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Commentary

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CONTRIBUTION OF DECLINING ANADROMOUS FISHES TO THE REPRODUCTIVE INVESTMENT OF A COMMON PISCIVOROUS SEABIRD, THE DOUBLE-CRESTED CORMORANT (*PHALACROCORAX AURITUS*)

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For female birds, reproduction is an energetically and nutritionally demanding process that is often constrained by proximate factors such as the availability of food and local environmental conditions (Perrins 1970, Martin 1987, Williams 2005). Clutch formation requires energy and other key resources for successful embryo development (Nager 2006). The daily protein investment alone has been estimated as 232% of the daily needs of a nonlaying female, in addition to large quantities of other essential resources such as lipids, calcium, and water (Meijer and Drent 1999, Nager 2006). To meet the steep demands of reproduction, many female birds rely on seasonally abundant resources (Winkler and Allen 1996, Siikamäki 1998). For the piscivorous coastal birds of New England, spawning anadromous fish are thought to fill this role.

New England is home to a variety of anadromous fishes that have historically migrated in large numbers between marine waters and coastal watersheds to complete their life cycles. This group includes iconic species such as Atlantic Salmon (*Salmo salar*), American Shad (*Alosa sapidissima*), and Rainbow Smelt (*Osmerus mordax*) as well as many others. Each spring, the region's coastal lakes and streams host the spawning runs of these species. For example, Alewife (*A. pseudoharengus*) and Blueback Herring (*A. aestivalis*), a group of anadromous clupeids collectively known as "river herring," typically aggregate in coastal lakes and streams to spawn from early March to early June (Walters et al. 2009). At the peak of the spawning run, they reach densities of 0.2–0.65 fish m^2 (Kissil 1974, Dalton et al. 2009). Their high density in these habitats and high caloric content make them a prey item with relatively high energetic payoff for consumers (Seefelt and Gillingham 2008). Moreover, their spawning runs generally coincide spatially and temporally with the breeding of many coastal birds (Poole 1989, Butler 1992) and provide a rich resource to many avian consumers striving to meet the peak metabolic demands of breeding (Nager 2006).

All of these fish species have historically been abundant in New England, but over the past century, dam building, habitat degradation, and commercial harvest have reduced the abundance of anadromous populations significantly: 91% of all studied anadromous fish stocks have declined, with 70% of stocks experiencing declines of 90% or more (Savoy and Crecco 1995, Limburg and Waldman 2009). River herring stocks exemplify this trend. Since 1985, commercial landings of river herring have fallen by >97%, from 6,000 to 143 metric tons (Atlantic States Marine Fisheries Commission [ASMFC] 1999, 2009). This decline is most likely attributable to some combination of direct fishing pressures, mortality incurred as bycatch (Kocik 2000), and predation by coastal predators such as cormorants (*Phalacrocorax* spp.) and Striped Bass (*Morone saxatilis*) (Savoy and Crecco 1995, Hartman 2003, Dalton et al. 2009). Three states in New England (Massachusetts, Rhode Island, and Connecticut) have reacted to this decline by enacting strict within-state harvest restrictions, in addition to a suite of interstate management measures aimed at protecting the remaining populations of river herring (ASMFC 2009). Currently, the full magnitude of this decline is still being realized and the broader ecological ramifications are poorly understood (Davis and Schultz 2009).

The results of previous studies indicate that anadromous fish like river herring make significant contributions to the diet of many of New England's coastal birds during reproduction. For example, breeding Double-crested Cormorants (*P. auritus*) consistently incorporate anadromous fish into their diet (Blackwell et al. 1995, 1997; Dalton et al. 2009). Ospreys (*Pandion haliaetus*; Poole 1989, Poole et al. 2002), Bald Eagles (*Haliaeetus leucocephalus*; Todd et al. 1982), and Red-breasted Mergansers (*Mergus serrator*; Stott and Olson 1973) have also been shown to consume a large proportion of the available river herring while breeding and nesting.

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Despite this clear evidence that coastal-breeding birds consume river herring and other anadromous fish (e.g., Todd et al. 1982, Poole et al. 2002), it is not clear how much influence the consumption of this particular prey has on the birds' reproductive success. Assessing the strength of this connection between consumption and reproduction is an essential next step in predicting how declines in anadromous fish will affect avian consumers. This information is urgently needed, because work in other regions such as the mid-Atlantic suggests that declines in a preferred prey can affect the distribution, diet, and population dynamics of avian consumers (Baker et al. 2004, Morrison et al. 2004, Viverette et al. 2007).

