

# The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central Connecticut, USA

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**Abstract:** The decline of anadromous alewife (*Alosa pseudoharengus*) threatens an important recreational and commercial fishery. While the cause of this decline is uncertain, predators could be trapping alewives at low abundance by preying on them during spawning migrations. Here we investigate the impact of predation by double-crested cormorants (*Phalacrocorax auritus*) on spawning adult alewives in south-central Connecticut, USA. We use a bioenergetic model together with estimates of cormorant diets and cormorant and alewife population sizes to estimate the consumption of alewives by cormorants both in Bride Lake, Connecticut, and regionally. We find that cormorants are important predators of spawning adult alewives at Bride Lake but do not have a notable impact on alewife mortality or population size. We also find that cormorants have little effect on alewife populations across south-central Connecticut because few alewives are consumed away from Bride Lake. We conclude that cormorants are important predators for anadromous alewives, but do not pose an immediate threat to the recovery of regional alewife stocks.

**Résumé :** Le déclin de gaspareau anadrome (*Alosa pseudoharengus*) menace une importante pêche sportive et commerciale. Bien que la cause du déclin soit incertaine, les prédateurs pourraient s'emparer des gaspareaux dans les conditions de basse densité en les capturant durant leur migration de fraie. Nous examinons ici la prédation par les cormorans à aigrettes (*Phalacrocorax auritus*) sur les gaspareaux adultes en fraie dans le centre-sud du Connecticut, É.-U. Un modèle bio-énergétique combiné à des estimations du régime alimentaire des cormorans et des densités des populations de cormorans et de gaspareaux nous a servi à estimer la consommation de gaspareaux par les cormorans à la fois dans le lac Bride, Connecticut, et dans la région avoisinante. Les cormorans sont d'importants prédateurs de gaspareaux adultes pendant la fraie au lac Bride, mais ils n'ont que peu d'effet marqué sur la mortalité ou la taille de la population de gaspareaux. Les cormorans ont aussi peu d'effet sur les populations de gaspareaux dans tout le centre-sud du Connecticut, parce que peu de gaspareaux y sont consommés sauf au lac Bride. En conclusion, les cormorans sont d'importants prédateurs des gaspareaux anadromes, mais ils ne représentent pas une menace immédiate pour la récupération des stocks régionaux de gaspareaux.

[Traduit par la Rédaction]

## Introduction

Anadromous alewife (*Alosa pseudoharengus*) are of notable ecological, economic, and historical importance in eastern North America. They impact freshwater ecosystems by importing marine-derived nutrients (Durbin et al. 1979; Garman and Macko 1998; MacAvoy et al. 2000) and structuring prey communities through predation (Post et al. 2008). The inshore fishery for anadromous alewives dates to precolonial times, and the offshore fishery, still a large source of bait for

Atlantic cod (*Gadus morhua*) and American lobster (*Homarus americanus*) fishermen, once landed nearly 25 000 mt annually (Munroe 2002).

Probably because of intense fishing pressure, alewives have declined throughout their native range since the 1960s (Munroe 2002). Several states have outlawed taking anadromous alewives, others are considering similar restrictions, and the US federal government has listed anadromous alewives as a species of concern across their range. Alewife stocks have continued to decline even as resource managers spend millions to restore anadromous fish spawning habitat. Managers suspect that bycatch from the Atlantic herring (*Clupea harengus*) fishery or predation by inshore predators is keeping alewife stocks at low abundance (Savoy and Crecco 1995).

Striped bass (*Morone saxatilis*) and double-crested cormorants (*Phalacrocorax auritus*, henceforth referred to as cormorants) are abundant inshore piscivores that could be preventing alewife recovery (Savoy and Crecco 1995). Striped bass and cormorant populations have increased dramatically in the past 20 years, and both species are more abundant now than ever in recent history (Wires et al. 2001; Hartman 2003). Hartman (2003) estimated that striped

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bass in the Hudson River could consume all of the young-of-the-year river herring (alewife and the closely related blueback herring, *Alosa aestivalis*) produced annually in that watershed, suggesting alewife population decline could be caused by increasingly abundant natural predators. Cormorants are also prodigious predators of fish and, where abundant, may impact alewife populations. Numerous studies have shown that cormorants can impact fish populations by altering population dynamics (Burnett et al. 2002; Rudstam et al. 2004), consuming a large proportion of the known population size (Derby and Lovvorn 1997), or by adding substantial incremental mortality to other known sources (Hebert and Morrison 2003; French McCay and Rowe 2004).

Blackwell et al. (1995, 1997) found that anadromous fish, including alewives, comprised a major but highly variable portion of the cormorants' diet in coastal Maine. We expect that based on their opportunistic foraging strategy (Hatch and Weseloh 1999), cormorants will feed heavily on alewives where spawning runs predictably concentrate thousands of fish in small bodies of water. The extent of such predation remains to be quantified.

