effects in the Gulf of Maine. Avian Conservation and Ecology 18(2):1. https://doi.org/10.5751/ACE-02440-180201

Short Communication

Effects of Atlantic butterfish (*Peprilus triacanthus*) in diets of Common Terns (*Sterna hirundo*): a case study of climate change effects in the Gulf of Maine

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ABSTRACT. Climate change and associated shifts in marine prey communities can alter food availability for foraging seabirds. This issue is illustrated in the Gulf of Maine by the northward shift of Atlantic butterfish (*Peprilus triacanthus*; hereafter butterfish) and their subsequent increase in seabird diets. Here, we examine effects of butterfish in diets of the Common Tern (*Sterna hirundo*), a threatened species in this region. Our objectives were to evaluate butterfish suitability for tern chick diet through observing handling time and feeding success, to examine effects of butterfish on tern chick growth, and to explore signs of adaptive foraging in adults. The diet and growth of Common Tern chicks were studied for three breeding seasons on Seavey Island, New Hampshire, USA in the Gulf of Maine. Prey items were identified during feedings and were grouped into five prey categories: butterfish, herring, hake, other fish, and invertebrates. Chicks were weighed to calculate growth rate, which was examined as a response to diet. Across prey categories, butterfish were handled by chicks for the greatest amount of time ($P < 0.001$) but were swallowed the least ($P < 0.001$). Furthermore, chick growth rates were negatively associated with proportion of butterfish in the diet ($P < 0.001$). There was significant variation in chick diet across different nests in two of the three years studied ($P < 0.05$ in 2018 and 2019), and some breeding pairs were never observed provisioning butterfish to their young. Although the mechanism underlying individual specialization is not known, chicks that are fed fewer butterfish are at an advantage. The provisioning (or not) of unsuitable prey is particularly important because seawater warming in the Gulf of Maine is expected to increase, and butterfish are likely to become even more prevalent in seabird diets.

Effets du stromaté à fossettes (*Peprilus triacanthus*) sur le régime alimentaire de la Sterne pierregarin (*Sterna hirundo*) : étude de cas des effets des changements climatiques dans le golfe du Maine

RÉSUMÉ. Les changements climatiques et les changements qui y sont associés dans les communautés de proies marines peuvent modifier la disponibilité de la nourriture pour les oiseaux marins. Cette réalité est illustrée dans le golfe du Maine par le déplacement vers le nord des stromatés à fossettes (*Peprilus triacanthus*) et leur augmentation subséquente dans le régime alimentaire d'oiseaux marins. Dans la présente étude, nous avons examiné les effets des stromatés sur le régime alimentaire de la Sterne pierregarin (*Sterna hirundo*), espèce menacée dans cette région. Nos objectifs étaient d'évaluer l'adéquation des stromatés au régime alimentaire des poussins de sternes en observant le temps de manipulation et le succès de l'alimentation, d'examiner les effets des stromatés sur la croissance des poussins et d'explorer les signes d'adaptation pour la recherche de nourriture chez les adultes. Le régime alimentaire et la croissance des poussins de Sterne pierregarin ont été étudiés pendant trois saisons de nidification sur l'île Seavey, au New Hampshire aux États-Unis, dans le golfe du Maine. Les proies ont été identifiées pendant le nourrissage et ont été regroupées en cinq catégories : stromaté, hareng, merluche, autres poissons et invertébrés. Les poussins ont été pesés pour calculer le taux de croissance, qui a été examiné en tant que réponse au régime alimentaire. Parmi les catégories de proies, les stromatés ont été manipulés par les poussins le plus longtemps ($P < 0,001$), mais ont été avalés le moins souvent ($P < 0,001$). De plus, le taux de croissance des poussins était négativement associé à la proportion de stromatés dans leur régime alimentaire ($P < 0,001$). Une variation significative du régime alimentaire des poussins a été observée entre les différents nids dans deux des trois années étudiées ($P < 0,05$ en 2018 et 2019), et certains couples nicheurs n'ont jamais été observés en train de fournir des stromatés à leurs jeunes. Bien que le mécanisme sous-jacent à la spécialisation individuelle ne soit pas connu, les poussins qui ont été nourris avec moins de stromatés ont été avantagés. L'approvisionnement (ou non) en proies inadaptées est particulièrement important car on prévoit que le réchauffement de l'eau dans le golfe du Maine s'accentuera, et les stromatés sont susceptibles de devenir encore plus fréquents dans le régime alimentaire d'oiseaux marins.