EXAMPLE FROM A COMMON PISCIVOROUS SEABIRD

Here, we evaluate the contribution of anadromous fish to the reproductive success of coastal piscivorous birds by focusing on the nutrients allocated for reproduction by the Double-crested Cormorant (hereafter "cormorant"). Like several previous authors (e.g., Fox et al. 1991, Kushlan 1993), we use the cormorant as a representative species for waterbirds because its diet is very similar to that of other predatory waterbirds, mixing locally abundant freshwater, estuarine, and marine fish species over a scale of several to several dozen kilometers from nesting sites. Though foraging behavior varies from species to species, all species share similar characteristics in selecting resources. We specifically chose to use the cormorant in this first assessment because of its relatively safe conservation status and colonial nesting behavior (Krohn et al. 1995).

We estimate the contribution of river herring to cormorant reproductive investments by measuring the naturally occurring stable-isotope ratios of cormorant egg material. Eggs provide a rich source of material for isotopic analysis and have previously been used to investigate the contributions of distinct prey items to the nutrients allocated for reproduction in cormorants and other piscivorous birds (Hobson 1995, 2006; Hobson et al. 2000). We combine stable isotope ratios from three elements, carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulfur ($^{34}S/^{32}S$) in a Bayesian mixing model (Moore and Semmens 2008, Jackson et al. 2009) to assess the relative contributions of the available prey groups to cormorant egg material. We take a comparative approach, contrasting the relative contribution of nutrients derived from river herring to eggs from colonies both near and far from substantial river herring runs. If river herring are an important resource for coastal breeding birds, we expect that they will contribute a large portion of the resources that cormorants allocate for reproduction and that their availability will dictate the degree to which they are utilized.

METHODS

Study site.—We chose two colonies of cormorants in southern New England as study sites (Fig. 1). Our site near a substantial river herring run was Long Ledge (41°29′N, 72°22′W), a small, rocky island off the central Connecticut coast that serves as a breeding ground for ~165 cormorant pairs (Dalton et al. 2009). Individuals nesting at this colony routinely forage at Bride Lake (41°33′N, 72°24′W), a 28.7-ha mesotrophic lake 4 km inland of Long Ledge that harbors one of the largest remaining Alewife runs in southern New England. Recent run sizes fluctuate between 67,000 and 130,000 adult fish (Walters et al. 2009), ~60% of the size of runs in the 1960s (Cooper 1961, Kissil 1974). At its peak, the spawning run attracts as many as 360 cormorants to Bride Lake per day (Dalton et al. 2009). Our second site, Spectacle Island (41°25′N, 72°80′W), is ~50 km west of Long Ledge. It is located a sufficient distance from a substantial river herring run to prevent nesting cormorants from efficiently preying on the aggregations of spawning fish. It therefore serves as a reference site where we expect that river herring will contribute negligibly to the reproductive investment of cormorants.

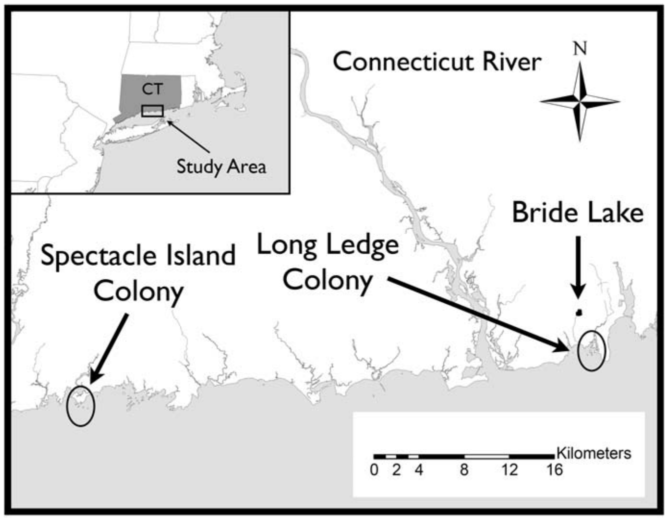

FIG. 1. Map showing the study area in Connecticut (inset: location in northeastern USA) and the two island colonies of Double-crested Cormorants, including the Long Ledge and Spectacle Island breeding colonies. Bride Lake, the site of a large Alewife spawning run, is shown in the bottom right.