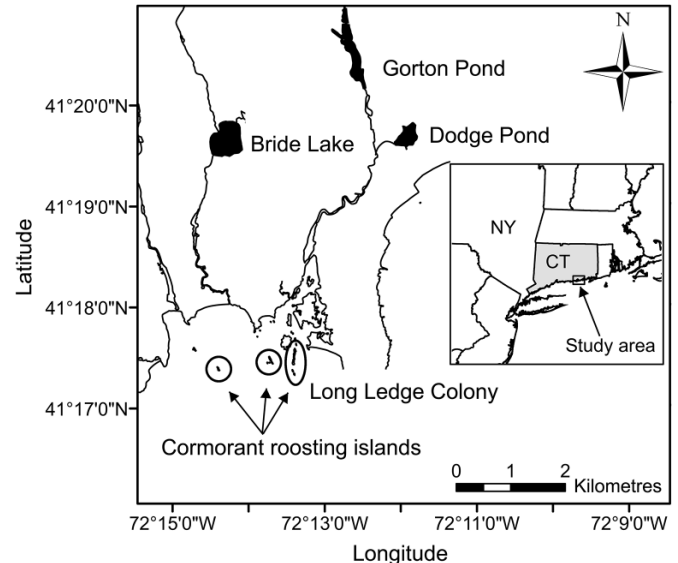
Here, we use a bioenergetic model to estimate the consumption of anadromous alewives by cormorants. The energetic model uses literature estimates of the daily per-cormorant energy intake and direct observation of cormorant population size, diet composition, and prey energy density. We focus our study on Bride Lake, in southern Connecticut, USA, one of the largest remaining alewife runs in Connecticut and host to large flocks of feeding cormorants during the alewife spawning season. Historical and current studies at Bride Lake provide detailed data on the lake's alewife population before and after the recent increase in local cormorant abundance (Kissil 1974; Davis 2004; Post et al. 2008). We use this data in conjunction with cormorant consumption estimates to obtain a high-resolution estimate of the magnitude and impact of cormorant predation on alewives at this lake. We then consider the implications of our result for the sustainability of regional alewife populations.

## Materials and methods

### Study site

Bride Lake is an 18.2 ha, 10.7 m deep (maximum depth) lake located in East Lyme, Connecticut (Fig. 1; Kissil 1974). There is no public access to Bride Lake because it is surrounded by two correctional facilities and a water treatment plant. The alewife run at Bride Lake is one of the largest remaining in Connecticut, and anadromous alewives obtain access to the lake by Bride Brook, a 3.5 km stream that empties into Long Island Sound at Rocky Neck State Park, Niantic, Connecticut. Daily counts of in-migrating alewives, obtained from the Connecticut Department of Environmental Protection, were made by hand in 2003 and 2004 and by electronic fish counter (Smith-Root, SR-1601) in 2005 and 2006. The fish counter was calibrated against hand counts in 2005. Hand counts were performed using a weir in Bride Lake, upstream of the fish counter, to collect in-migrating alewives. Every 24 h, alewives were picked from the weir by hand net, counted, and then moved into Bride Lake. The weir remained in place throughout in-migration, preventing

**Fig. 1.** Map showing the study area in Connecticut (inset: location in northeastern USA), including the focal alewife (*Alosa pseudoharengus*) run at Bride Lake, as well as nearby runs at Dodge Pond and Gorton Pond. The three roosting islands for double-crested cormorants (*Phalacrocorax auritus*) feeding at Bride Lake (including the Long Ledge breeding colony) are illustrated in the lower left portion of the map.



spawned-out alewives from leaving Bride Lake until in-migration was complete. The end of in-migration was determined based on historical run dates and daily in-run counts. Several days separated the end of in-migration and the beginning of out-migration. We will refer to the 24 h count of alewives entering Bride Lake as the daily escapement.

The annual alewife mortality in Bride Lake was determined by subtracting the count of alewives leaving Bride Lake from total annual escapement. The count of alewives leaving Bride Lake was obtained from the Smith-Root counter after the weir was removed. Because of concern that unusually high flow might endanger out-migrating alewives (a local and USA federal species of concern), we have no similar estimate of mortality in 2006.

We studied cormorants both at Bride Lake and at several nearby islands in Long Island Sound (Fig. 1). These islands are unvegetated, rocky outcroppings less than 4.0 km from Bride Lake. One of these islands, Long Ledge, serves as a breeding colony for 155–170 pairs of cormorants, while all other islands are used as roosts by nonbreeding cormorants.

### Cormorant population estimates

We separately estimated the number of cormorants feeding at Bride Lake and the number of cormorants that potentially could feed at Bride Lake. Estimates of the number of cormorants feeding at Bride Lake were made in both 2005 and 2006 by shore-based observers using binoculars and a spotting scope. In 2005, we performed counts at least once a week between 8 April and 1 May, and in 2006 we performed these counts at least once a week between 5 March and 22 May and at least twice a week between 22 March and 7 May. Counts were performed continuously for several hours. Between 2 h after sunrise and 2 h before sunset, the

count of cormorants on Bride Lake never varied by more than 10 birds. We also surveyed cormorant abundance at two nearby alewife spawning sites (Dodge Pond and Gorton Pond) on each Bride Lake count date. These counts were conducted at the beginning and end of each Bride Lake count and frequently once in the middle of the count as well.