Key Words: *Atlantic butterfish; climate change; Common Tern; diet; forage fish; growth rate; ocean warming; range shift*

INTRODUCTION

Climate change affects physical conditions of marine systems, eliciting community responses in which some species may shift their distribution or phenology (Doney et al. 2012, Poloczanska et al. 2013, Sydeman et al. 2015). However, not all species in a community respond in the same manner or magnitude, and asymmetries in species' responses to climate change can alter predator-prey interactions through changes in size, location, and

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overlap of an organism's spatial range (Selden et al. 2018). For species that are central place foragers, these shifts in prey distribution can increase the distance between the predator's foraging zone and its desired prey, ultimately altering food availability (Durant et al. 2007). Some species adapt to these changes by replacing historically preferred prey with different species or by adjusting their spatial range according to changes in their environment (Grémillet and Boulinier 2009).

Instances of predator-prey mismatch as a response to shifting prey communities have been observed in the Gulf of Maine (GOM; Staudinger et al. 2019), which is warming faster than 99% of the world's oceans (Pershing et al. 2015). In these prey communities, climate-driven ecosystem changes have resulted in more temperate species and fewer subarctic organisms (Pershing et al. 2021). One such change to the GOM prey community can be seen in distributional shifts of Atlantic butterfish (*Peprilus triacanthus;* hereafter butterfish), a subtropical to temperate fish that is found in Northwest Atlantic waters ranging from Florida, USA to Nova Scotia, Canada (Adams et al. 2015). Butterfish is vulnerable to distributional shift because it is a highly mobile habitat generalist with broad larval dispersal (Hare et al. 2016) and migrates in response to fluctuating water temperature (Hudson and Peros 2013). Consequentially, this warm-water fish has shown significant northward shift in mean latitude in recent decades (Suca et al. 2021), including range expansion into the GOM (Adams 2022). Butterfish were detected in the GOM as early as 1982 (Adams 2022). However, more recently, they are increasing in diets of seabirds within this region (Kress et al. 2017) and are replacing historically preferred prey of seabirds (Scopel et al. 2019). Despite being captured more frequently, butterfish may prove to be unsuitable prey for seabirds because of its dorsoventrally deep-bodied shape, which makes it difficult for gape-limited seabirds to swallow (Kress et al. 2017). This issue is of particular concern for foraging seabirds in the GOM because, in coming decades, habitat suitability for butterfish is predicted to be high in this region (McHenry et al. 2019).

Here, we explore effects of butterfish in the diet of Common Terns (*Sterna hirundo*) at a breeding site in the GOM. Common Terns are the most widely distributed tern in the GOM and in North America. These birds were overharvested and displaced from their colonies during the 20th century; today, they are considered a Regional Species of Greatest Conservation Need in the U.S. Northeast region (Terwilliger Consulting 2015). Breeding Common Terns are central place foragers constrained by foraging distance away from their young (with a typical clutch size of 2–3 eggs; Arnold et al. 2020). In the GOM, they capture a variety of prey from foraging areas surrounding their breeding colonies, including small and juvenile fishes (particularly species of herring and hake [*Clupea, Alosa, Urophycis,* and *Merluccius* species]) and invertebrates such as insects, euphausiids, and squid (Hall et al. 2000, Arnold et al. 2020). Understanding effects of climate-mediated changes on Common Tern prey is particularly important for the protection of this management-dependent seabird, as prey availability is an essential component underlying seabird reproductive success during the breeding season (Schaffner 1986, Cairns 1988, Suddaby and Ratcliffe 1997). Effects of climate change and overfishing on prey availability, as well as increased butterfish in the diet, are specifically cited as threats to breeding terns in New Hampshire, USA (Carloni 2015).