Sample collection.—Eggs ($n = 16$) were collected on two sampling dates: 27 April and 7 May 2006. A single egg from each nest was wrapped in aluminum foil and placed on ice, then frozen within 6 h of collection (Gloutney and Hobson 1998). The freshness of each egg was determined visually, and, to minimize isotopic turnover, only eggs estimated to be in the first 10 days of incubation were subsequently analyzed. To develop isotopic values for potential prey groups, we collected a diverse array of local fish species, using diadromous-fish traps, boat electrofishing, trawling, and hook-and-line sampling. We collected prey species between March and June 2006 to avoid temporal mismatching of prey and predator samples (MacAvoy et al. 2001, Post 2002). All samples were collected under Connecticut Department of Environmental Protection Scientific Collection Permit number 0508021 and U.S. Fish and Wildlife Scientific Collection Permit MB103687-1.

Laboratory analysis.—Preliminary analysis of carbon and nitrogen isotope data indicated that they would not be sufficient to discriminate between marine and estuarine sources. Thus, samples were prepared and analyzed for naturally occurring stable isotope ratios of carbon, nitrogen, and sulfur. Because of the difficult and costly nature of assessing naturally occurring sulfur isotope ratios, including this element in our analysis slightly decreased our total sample size, but it greatly improved our ability to discriminate among marine, estuarine, and freshwater sources (Peterson et al. 1985, Connolly et al. 2004). Standard isotope techniques were used for sample preparation and analysis (Post 2002). Prey samples were dried at 45°C for >48 h and powdered whole using a freezer mill. For egg samples, the albumen and yolk were separated, dried, and powdered. To avoid possible bias, lipids were extracted from yolk samples using methanol-chloroform, and $\delta^{13}C$ values from all prey samples were corrected for lipid bias following Post et al. (2007). Isotope analysis was performed with a Thermo Finnigan Delta Plus Advantage stable-isotope mass spectrometer at the Earth Systems Center for Stable Isotope Studies (ESCSIS) at Yale Institute for Biospheric Studies. Isotope ratios are reported in relation to international standards. All stable isotope values are reported in delta notation, where $\delta^{13}C$, $\delta^{15}N$, or $\delta^{34}S = ([X_{\text{sample}}/X_{\text{standard}}] - 1) \times 1{,}000$ and X is ^{13}C:^{12}C, ^{15}N:^{14}N, or ^{34}S:^{32}S. Lipid-free yolk was used to determine $\delta^{13}C$ and $\delta^{34}S$, and nonextracted yolk was used to establish $\delta^{15}N$ values for the eggs following Hobson et al. (1997).

Isotopic calculations.—We assessed the relative contributions of the available prey sources to individual eggs and colony groups using the Stable Isotope Analysis in the R (SIAR) 4.0 package (Parnell et al. 2008, R Development Core Team 2009). This recently developed isotope mixing model builds on previous linear mixing models of Phillips and Gregg (2003) by using a Bayesian statistical framework (Moore and Semmens 2008, Jackson et al. 2009). The package essentially fits a mixing model using a Markov-chain Monte Carlo method, generating posterior probability distributions for each prey source's contribution to a predator mixture. This method capitalizes on the strengths of Bayesian statistics by explicitly incorporating variation in source and fractionation values, thereby providing a more precise estimate of the proportional contribution of sources to a given mixture.

For our analysis, individual prey items were grouped by location of collection and natural history into five aggregate end members: river herring, estuarine fish, freshwater fish, marine fish, and White Perch (*Morone americana*) (Table 1). Because marine fish and river herring had similar isotopic signatures (Fig. 2), we also included outside information in the form of an informative prior as a means of aiding analysis (Moore and Semmens 2008). Cormorants are noted income-breeders (Hobson 2006), and their maternal investments (e.g., egg material) should correspond to diet. Therefore, we used diet data obtained from pellets collected from Long Ledge colony between April and May 2006 to develop our prior for Long Ledge (see Dalton et al. 2009). We were unable to obtain diet data for Spectacle Island for 2006, so an uninformative prior was used for analysis of that population. Generally, the use of our prior for Long Ledge sharpened the peaks of our posteriors but did little to alter the means, which suggests that our isotope data were informative and drove our results.