The number of cormorants within foraging range of Bride Lake (henceforth referred to as the local cormorant population) was assessed in 2006 by counting the number of cormorants roosting within 20 km of Bride Lake (studies on the Great Lakes, e.g., Neuman et al. 1997) show that most cormorant foraging occurs within this distance of breeding colonies). These counts included breeding birds on Long Ledge, as well as migrant cormorants roosting on other islands. These birds represented all cormorants feeding in bodies of water near or on the Connecticut shoreline between the Niantic and Connecticut rivers.

Daily cormorant movements were assessed by visual observation. Throughout the spawning season, cormorants were observed leaving roosting islands at dawn and returning at dusk. Because of the proximity of Bride Lake and Long Ledge, cormorants could be observed throughout the flight between the two sites at both dawn and dusk. We never observed a cormorant leave Bride Lake and fly to any roosting site not included in our observations.

### Cormorant diets

We estimated the diet of the local cormorant population based on otoliths recovered from cormorant pellets collected at roosts. The identification and measurement of otoliths from cormorant pellets is a method biased by otolith wear and unpredictable retention (Harris and Wanless 1993; Blackwell et al. 1995; Leopold et al. 1998). Nonetheless, we chose to use this method because it is minimally invasive and less prone to spatial and temporal sampling bias per unit effort than other methods, such as stomach dissection or flushing (Harris and Wanless 1993; Votier et al. 2003, reviewed in Wires et al. 2001).

Cormorant pellets were collected from West Brother Island on 9 April ( $n = 28$ ), 27 April ( $n = 38$ ), and 7 May 2006 ( $n = 21$ ). We were unable to find cormorant pellets at other roosting sites in the study area. We chose these three dates to represent the cormorant diet before (9 April), during (27 April), and after (7 May) the peak of alewife abundance in Bride Lake. We collected each pellet in a separate zip-lock bag and preserved all pellets at  $-20\text{ }^{\circ}\text{C}$  within 4 h of collection. For analysis, we dissolved each pellet in  $1.0\text{ mol}\cdot\text{L}^{-1}$  NaOH for 24 h and removed all of the otoliths from each pellet under a dissecting microscope. We paired as many otoliths as possible from each pellet according to the specific identity, measured size, and whether the otolith was from the right or left side of the fish. We identified each otolith or pair of otoliths to the lowest possible taxon using several guides to otoliths of Atlantic fishes (Broudeur 1979; Harkonen 1986; Campana 2004) and a reference collection of otoliths from 27 species of freshwater, estuarine, and marine fish that we considered potential food sources for cormorants.

For analysis, we regarded either a pair of otoliths or one unpaired otolith as representative of a single fish in the cor-

morant diet. We measured the total length of each otolith or otolith pair using an optical micrometer. We defined total otolith length as the straight-line distance between the furthest extents of the otolith along its anterior–posterior axis. We estimated the total length (TL) of the consumed fish using taxon-specific otolith length – TL regressions, which we calculated from measurements of reference specimens and published data (Appendix A, Table A1). We then estimated the weight (FW, in g) of each consumed fish using TL–FW regressions from our reference collection and published sources (Appendix A, Table A1). We did not calculate FW for unknown otoliths (<5% of all collected otoliths) and non-fish food items (two unidentified shrimp). For the local cormorant population's diet, we estimated the proportion by weight and frequency of occurrence of each fish taxon for each of our three sampling dates.

To account for the effect of digestive wear on fragile alewife otoliths, we used a linear scalar to correct the average estimated alewife length in the cormorant diet upwards to match that of alewives found entering Bride Lake. We did not perform this correction on other diet items, the otoliths of which are less prone to digestive erosion.

In both 2005 and 2006, we sampled the fish community of Bride Lake using purse seines, beach seines, gill nets, and hook and line. Personnel from Connecticut Department of Environmental Protection monitored the movement of fish in and out of the lake on a daily basis. All of the fish species found in or moving into Bride Lake taken together (excluding alewives) accounted for less than one percent of the diet of cormorants roosting nearby. This result strongly suggests that while cormorants may consume a few freshwater fish at Bride Lake, the vast majority of their diet there is alewife.

### Bioenergetics model

We estimated the consumption of alewives both by cormorants at Bride Lake (2005 and 2006) and by the local population of cormorants (2006 only). Our consumption estimates are based on the daily energy intake of a single cormorant, daily estimates of cormorant population size, the empirically determined energy density of prey items, and the proportion of the cormorants' diet composed of alewife.

We estimated the daily energy intake of a single cormorant using a model for daily energy expenditure, or field metabolic rate (FMR), of seabirds (Ellis and Gabrielsen 2002) and a digestive efficiency factor from Brugger (1993). We multiplied this energy intake by daily estimates of cormorant population size at Bride Lake and Long Ledge, using linear interpolation to estimate population between actual counts. This total daily energy intake (kJ) was divided by prey energy density ( $\text{kJ}\cdot\text{g}^{-1}$ ) to calculate total daily fish consumption (g, wet mass). Total alewife consumption was then estimated by multiplying fish consumption by the cormorant diet proportion composed of alewives.

We created maximum and minimum estimates for each model input to produce the widest possible range of consumption estimates. Each estimate of alewife consumption was recalculated using all minimum values and all maximum values for model inputs (Table 1). (For more detail on our energetics modeling approach, see Appendix B.)