We examined suitability and effects of butterfish in diets of Common Terns to evaluate current and potential future impacts of increasing butterfish abundance with warming temperatures in the GOM. Our specific objectives were:

1. To evaluate the suitability of butterfish for chick consumption, using handling time and feeding success as measures of prey suitability. We hypothesized that due to their deep-bodied morphology, butterfish would be difficult to handle and ultimately less likely to be successfully swallowed compared to other prey items, rendering them unsuitable prey for tern chicks.
2. To examine effects of butterfish on tern chick growth. We expected that increased rates of butterfish provisioned to tern chicks by their parents would negatively affect chick growth.
3. To explore variability in butterfish provisioning among breeding pairs of adults. We examined diet composition across nests and hypothesized that variability in the proportion of butterfish provisioned may be an indicator of an adult's capacity to respond adaptively to the increasing presence of butterfish in the GOM prey community.

METHODS

Study area

We collected data from Common Terns at a mixed-species tern nesting colony on Seavey Island, New Hampshire, USA (42°58' N, 70°37' W), located approximately 10 km offshore in the southwestern GOM. The island serves as the site of New Hampshire's threatened and endangered tern restoration efforts. Research and management have been conducted on the island every summer (May–August) since 1997. Data presented here were collected on Seavey Island in June and July 2017, June to August 2018, and July and August 2019. During these years, Seavey Island annually supported 2000–3000 pairs of Common Terns, 60–90 pairs of Roseate Terns (*S. dougallii*), and 1–2 pairs of Arctic Terns (*S. paradisaea*).

Common Tern chick diet

Feeding watches were made either in-person with binoculars from observation blinds or remotely using video footage recorded from an AXIS P5635-E Mk II PTZ Network Camera. Observations occurred between 5:30 and 21:30. Chicks monitored during feeding watches were banded and regularly marked on the breast with colored ink, allowing us to identify individuals and their corresponding nest identity (ID). We could not consistently identify individual adults during feeding watches, so our diet data were collected at the nest level, representing each pair of adults. The majority of nests were monitored for ≥ 5 h over the course of the breeding season. For nest-level analyses, we removed seven nests (of 53 total) that were observed for < 5 h, finding that the low watch times resulted in feeding rate outliers.

For each chick feeding event, we visually identified prey to the lowest taxonomic resolution possible. Prey items recorded were grouped into five categories: (1) butterfish, (2) herring (comprising *Clupea harengus* and *Alosa* spp.), (3) hake (comprising *Urophycis chuss, U. tennuis,* and *Merluccius bilinearis*), (4) other fish (in order of relative proportion:

Ammodytes spp., *Fundulus heteroclitus, Tautogolabrus adspersus, Enchelyopus cimbrius,* other gadid species [likely *Melanogrammus aeglefinus, Pollachius virens,* and *Gadus morhua*], *Cyclopterus lumpus, Menidia menidia, Catostomus commersonii,* and *Syngnathus fuscus*), and (5) invertebrates (primarily euphausiids, insects, and squid). Thirty-five percent of prey items were unidentifiable and were excluded from analyses. Prey size was quantified by visually estimating the length of prey relative to that of the adult tern's bill, using units of "bill length."