A key assumption of stable isotope analysis is that the isotope ratios of a consumer's diet are translated into its tissues in a predictable fashion (Peterson and Fry 1987, Post 2002). To account for this, use of fractionation factors from related species

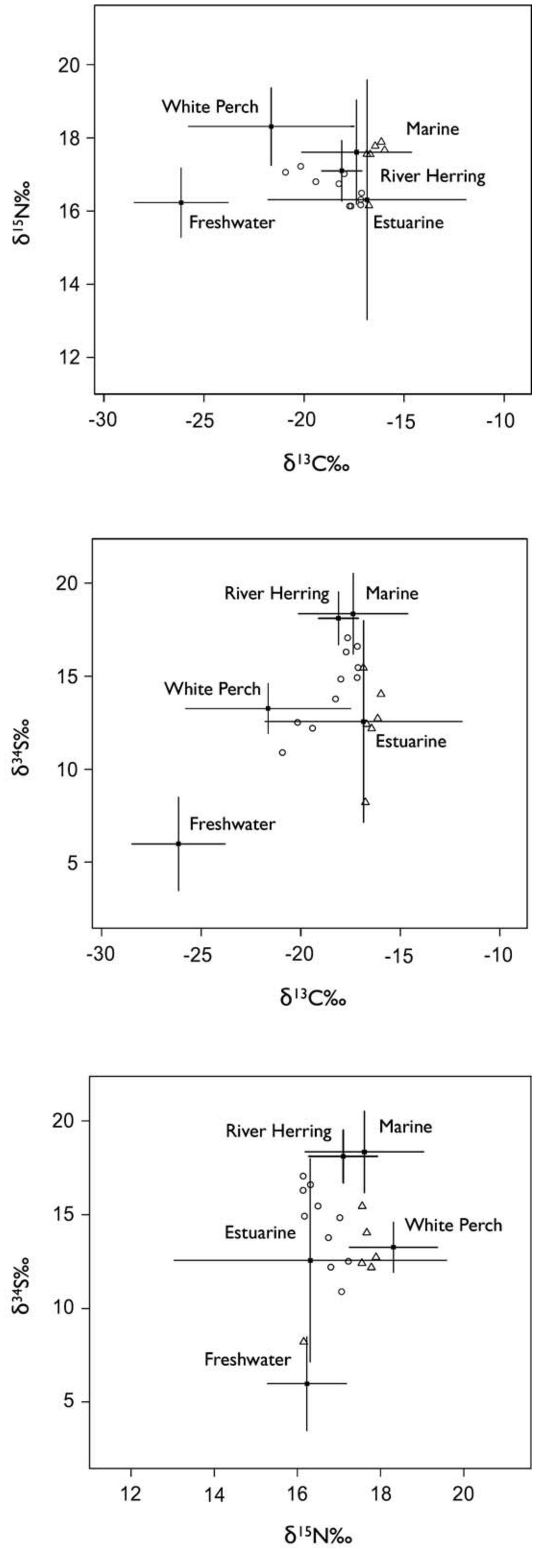

FIG. 2. SIAR model inputs showing means (± SD) for prey-group end members: river herring (n = 5), marine (n = 13) freshwater (n = 5), estuarine (n = 12), and White Perch (n = 5). Individual Double-crested Cormorant egg samples are also shown. Circles represent Long Ledge eggs and triangles Spectacle Island eggs. Egg values are corrected for trophic fractionation.

TABLE 1. Sample size, isotopic mean, and isotopic standard deviation for each prey-group end member. Prey groups are river herring (*Alosa pseudoharengus, A. aestivalis*), marine fish (*Pseudopleuronectes americanus, Stenotomus chrysops, Tautoga onitis, Tautogolabrus adspersus*), freshwater fish (*Fundulus diaphanus, Lepomis macrochirus, Micropterus salmoides, Perca flavescens*), estuarine fish (*Fundulus heteroclitus, Gasterosteus aculeatus, Menidia menidia, Peprilus triacanthus*), and White Perch (*Morone americana*).