**Table 1.** Parameter estimates and range of variation in parameter estimates (minimum–maximum values) used in bioenergetics models.

| Input  | Midpoint used                   | Min. and max. values                 |
|--|---------------------------------|--------------------------------------|
| Cormorant body mass (g)                        | 2050 <sup>a</sup>               | 1861 <sup>b</sup> –2442 <sup>b</sup> |
| FMR (kJ·cormorant <sup>-1</sup> ) <sup>c</sup> | 2390 <sup>d</sup>               | 1581 <sup>e</sup> –3817 <sup>d</sup> |
| Count  | Direct counts and interpolation | ±10% <sup>g</sup>                    |
| Digestive efficiency                           | 0.779 <sup>f</sup>              | 0.75–0.79 <sup>f</sup>               |
| Alewife energy density (kJ·g <sup>-1</sup> )   | 5.86                            | 5.71–6.01 <sup>g</sup>               |
| Alewife body mass (g)                          | 152                             | 147–158 <sup>g</sup>                 |

<sup>a</sup>Glahn and Brugger 1995.<sup>b</sup>Kury 1969.<sup>c</sup>Field metabolic rate.<sup>d</sup>Ellis and Gabrielsen 2002.<sup>e</sup>Gremillet et al. 2003.<sup>f</sup>Brugger 1993.<sup>g</sup>± standard error.

## Results

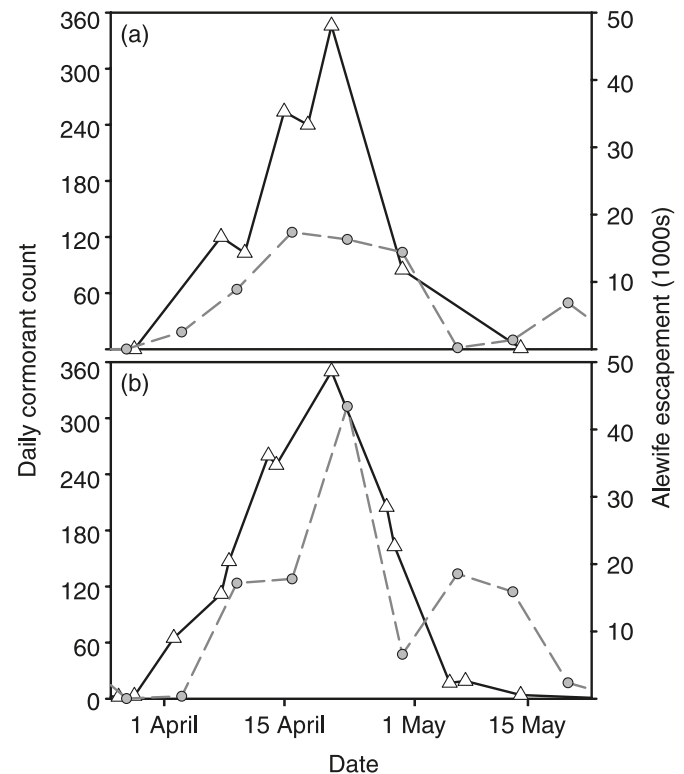
### Cormorant and alewife populations

The number of cormorants feeding at Bride Lake was similar in 2005 and 2006 (Fig. 2). In both years, cormorants began feeding at the lake around 1 April, were most abundant (about 350 birds) around 22 April, and were largely gone by 10 May. Daily counts averaged 5% higher in 2006 than in 2005. The number of cormorants roosting on islands near Bride Lake (2006 only; not illustrated) largely paralleled the trend at the lake itself, but peaked later, at 600 cormorants, on 29 April.

Cormorants that fed at Bride Lake during the alewife spawning season spent most of the available daylight on the lake. Their abundance there was consistent from midmorning until early evening. Flocks typically foraged in three feeding bouts: morning, midday, and early evening. Each feeding bout lasted between 1 and 2 h. Between bouts, cormorants rested on the lake surface or in trees overhanging the lake. Most birds departed the lake in flocks immediately after the third foraging bout, at the end of the day. All flocks were observed flying directly from Bride Lake to the studied roosting sites in Long Island Sound. At dawn, flocks of some cormorants, though not all at the roosting site, were observed flying directly to Bride Lake from Long Ledge. Cormorant abundance at other nearby alewife runs never approached that at Bride Lake, with no more than 10 birds on Dodge Lake or Gorton Pond at any time.

Total annual alewife escapement into Bride Lake was 116 851, 81 350, 68 761, and 129 114 in 2003, 2004, 2005 and 2006, respectively (mean across all years = 99 019). Escapement was nearly twice as high in 2006 as in 2005, with much of that additional escapement occurring during 7–10 May. No similar late peak in escapement occurred in 2005. In 2005, and for most of 2006, cormorant abundance at Bride Lake closely tracked daily alewife escapement (Fig. 2). In 2006, however, there was no late peak in cormorant abundance to match the substantial movement of alewives into Bride Lake from 7 to 10 May. In 2005, the overall mortality rate for adult alewives in Bride Lake was 62% (42 888 fish).