To assess the suitability of butterfish as prey for Common Tern chicks, we recorded handling time and feeding success. Handling time was defined as number of seconds that a chick held a prey item in its bill before it was swallowed, discarded, or stolen. Handling times were included in analyses regardless of whether prey were swallowed. Feeding success was defined as the proportion of each prey category that was successfully swallowed by chicks; discarded or stolen prey were considered unsuccessful feedings. To test for differences in both handling time and feeding success across prey categories, we used analysis of variance with post-hoc Tukey honestly significant difference (HSD) tests. We used linear regression to assess the relationship between prey size and handling time within each prey category. Statistical analyses were conducted in R (version 4.0.2; R Core Team 2021) and JMP (JMP Pro 15.0.0).

Common Tern chick growth rates

We weighed individual chicks at least twice between 3 and 15 days of age, the period over which chick weight increases linearly and a linear growth rate could be calculated (Arnold et al. 2016). For nests with more than one chick, we used the growth rate of the fastest growing sibling in analyses, as one chick typically received most feedings, and that chick's growth was therefore more representative of the composition of the diet. Furthermore, in 60% of nests with more than one chick, one sibling tended to die quickly (within one week of hatching in our study population), limiting the potential to collect diet and growth data for multiple chicks in one nest. For growth-diet comparisons, we used feeding data when chicks were between 0 and 15 days old, as these feedings were most relevant to the period of linear chick growth. To assess effects of butterfish in diets on chick growth while accounting for overall feeding rates, we conducted a least-squares regression of chick growth rate, including the effects of proportion of butterfish in the diet, overall feeding rate, and the interaction between those variables. Although we also measured juvenile survival (to 15 days of age) at our study site, this metric was highly influenced by non-dietary factors, including severe weather and predation events. We therefore chose to focus our investigations on chick growth rate as the response metric most immediately influenced by shifts in diet.

Variability in butterfish provisioning

We examined variability in number of butterfish in diets across years and across nests within each year of study. For these analyses, we grouped prey items into two categories: butterfish and all other prey. We compared the number of butterfish relative to all other prey provisioned across the three years of study using a χ^2 test. To examine variability in butterfish provisioning by different nesting pairs of adults, we compared number of butterfish and other prey by nest ID within each of the three years using a two-tailed Monte Carlo estimate of Fisher's exact test (Mehta and Patel 2013).

RESULTS

We conducted feeding watches of individual Common Tern nests in 2017 (N = 11, watched on average [± standard deviation, SD] for 18 ± 13 h), 2018 (N = 13, 20 ± 16 h), and 2019 (N = 22, 43 ± 24 h). We successfully identified 110 prey items in 2017, 212 prey items in 2018, and 656 prey items in 2019. Over the three years combined, we observed 92 butterfish, 277 herring, 477 hake, 58 other fish, and 74 invertebrates. Overall, butterfish comprised 17% of the diet in 2017, 19% in 2018, and 5% in 2019.

Suitability of butterfish for chick consumption

Handling time varied significantly among prey categories ($F_{4, 499}$ = 63.9, P < 0.001; Fig. 1). A post-hoc Tukey HSD test indicated that butterfish took significantly longer for chicks to handle (mean ± SD: 328 ± 424 s) than herring (13 ± 35 s), hake (2 ± 6 s), other fish (28 ± 49 s), and invertebrates (3 ± 11 s), with no significant differences among the four latter categories. Feeding success also varied significantly across prey categories ($F_{4, 925}$ = 195.0; P < 0.001; Fig. 1). A post-hoc Tukey HSD test revealed that butterfish were significantly less likely to be swallowed (21 ± 41% swallowed) than herring (95 ± 23%), hake (98 ± 13%), other fish (79 ± 41%), or invertebrates (86 ± 35%), again with no significant differences among the four latter categories. Butterfish was the only prey category that did not exhibit a significant relationship between prey size and handling time (butterfish: r^2 = 0.05, P = 0.10; herring: r^2 = 0.13, P < 0.001; hake: r^2 = 0.03, P < 0.01; other fish: r^2 = 0.37, P < 0.01; invertebrates: r^2 = 0.12, P = 0.02).