Source	*n*	δ^{13}C	δ^{15}N	δ^{34}S
River herring	5	−18.11 (0.02)	13.6 (0.22)	17.61 (0.43)
Marine	13	−17.37 (1.28)	14.11 (0.62)	17.85 (0.93)
Freshwater	5	−26.14 (1.06)	12.73 (0.32)	5.48 (1.12)
Estuarine	12	−16.85 (2.42)	12.81 (1.60)	12.06 (2.65)
White Perch	5	−21.64 (2.01)	14.81 (0.40)	12.76 (0.37)

with comparable ecology has been advocated (Inger and Bearhop 2008). For δ^{15}N, we used estimates for the carnivore model derived by Hobson (1995; mean ± SD = 3.5 ± 0.35‰), because that study is the only published experimental report of fractionation factors between diet and egg tissues; this value agrees with the more general values for trophic fractionation (Post 2002, McCutchan et al. 2003). For δ^{13}C and δ^{34}S, isotopic fractionation values were also taken from the literature. The mean fractionation and standard deviations used for δ^{13}C are typically enriched but not significantly different from zero (Post 2002). We used fractionation values from lipid-free yolk of another carnivore of 0.0 ± 0.5‰ (Hobson 1995). Few published studies have explored fractionation of sulfur isotopes; we used 0.5 ± 0.56‰ for δ^{34}S, which is consistent with the existing literature (McCutchan et al. 2003).

To determine how variation in the fractionation values taken from the literature affected the output of the model, we performed a local sensitivity analysis (Appendix). The estimated mean contribution of each prey group to each colony changed little in response to a ±1 SD change in mean fractionation values. The largest change was to the estuarine fish contribution to Long Ledge eggs (−6.47%), in response to a decrease in the mean nitrogen-fractionation value. The estuarine fish and White Perch groups were consistently the most variable; however, all other changes were less than ±4%, and most were plus or minus 0–2%. These robust results are likely attributable to the fact that SIAR explicitly incorporates a range of fractionation values in its analysis.

RESULTS

We found that river herring were an important contributor to the eggs of cormorants nesting near large runs of anadromous Alewife. For the Long Ledge cormorant colony (the group near Bride Lake), nutrients derived from river herring represented the largest proportional contribution of all prey sources, with a mean posterior probability of 35% (range: 17–52% for the 5th and 95th percentiles; Fig 3A) for all eggs from the colony. The contribution of river herring to individual eggs was, however, somewhat variable. The lowest individual mean was 18% (range: 7–29%), for egg 5; and the highest individual mean was 52% (range: 27–75%), for egg 2.

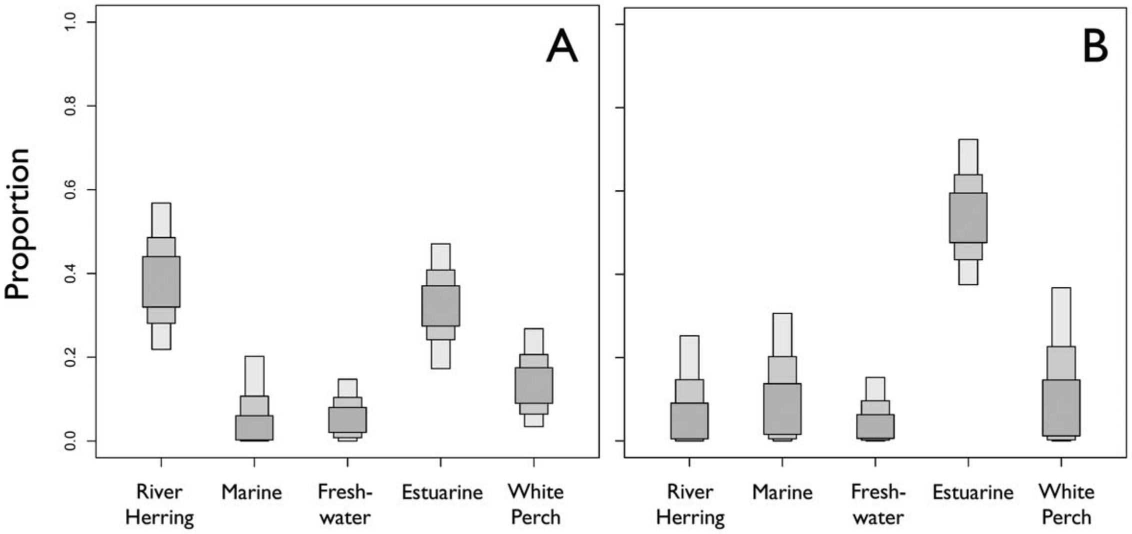

FIG. 3. Posterior probability intervals for prey-source contributions to Double-crested Cormorant egg samples from (A) Long Ledge and (B) Spectacle Island. The 95th (light gray), 75th (gray), and 50th (dark gray) percentiles are shown for individual eggs typical of the group (egg 4 and egg 15).