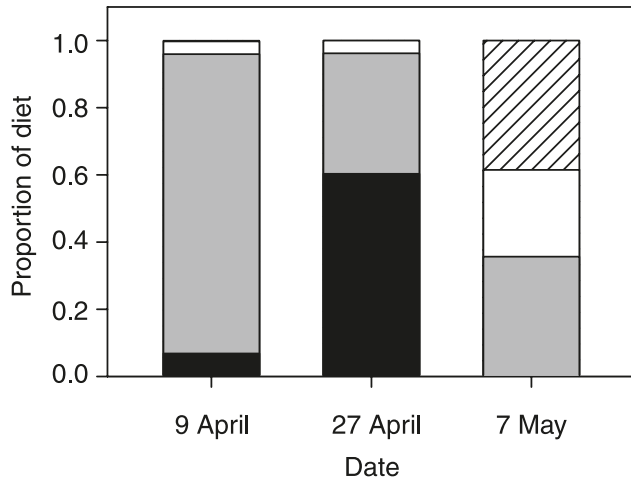
**Fig. 2.** Comparison of alewife (*Alosa pseudoharengus*) escapement and double-crested cormorant (*Phalacrocorax auritus*) abundance at Bride Lake in 2005 (a) and 2006 (b). Alewife counts (circles, broken line) represent the total number of alewives entering Bride Lake in the previous 7 days. Cormorant counts (triangles, solid line) represent actual full-day cormorant counts made at Bride Lake on each demarked date.



### Cormorant diet

In 2006, we assessed the diet of cormorants roosting on islands within foraging range of Bride Lake (the local cormorant diet). Before the peak in alewife abundance at Bride Lake, alewives made up a small proportion of the local cormorant diet (7% by weight, frequency = 0.25). During the

**Fig. 3.** The estimated diet of cormorants (*Phalacrocorax auritus*) roosting near Bride Lake. The estimated diet is the proportion (by weight) of fish eaten by cormorants roosting near Bride Lake and is presented for alewife (*Alosa pseudoharengus*; black), white perch (*Morone americana*; gray), marine fish (open), and other freshwater fish (hatched).



height of the alewife run, alewives made up more than half (60% by weight, frequency = 0.67) of the local cormorant diet. By 7 May, however, pellets collected from cormorant roosts contained no evidence of alewives (Figs. 3, 4).

For the entire sampling period, white perch (*Morone americana*) were the most abundant fish by weight in the local cormorant diet (Figs. 3 and 4). White perch were most prevalent in early April (89% by weight, frequency = 0.63), but were less abundant at each subsequent sampling date. Other freshwater fish species were never more than a minor portion of the diet of these cormorants. Saltmarsh fish species (*Fundulus* spp. and *Menidia menidia*) and other marine fish were increasingly abundant in cormorant diets through the spring sampling period, but never accounted for more than 25% of fish consumed (by weight; Fig. 3).

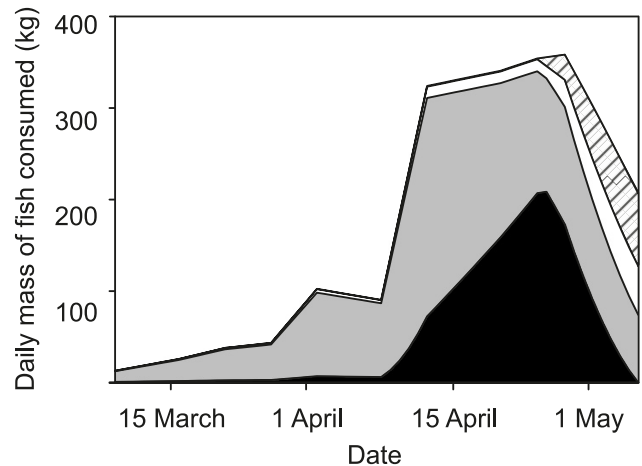
Our intensive fish sampling efforts in Bride Lake found alewives, bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), white sucker (*Catostomus commersonii*), and banded killifish (*Fundulus diaphanus*) in the lake. All of these species together (excepting alewives) accounted for less than one percent of the fish eaten by cormorants roosting near Bride Lake in 2006. We found no evidence of white perch in Bride Lake, but they are common in the Connecticut River, a nearby river where flocks of cormorants from this population feed.

#### Cormorant consumption and alewife mortality estimates

We estimate that cormorants at Bride Lake consumed 20 687 alewives in 2005 (range 11 417–39 923) and 23 705 alewives in 2006 (13 083–45 747). At Bride Lake, cormorant consumption of alewives increased 15% from 2005 to 2006; however, the proportion of alewives entering Bride Lake that were consumed by cormorants decreased from 30% in 2005 to 18% in 2006. In 2005, we estimate that 48% of overall alewife mortality was caused by cormorants.

In 2006, we estimate that all cormorants roosting within

**Fig. 4.** The daily estimated fish consumption by cormorants (*Phalacrocorax auritus*) roosting near Bride Lake. Consumption is estimated for alewife (*Alosa pseudoharengus*; black), white perch (*Morone americana*; gray), marine fish (open), and other freshwater fish (hatched).



foraging range of Bride Lake (the local cormorant population) consumed 22 954 (range 10 797–49 968) alewives. This estimate was 3% lower than our estimate for cormorants at Bride Lake alone in the same year. This result strongly suggests that cormorants roosting near Bride Lake obtain few alewives at other runs (despite the presence of several nearby).