Effect of butterfish on chick growth rate

Growth rate of individual Common Tern chicks was negatively associated with proportion of butterfish provisioned when analyzed using least-squares regression (â = −11.8, standard error [SE] = 2.3, t = −5.2, P < 0.01). There was no significant correlation between chick growth rate and overall feeding rate (â = 1.5, SE = 0.8, t = 1.8, P = 0.09). However, there was a significant negative association between growth rate and the interaction of butterfish proportion and overall feeding rate (â = −37.7, SE = 13.8, t = −2.7, P = 0.01; Fig. 2).

Variability in butterfish provisioning

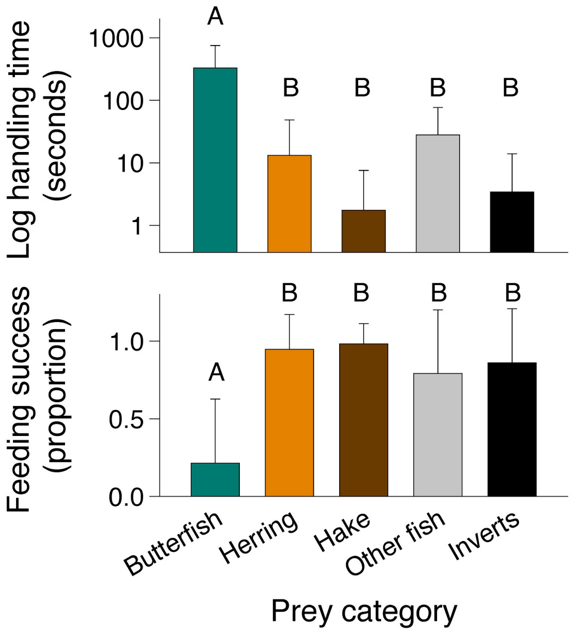
The number of butterfish relative to all other prey in chick diets varied across the three years (χ^2 = 54.7, degrees of freedom = 2, P < 0.01). We found a significant relationship between diet and nest ID in 2018 (P < 0.01) and 2019 (P = 0.04), but not in 2017 (P = 0.57) using a Monte Carlo version of Fisher's exact test.

When considering inter-nest variability in butterfish feeding for each year, the mean percentage (± SD) of chick diet that consisted of butterfish was 11 ± 13% in 2017 (ranging from 0–40%), 30 ± 30% in 2018 (ranging from 0–100%), and 4 ± 6% in 2019 (ranging from 0–20%; Fig. 3).

DISCUSSION

Common Tern chicks spent substantial time handling butterfish but infrequently gained nutritive rewards, with only 21% of butterfish being successfully swallowed (Fig. 1). Butterfish was the only prey category for which prey size had no significant effect on handling time.

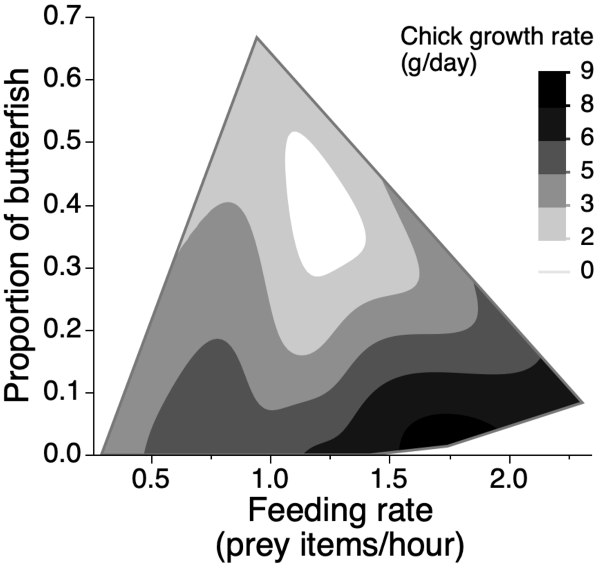
Fig. 1. Suitability of Atlantic butterfish (*Peprilus triacanthus*) and other prey categories in the diet of Common Tern chicks (*Sterna hirundo*) in the Gulf of Maine as measured by handling time (top; logarithmic scale) and feeding success (bottom). Different letters signify significant differences among prey categories according to Tukey HSD tests (P < 0.001 for both handling time and feeding success comparisons).