Estuarine fish made the second-largest contribution to Long Ledge eggs, with a mean contribution of 27% (range: 16–40%). Generally, fish that received nutrients from river herring also consumed a large proportion of estuarine nutrients. The highest contribution of estuarine nutrients was 39%, to egg 10 (range: 28–50%). The lowest contributions were 16%, to egg 6 (range: 3–28%), and 18%, to egg 5 (range: 4–36%).

The posterior distributions of the other three prey groups indicated lower proportional contributions. Freshwater fish contributed negligibly to 7 of 10 eggs, with a mean contribution across the colony of 11% (range: 6–16%). The mean contribution of marine fish was 10% (range: 0–25%), and the mean contribution of White Perch was 17% (range: 5–28%). The contribution of White Perch to individuals eggs was quite variable, with a contribution of >20% for half of the eggs (4, 5, 6, 7, and 8).

Generally, individuals from Long Ledge relied on river herring and estuarine fish for the bulk of their reproductive investments (on average 62%), with other prey categories making minor contributions to every egg. This pattern of resource contribution was consistent across the Long Ledge individuals except for eggs 5 and 6, which received greater-than-average contributions from both freshwater fish and White Perch.

For the Spectacle Island colony, where river herring are not locally abundant, we found a strikingly different pattern than that for Long Ledge. As expected, river herring were a small portion of the Spectacle Island colony's reproductive investments. The mean contribution of river herring to this colony was 11% (range: 0–26%) (Fig. 3B). Egg 11 had the largest contribution from river herring, with river herring making up 20% (range: 0–39%) Given that the range for the colony contains zero, it is possible that river herring did not contribute to Spectacle Island cormorant reproduction at all.

Spectacle Island eggs were composed primarily of estuarine fish, which contributed a mean of 54% (range: 6–63%) to eggs in the colony. The smallest percent contribution from estuarine resources to a Spectacle Island egg was 30% (range: 15–46), to egg 11. All other eggs from this colony were >50% derived from estuarine fish.

Marine fish were responsible for the second-largest contribution of the nutrients to Spectacle Island eggs, with a mean contribution of 17% (range: 2–34%). Both egg 11 (35%) and egg 13 (24%) received a larger-than-average portion of their nutrients from marine sources. The range for marine-source contributions was slightly larger than that for the estuarine fish, with mean contributions to individual eggs ranging from 4% to 35%.

Like the Long Ledge eggs, the Spectacle Island eggs received relatively few nutrients from freshwater prey, with a mean across all eggs of 6% (range: 0–14%). Freshwater prey made the smallest contribution to all eggs except egg 12, for which freshwater-derived nutrients made up 15% of the egg material. White Perch contributed slightly more than freshwater prey, with a mean contribution of 11% (range: 0–28%). White Perch contributed more to all eggs except egg 12, the opposite of the pattern for freshwater prey.

Between the two colonies, every source made a contribution to a few eggs. However, the range of a few sources consistently included zero, which suggests that the actual contribution of these sources to the egg may have been zero. This includes freshwater fish for both colonies, river herring and White Perch for Spectacle Island, and marine fish for Long Ledge cormorants.

DISCUSSION

Our study is the first to demonstrate that where river herring are available, they are the principal source of nutrients allocated for reproduction by breeding cormorants. Every egg from the colony near the large river herring run (Long Ledge) contained a high percentage nutrients derived from river herring (colony mean = 35%; individual mean range: 18–52%). This is consistent with the results of previous studies that identified river herring as a potentially important prey for cormorants and other coastal birds of New England (Stott and Olson 1973, Todd et al. 1982), including a previous study of the Long Ledge colony that found that river herring composed 43% of the diet (by weight) of cormorants during the breeding period (Dalton et al. 2009). Our study goes one step further, directly linking consumption of river herring to reproductive investment in eggs, and establishes a clear link between river herring abundance and cormorant reproduction.