#### Discussion

Cormorants are major predators of alewives at Bride Lake. We estimate that cormorants on Bride Lake consumed 20 687 (11 417–39 923) and 23 705 (13 083–45 747) adult alewives in 2005 and 2006, respectively, which represents 30% (17%–58%) and 18% (10%–35%) of the alewives spawning in Bride Lake in those years and 48% (27%–93%) of the overall mortality in 2005. The arrival of large flocks of cormorants at Bride Lake in spring is concurrent with the escapement of the largest schools of alewives. From our observations on the local cormorant diet, the diversity of fish in Bride Lake, and cormorant feeding strategies, we conclude that large flocks of cormorants use Bride Lake to exploit the high density of alewives there in spring.

Though cormorants are important predators of alewives at Bride Lake, our results suggest that they are not an immediate threat to alewife populations, both at Bride Lake and regionally. In the mid-1960s, when cormorants were largely absent from Connecticut, Kissil (1974) estimated that alewife spawning mortality at Bride Lake was 53%. This estimate was obtained from 2 years of visual counts of alewives entering and leaving Bride Lake at a fish ladder. Assuming that background mortality of alewives is density-independent, we can estimate the maximum potential mortality impact of cormorants by adding their consumption (20 687) to the 53% background rate (36 601). This approach estimates the hypothetical, completely additive mortality as 83% (57 289 alewives). This estimate is substantially higher (14 401 alewives) than the recorded mortality of 62% (42 888 ale-

wives). Comparing the recorded alewife mortality in 2005 with Kissil's estimate of background mortality suggests that only 6286 of the alewives consumed by cormorants are additive to background mortality. Based on a total consumption of 20 687 alewives, this result suggests that 70% of cormorant consumption is compensatory to background rates. Further, though cormorants consume a large proportion of spawning alewives, O'Gorman et al. (2004) have shown that alewives can produce very large year classes at low density. Thus, even a greatly reduced number of spawning adult alewives could produce a relatively large number of young of the year. This inference, combined with the mortality rate data from Bride Lake, strongly suggests that predation by cormorants is not the single cause of declining alewife escapement at Bride Lake.

Our observations also suggest that cormorants do not impact regional alewife populations. Cormorants are absent from other local spawning lakes (Dodge and Gorton ponds), and our diet analysis shows that consumption by all cormorants within foraging range of Bride Lake is no greater than that at Bride Lake alone. Even if cormorants from beyond the normal foraging range fed at Bride Lake (not supported by our observations), this pattern would indicate that the impact of cormorants along an even longer stretch of the Connecticut coastline was no greater than that at Bride Lake alone. Since cormorants do not appear to have greatly impacted the alewife population at Bride Lake, where the concentration of cormorants is extraordinary, we consider it very unlikely that they impact alewife populations elsewhere. Cormorants could impact alewife populations if their abundance at spawning sites were much greater than at Bride Lake. However, evidence from this study and observations at other sites suggest that is rarely the case.

While we do not see current cormorant predation as a threat to existing alewife populations, declining and highly variable alewife escapement combined with increasing predator abundance could undermine long-term management of alewife populations. Because generalist predators like striped bass and cormorants can switch food sources, their population dynamics are typically not sensitive to changes in any single prey item. The predation pressure imposed by cormorants and striped bass on alewives should remain constant, even as alewife populations continue to decline. Our results support this hypothesis, as an 87% change in alewife escapement in Bride Lake (2005 to 2006) was countered by only a 5% change in the average daily cormorant count.

Constant predation on declining alewife populations may undermine the alewife's ability to sustain itself. Hartman (2003) has shown that striped bass in the Hudson River can consume all of that river's annual production of river herring biomass. While O'Gorman et al. (2004) demonstrate that alewives can produce large year classes at low spawning stock density, we hypothesize that alewives will not be able to produce sustainable year classes below a critical spawner density. Given continuing alewife population declines, this scenario could occur at Bride Lake in years of particularly low alewife escapement, when cormorants could consume nearly all adult alewives. Such single-lake-scale events, repeated with enough frequency over time and across lakes, would greatly impact regional alewife populations. Thus, while our results show that cormorants pose no immediate

threat to alewife populations, we suggest that double-crested cormorants, as generalist predators, could detrimentally impact regional alewife populations by exploiting local populations.

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## Appendix A

Table A1 appears on the next page.

**Table A1.** Otolith length (OL) to total length (TL) regression parameters; TL to fresh weight (FW) regression parameters; and energy density (ED) estimates.