This result indicates that difficulty handling and ingesting butterfish is not a function of total length, but is likely driven by dorsoventral body depth, which, although not directly measured here, typically exceeded the gape of tern chicks across the range of butterfish sizes provisioned by adults. We also observed occasions during which chicks ignored other prey items offered to them while they were preoccupied handling butterfish, compounding nutritive costs of butterfish provisioning. Unconsumed butterfish were often discarded near the nest, where they were either picked up by a neighbor or left long enough to desiccate and decay.

Chicks that were fed higher proportions of butterfish had lower growth rates, likely due to the low probability of successful feeding and the associated energetic costs of long handling times. Although we expected to find that increased overall feeding rates would correlate with higher growth rates in chicks, we found this relationship to be positive but not significant. However, when considering the significant interaction between proportion of butterfish and overall feeding rate (Fig. 2), we found that increased feeding rates were associated with increased growth rate as expected, but only when proportions of butterfish in diets were low. When proportions of butterfish in diets were high, there was no association between feeding rate and chick growth. The association of butterfish provisioning with reduced growth rates in Common Tern chicks is particularly concerning, given the strong linkage between chick growth and survival in seabirds (Maness and Anderson 2013, Kress et al. 2017). Furthermore, post-fledging body mass has been linked to subadult survival in this species, and if chicks fail to put on weight prior to migration, we may see fewer young, prospecting birds returning to this colony in the future (Braasch et al. 2009).

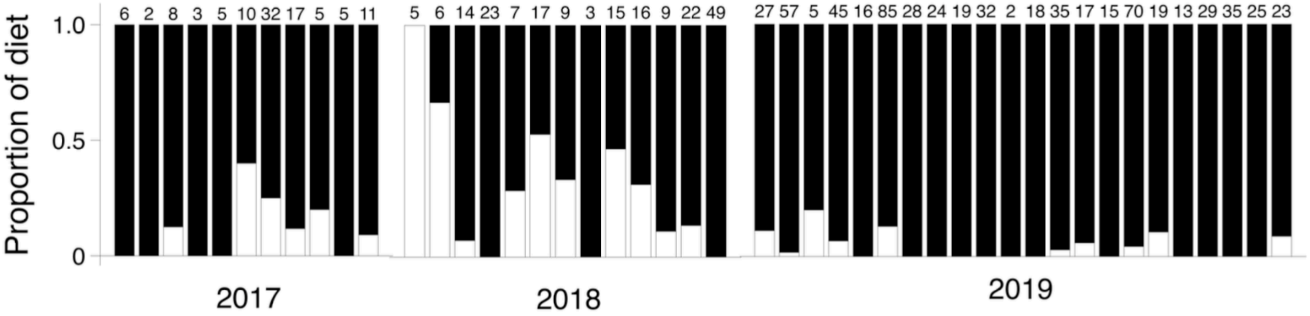
Fig. 2. Contour plot of chick growth rate (g/day) as it relates to overall feeding rate (feedings/h) and proportion of Atlantic butterfish (*Peprilus triacanthus*) in the diet of Common Tern chicks (*Sterna hirundo*) in the Gulf of Maine.



Given that butterfish appear to be highly unsuitable prey for tern chicks, the question remains as to why tern adults feed their chicks this fish. We speculate that when encountering juvenile butterfish on foraging grounds, adult terns may capture this fish because it appears similar to other common, high-quality prey such as juvenile herring and hake, which are similar in length and also laterally compressed. However, once captured, we would presume that the deep-bodied morphology of butterfish would be apparent to an adult tern. This mismatch led us to question whether adults are sensitive to prey suitability.