In contrast to our samples from Long Ledge, those from the colony located farther from a substantial river herring run (Spectacle Island) contained a considerably lower proportion of nutrients derived from river herring (colony mean = 11%; individual mean range: 0–26%). This indicates that where river herring are absent, cormorants subsidize their diet with alternative prey to compensate for the 35% of egg nutrients that would otherwise come from river herring. The majority of this difference is recovered by consuming estuarine fish, for which the average percent incorporation doubled, increasing from a mean of 27% at Long Ledge to 54% at Spectacle Island. Although the caloric content and local density of prey items such as these vary throughout the year, data from Dalton et al. (2009) suggest that in the spring, estuarine fish have an energy density that is 20% lower, on average, than that of river herring. Moreover, local densities of estuarine fish are two orders of magnitude lower, on average, than that of spawning Alewife (Hughes et al. 2002). Both of these factors make estuarine fish much less profitable to foraging cormorants.

Together, these two results suggest that the decline of anadromous fish populations could detrimentally affect New England's waterbirds. Reproduction is a period of peak metabolic demand (Nager 2006), and decreasing resource availability during this period might negatively affect their reproductive success by limiting egg production or by reducing resources available for incubation and nestling provisioning (Martin 1987, Nilsson and Svensson 1993). For New England's cormorants, a reduction in egg production is most likely attributable to the close matching of the phenology of egg laying and river herring migration. For other species with slightly different schedules (e.g., Bald Eagles, which lay in early March), the loss of river herring prey may affect other portions of their reproductive budgets, such as chick rearing.

Research in the Pacific Northwest has directly linked the abundance of anadromous fish to the diet and behavior of >40 vertebrate consumers (Willson et al. 1998) and has demonstrated direct effects of salmon numbers on the fitness of key regional consumers (Ainley et al. 1994, Merrick et al. 1997, Roth et al. 2007). Although we argue that a similar link exists between river herring and coastal waterbirds because of the energetic payoff of river herring and phenological matching of their migration to waterbird breeding, establishing a direct connection between anadromous fish and waterbird fitness remains a research need in these ecosystems.

Although we have focused on the Double-crested Cormorant, a species of low conservation concern (Krohn et al. 1995), our results suggest that access to river herring is likely important to the other regional avian consumers, many of which are of regional conservation concern, including Osprey, Bald Eagle, herons (*Ardea* spp.), and egrets (*Egretta* spp.). We suggest that our research serve as a charge to establish an empirical link between anadromous fish and their fitness effects for waterbirds of conservation concern in New England.

Our findings suggest that declining populations of anadromous fish will likely have important effects on coastal ecosystems. Not only will the decline mean a loss of nutrient subsidies for freshwater systems that come from river herring gametes, carcasses, and excretion (Durbin et al. 1979, Garman and Macko 1998, Post and Walters 2009, Walters et al. 2009), but shifts in predation pressure by cormorants and other predators could potentially affect community and ecosystem dynamics (Hartman 2003, Rudstam et al. 2004). We have provided strong evidence that the consumption of estuarine fish by cormorants without access to river herring is roughly double that of cormorants with access to river herring runs. Given the broad importance of anadromous fish to consumers (Gende and Willson 2001, Obermeyer et al. 2006, Christie and Reimchen 2008), it is likely that their continued decline will have a variety of serious implications for New England's coastal ecosystems.

Acknowledgments

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Appendix. Results of the local sensitivity analysis. Values shown are percent changes in SIAR estimates resulting from a change of ±1 SD in each fractionation value from its mean.

		ΔC		ΔN		ΔS	
	Source	+1 SD	−1 SD	+1 SD	−1 SD	+1 SD	−1 SD
Long Ledge	River herring	−0.25	−0.20	−1.05	0.47	−2.56	2.80
	Marine	−0.21	−0.16	−1.19	2.55	−0.80	0.78
	Freshwater	2.75	−1.69	−0.21	−0.45	1.28	−1.04
	Estuarine	−3.37	2.41	3.58	−6.47	1.44	−2.09
	White Perch	1.08	−0.36	−1.12	3.89	0.64	−0.45
Spectacle Island	River herring	1.14	−0.74	1.31	−1.24	−0.13	0.05
	Marine	2.62	−1.94	−1.98	−0.20	−0.46	0.27
	Freshwater	−2.34	2.26	1.22	−0.79	0.82	−0.98
	Estuarine	1.56	−3.41	3.21	0.01	−0.66	1.02
	White Perch	−2.97	3.83	−3.76	2.22	0.43	−0.36