| Species                                  | OL to TL regression form:<br>TL = A · OL + B |       |       |                | TL to FW regressions form:<br>log(W) = A + B[log(TL)] |       |      |                | ED estimates |         |      | Reference <sup>a</sup> |
|--|--|-------|-------|----------------|---|-------|------|----------------|--------------|---------|------|------------------------|
|  | n  | A     | B     | R <sup>2</sup> | n   | A     | B    | R <sup>2</sup> | n            | Mean ED | SE   |                        |
| <i>Fundulus heteroclitus</i>             | 27   | 49.9  | -9.17 | 0.90           | 31  | -5.39 | 3.28 | 0.98           | 26           | 4.98    | 0.07 |                        |
| <i>Labridae</i> spp.                     | 13   | 88.4  | -70.2 | 0.94           | 11  | -4.67 | 2.92 | 0.97           | 5            | 5.12    | 0.13 |                        |
| <i>Peprilus triacanthus</i>              | 7  | 27.1  | 8.97  | 0.98           | 6   | -5.93 | 3.48 | 0.94           | —            | —       | —    |                        |
| <i>Stenotomus chrysops</i>               | 6  | 33.2  | -31.8 | 0.99           | 5   | -6.08 | 3.58 | 0.96           | 2            | 5.72    | 0.28 |                        |
| <i>Alosa pseudoharengus</i>              | 31   | 95.5  | -68.1 | 0.97           | 369   | -5.3  | 3.12 | 1              | 20           | 5.86    | 0.15 |                        |
| <i>Morone americana</i>                  | 14   | 28.7  | -57.2 | 0.95           | 1706  | -1.43 | 2.89 | 0.92           | 4            | 3.79    | 0.19 | 1                      |
| <i>Menidia menidia</i>                   | 6  | 58.3  | 0.99  | 0.98           | 10  | -4.65 | 2.75 | 0.97           | —            | —       | —    |                        |
| <i>Anguilla rostrata</i>                 | 3  | 193.1 | -84.8 | 0.89           | 48  | -5.69 | 2.98 | 0.99           | —            | —       | —    | 2                      |
| <i>Perca flavescens</i> (7)              | 5  | 24.2  | 25.6  | 0.98           | 372   | -3.76 | 2.43 | NA             | —            | —       | —    | 3 <sup>e</sup>         |
| <i>Myoxocephalus aeneus</i> <sup>b</sup> | 51   | 1.42  | -2.8  | 0.97           | 119   | -4.93 | 3.03 | 0.99           | —            | —       | —    | 4                      |
| <i>Paralichthys</i> spp.                 | 7  | 68.9  | -68   | 0.91           | NA  | -5.25 | 3.1  | 0.99           | —            | —       | —    | 5, 6                   |
| <i>Oncorhynchus mykiss</i>               | 13   | 91.8  | -52   | 0.86           | 121   | -6.3  | 2.76 | NA             | —            | —       | —    | 7                      |
| <i>Morone saxatilis</i>                  | 4  | 41.9  | -99.8 | 0.98           | 1364  | -5.08 | 3.07 | NA             | —            | —       | —    |                        |
| Combined demersal <sup>c</sup>           | —  | —     | —     | —              | —   | —     | —    | —              | 21           | 4.94    | 0.17 |                        |
| Combined freshwater <sup>d</sup>         | —  | —     | —     | —              | —   | —     | —    | —              | 10           | 4.94    | 0.23 |                        |

<sup>a</sup>References are as follows: (1) Marcy, B.C., Jr., and Richards, F.P. 1974. Age and growth of the white perch, *Morone americana*, in the lower Connecticut River. Trans. Am. Fish. Soc. **103**: 117–120. (2) Carlander, K.D. 1950. Handbook of freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa. (3) Carlander, K.D. 1997. Handbook of freshwater fishery biology. Vol. III. Iowa State University Press, Ames, Iowa. (4) Roseman, E.F., Tomichek, C.A., Maynard, T., and Burton, J.A. 2005. Relative abundance, age, growth, and fecundity of grubby, *Myoxocephalus aeneus*, in Niantic River and Niantic Bay, Long Island Sound. J. Sea Res. **53**: 309–318. (5) Grimes, B.H., Huish, M.T., Kerby, J.H., Moran, D., and Pendleton, E. 1974. Summer and winter flounder. USFWS Biological Reports, **82** (11.112). (6) Powell, A.B. 1974. Biology of the summer flounder, *Paralichthys dentatus*, in Pamlico Sound and adjacent waters, with comments on *P. lethostigma* and *P. albigutta*. M.S. thesis, University of North Carolina, Chapel Hill, N.C. (7) Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vol. I. Iowa State University Press, Ames, Iowa.

<sup>b</sup>Form:  $\ln(TL) = A \cdot \ln(OL) + B$ .

<sup>c</sup>Species include *Labridae* spp. ( $n = 5$ ), *Microgadus tomcod* ( $n = 4$ ), *Gadus morhua* ( $n = 2$ ), *Stenotomus chrysops* ( $n = 2$ ), *Centropristis striata* ( $n = 7$ ), and *Pseudopleuronectes americanus* ( $n = 1$ ).

<sup>d</sup>Species include *Lepomis macrochirus* ( $n = 7$ ) and *Fundulus diaphanous* ( $n = 3$ ).

<sup>e</sup>Length adjusted to convert TL to fork length.

## Appendix B. Bioenergetic modeling approach: overview

We calculated cormorants' seasonal consumption of alewives using bioenergetic modeling. We first estimated the total daily energy intake of the cormorant population from literature energy estimates and empirical population counts. We converted daily energy intake to total daily alewife consumption based on the energy density of prey items and the diet proportion composed of alewives. We summed daily consumption estimates across all alewife spawning dates to calculate total seasonal consumption.

Because all model inputs incorporate some uncertainty, we estimated maximum and minimum values for each parameter. Our methodology for estimating these maximum and minimums is described below.