We quantified variability in butterfish provisioning within the sampled population and found that number of butterfish in diets varied significantly among nesting pairs in 2018 and 2019, although not in 2017 (potentially due to smaller sample size in that year; Fig. 3). This finding highlights that adult terns breeding on the same island during the same season feed their chicks significantly different diets. In all three years, there were breeding pairs that were never observed provisioning butterfish to their chicks, even in 2018, when the relative abundance of butterfish in the diet of terns at this colony was highest. Adult terns adjust the size of prey provisioned when foraging, depending on nutritive needs of nestlings (Quiring et al. 2021), and our results suggest they are species-selective as well. However, these signs of individual specialization may not signal active butterfish avoidance, but could be driven by numerous factors, including

Fig. 3. Proportion of Atlantic butterfish (*Peprilus triacanthus;* white), and other prey items (black) in the diet of Common Tern chicks (*Sterna hirundo*) in the Gulf of Maine in 2017, 2018, and 2019, with each bar representing a single nest, and the number of prey observations per nest recorded above each bar.



other characteristics of the prey field (e.g., the distribution and abundance of high-quality prey) as well as characteristics of individuals birds (e.g., age, sex, physiological fitness, and site fidelity; Phillips et al. 2017, Nisbet et al. 2020). While the actual mechanism of dietary variation at this colony is a topic of ongoing investigation, chicks of terns that capture fewer butterfish, by whatever mechanism, are at an advantage. This consequence provides some means for adaptive response in the face of shifting prey communities in the GOM, contingent on continued availability of suitable prey into the future.

CONCLUSION

The effect of butterfish on Common Tern chicks described here highlights the significant role that prey species composition plays in the reproductive outcomes of terns. Continued monitoring of tern diets will be key to evaluating how and whether these seabirds are able to respond to changes in their prey communities, which are simultaneously affected by climate change and commercial fishing in the GOM (Pershing et al. 2021). Seabird diet data such as those presented here can fill gaps in fish stock assessments (Sydeman et al. 2022), including GOM fisheries for butterfish and other common prey species (e.g., Atlantic herring; Scopel et al. 2018, Deroba et al. 2019). We additionally suggest that seabird diet data can contribute to a more holistic approach to fisheries management (e.g., ecosystem-based fisheries management; Pikitch et al. 2004) that incorporates the needs of predators such as seabirds (Townsend et al. 2019). Through such an approach, juvenile fishes that are important both commercially and ecologically (Pikitch et al. 2014) can be monitored and protected to sustain marine ecosystems as a whole (Pikitch et al. 2004).

Acknowledgments:

The handling of live birds was permitted under protocol #160403 approved by University of New Hampshire's Institutional Animal Care and Use Committee, and permit 06543 under the U.S. Geological Survey's Bird Banding Laboratory. We thank the Avian Ecology and Conservation editors and reviewers for their feedback. We thank A. Caldwell for comments on a previous version of this manuscript, and University of New Hampshire statistical consulting services for advice on statistical analyses. We thank M. Marchand (New Hampshire Fish and Game Department, Nongame and Endangered Wildlife Program) and J. Seavey (Shoals Marine Laboratory) for their leadership in New Hampshire tern conservation efforts. We thank field technicians C. Bowman, A. Caldwell, E. Ford, A. Litterer, and T. Ouellette for their assistance in monitoring tern diet and reproductive responses in the field. The Isles of Shoals Tern Conservation Program is supported by the New Hampshire Fish and Game Department's Nongame and Endangered Wildlife Program, the United States Fish and Wildlife Service New Hampshire State Wildlife Grants, and the Shoals Marine Laboratory. Findings and conclusions in this article are those of the authors and do not necessarily represent the views of supporting agencies. This paper is contribution 196 to the Shoals Marine Laboratory. The site of this study occupies N'dakinna, traditional homelands of the Wabanaki People. We recognize both their historical and contemporary presence in this area, in defiance of forced removal by colonizers.

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