### I. Calculating total daily cormorant energy intake

#### Overview

We calculated the daily energy intake of a single cormorant by multiplying the estimated daily per-cormorant energy expenditure by a digestive efficiency ratio. The total energy intake of cormorant populations was then estimated by multiplying per-cormorant energy intake by daily estimates of cormorant population size.

#### Estimating per cormorant energy expenditure

We used the all seabirds field metabolic rate (FMR) regression of Ellis and Gabrielsen (2002) to estimate the daily energy expenditure (DEE) per cormorant as follows:

$$DEE = 16.69 M^{0.651}$$

where  $M$  is the mass (g) of a cormorant.

Based on an estimated cormorant mass of 2051 g, this regression calculated FMR at 2391 kJ-cormorant<sup>-1</sup>·day<sup>-1</sup>. We used the standard errors provided by Ellis and Gabrielsen (2002), together with estimates of minimum and maximum cormorant mass (Table 1), to create a range of potential daily energy expenditures (1581–3817).

#### Digestive efficiency

To calculate energy intake per cormorant per day, we divided the estimated daily energy expenditure (FMR) by Brugger's (1993) empirically determined cormorant digestive efficiency of 0.779. To create a range of potential values, we used Brugger's minimum DE estimate (for bluegill; 0.75) and maximum DE estimate (for channel catfish (*Ictalurus punctatus*); 0.79).

#### Cormorant population size

We estimated the total daily energy intake by cormorant populations by multiplying the per-cormorant energy intake by the number of cormorants in each population. We interpreted linearly between our known counts to create daily cormorant population size estimates for Bride Lake and the local population (see main text for counting methodology). We created maximum and minimum population size estimates by varying daily counts  $\pm 10\%$  from the actual counts for Bride Lake and  $\pm 20\%$  for the local cormorant population.

## II. Estimating daily alewife consumption

### Overview

From the total daily cormorant energy intake, we calculated fish consumption (in g) by dividing the total energy intake (in kJ) by the estimated energy density of prey items (in kJ·g<sup>-1</sup>). We then estimated alewife consumption (in g) by multiplying total fish consumption by the cormorant diet proportion composed of alewives. The count of alewives consumed was calculated by dividing the total estimated mass of alewife eaten by the average mass of an alewife.

### Energy density of prey items

We empirically estimated the energy density (ED) of each prey taxon from whole fish wet weight:dry weight ratios and the equations of Hartman and Brandt (1995) (Appendix A). Measured fish were sampled by beach and purse seine, hook and line, and minnow traps, and fish were collected from locations where cormorants from Long Ledge were observed feeding. Alewives were collected directly from Bride Lake at the peak of the alewife run. In all cases, fish sampling was concurrent with cormorant diet sampling and population estimation. We obtained empirical ED estimates for species composing 88% of the cormorant diet.

For cormorants feeding at Bride Lake, prey ED was modeled as equal to our ED estimate for alewife, 5.92 kJ·g<sup>-1</sup>. For the local cormorant population, prey ED was estimated as the average energy density of all prey, weighted by proportion in the cormorant diet. For dates where diet samples were available, we calculated these estimates directly from diet proportions. Linear interpolation between known dates was used to create daily weighted ED averages for dates with no diet samples.

A range of maximum and minimum energy density estimates was calculated based on the standard error of our ED measurements.

### Diet proportion

At Bride Lake, the proportion of the diet composed of alewives was assumed to always equal one (see note in main body of paper). For the local cormorant population, diet proportion was determined directly from cormorant diet samples (see main text for detail on methodology). For dates with no diet samples available, linear interpolation between known samples was used to create daily diet proportions.

A range of maximum and minimum alewife diet proportions was created for the local cormorant population by varying the daily proportion of alewives in the diet  $\pm 10\%$ .

### Mass of alewives

The mass of an alewife was calculated from measurements of alewives sampled entering Bride Lake. Alewives were collected from Bride Lake via established weirs used for population estimation. If possible, alewife mass was obtained from chilled fish within 4 h of mortality. Some fish were frozen (again, within 4 h) and then weighed. A range of possible alewife masses was created based on the standard error of our Bride Lake sample.

### III. Other models

Without detailed behavioral data, cormorant energy intake can be estimated by three methods. One combines an estimate of basal metabolism with an FMR:BMR (basal metabolic rate) ratio to estimate the per-cormorant daily energy intake (e.g., Kendeigh et al. 1977). A second method avoids the issue of prey energy density by estimating cormorant consumption as a percentage of body weight (e.g., 20%, Rudstam et al. 2004; 22%, Glahn and Brugger 1995). Each of these two models produced consumption estimates less than 20% different than the midpoint consumption estimate and within the range of standard error for the FMR-based model of Ellis and Gabrielsen (2002).

In short, we chose to use the FMR model because it maximized the potential insights from available data without sacrificing precision. Unlike a percentage of body weight model, the FMR model enables the modeler to adjust consumption estimates based on shifts in prey energy, like that which occurs when cormorants switch from alewives to lower energy density food sources (see Appendix A for magnitude of difference). Additionally, the FMR model incorporates less uncertainty than the basal metabolism model, which requires an FMR:BMR multiplier — a highly sensitive model parameter.

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