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Quantifying alosine prey in the diets of marine piscivores in the Gulf of Maine

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The objectives of this work were to quantify the spatial and temporal distribution of the occurrence of anadromous fishes (alewife *Alosa pseudoharengus*, blueback herring *Alosa aestivalis* and American shad *Alosa sapidissima*) in the stomachs of demersal fishes in coastal waters of the north-west Atlantic Ocean. Results show that anadromous fishes were detectable and quantifiable in the diets of common marine piscivores for every season sampled. Even though anadromous fishes were not the most abundant prey, they accounted for *c.* 5–10% of the diet by mass for several marine piscivores. Statistical comparisons of these data with fish diet data from a broad-scale survey of the north-west Atlantic Ocean indicate that the frequency of this trophic interaction was significantly higher within spatially and temporally focused sampling areas of this study than in the broad-scale survey. Odds ratios of anadromous predation were as much as 460 times higher in the targeted sampling as compared with the broad-scale sampling. Analyses indicate that anadromous prey consumption was more concentrated in the near-coastal waters compared with consumption of a similar, but more widely distributed species, the Atlantic herring *Clupea harengus*. In the context of ecosystem-based fisheries management, the results suggest that even low-frequency feeding events may be locally important, and should be incorporated into ecosystem models.

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Key words: alewife; demersal fish; Gulf of Maine; river herring; trophic interaction.

INTRODUCTION

Anadromous fishes have declined throughout their range largely because dams impede access to spawning and nursery habitats (ASMFC, 1998, 1999; Limburg & Waldman, 2009; Hall *et al.*, 2011, 2012). In response to documented declines, large-scale riverine and estuarine restoration efforts are underway to re-establish migratory access throughout North America (Opperman *et al.*, 2011). The goal of such efforts is to restore populations of anadromous species to their historical levels (Baird, 1885; Belding,

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1921; Hall *et al.*, 2011, 2012). If successful, these efforts have the potential to change the marine ecosystems to which the restored habitats are connected.

Paralleling this restoration movement is an emerging interest in the importance of migrating anadromous species as prey for commercially managed marine fishes (marine piscivores) in estuarine and coastal waters (Ames, 2004; Wilson *et al.*, 2009; Hall *et al.*, 2012; Ames & Lichter, 2013). Implications of predator–prey relationships among anadromous species in marine ecosystems have been evaluated for a number of thematic topics, including survival of stocked fishes, climate change effects on ecosystem dynamics and ecosystem stability (Hvidsten & Lund, 1988; Beamish *et al.*, 1992; O'Gorman & Emmerson, 2009; Sturdevant *et al.*, 2012). The energetic contribution that seasonal pulses of anadromous prey contribute to marine ecosystems is not well studied and thus its significance is unknown.

Historically, the most abundant anadromous fishes in the Gulf of Maine (GOM) were probably river herring of the sub-family Alosinae (Saunders *et al.*, 2006), including alewife *Alosa pseudoharengus* (Wilson 1811), blueback herring *Alosa aestivalis* (Mitchill 1814) and American shad *Alosa sapidissima* (Wilson 1811). Reviews of fisheries data indicate that millions of *A. pseudoharengus*, *A. aestivalis* and *A. sapidissima* were harvested annually (Baird, 1885; Saunders *et al.*, 2006; Limburg & Waldman, 2009). Hall *et al.* (2012) estimated a historic flux of between 10×10^6 and $1{\cdot}4 \times 10^9$ *A. pseudoharengus* per year into the marine ecosystem. Those historical runs represented a substantial and localized flux of prey species on a seasonal basis. Studies documenting predation on anadromous fishes have largely been conducted in a broader biological, behavioural or ecological context (Beamish *et al.*, 1992; Creaser & Perkins, 1994; Blackwell & Juanes, 1998; Bowman *et al.*, 2000; Hartman, 2003). There are, however, several historical accounts (Baird, 1885; Belding, 1921) and modern theories (Dadswell, 1985; Ross & Biagi, 1991; Ames, 2004; Hall *et al.*, 2011; Ames & Lichter, 2013; Willis *et al.*, 2013) proposing that demersal fishes, especially Atlantic cod *Gadus morhua* L. 1758, once relied substantially on alosines as a part of their diet at specific times and places. As a generalist feeder, it is not unreasonable to infer that *G. morhua* might consume alosine prey when encountered (Link & Garrison, 2002; Smith *et al.*, 2007; Link *et al.*, 2009). Ames & Lichter (2013) further hypothesize that *G. morhua* migration patterns were influenced by pulses and eventual absence of juvenile alosines in coastal waters. In addition, because the dominant alosines are relatively small bodied (20–30 cm total length, L_T), these fishes probably serve as prey for a wide diversity of marine and estuarine piscivores including the anadromous striped bass *Morone saxatilis* (Walbaum 1792), bluefish *Pomatomus saltatrix* (L. 1766) and spiny dogfish *Squalus acanthias* L. 1758 (Juanes *et al.*, 1993; Blackwell & Juanes, 1998; Buckel *et al.*, 1999; Hartman, 2003; Smith & Link, 2010). Yet, the trophic significance of anadromous species to their marine predators is not entirely understood.

To improve the management and conservation of anadromous fishes and their marine predators as restoration efforts advance, it is imperative to understand the ecological link between anadromous fishes and the marine ecosystems in which they spend the greatest portion of their lives. Important unanswered questions remain, including whether increased spawning habitat availability and numbers of juvenile anadromous fishes will lead to more adult spawners in the future, or if restoration efforts will simply provide more food for marine predators thereby reducing future anadromous fish recruitment. By gathering additional empirical evidence on these interactions, informed expectations can begin regarding restoration efforts.

Anadromous fishes display complex and unique migration patterns to and from riverine systems; sampling must be designed around these patterns to understand the extent of predation on these species. Typically, movements of anadromous fishes occur in pulses during spring and autumn. Adult anadromous fishes move from marine systems and enter freshwater systems during spring spawning migrations; juveniles typically migrate from their natal river to sea during late summer into autumn in migrations partitioned by species and latitude (Loesch & Lund, 1977; Mullen *et al.*, 1986; Weiss-Glanz *et al.*, 1986). In Maine, juvenile *A. pseudoharengus* appear to have two seaward migration modes: an early mode during July and August, and a later mode in November (Saunders *et al.*, 2006; Iafrate & Oliveira, 2008). Juvenile *A. aestivalis* also migrate in the autumn with a single mode of migration occurring primarily during October, co-occurring with *A. pseudoharengus* emigration (Loesch, 1987; Saunders *et al.*, 2006). *Alosa sapidissima* tend to leave the rivers during a time frame that overlaps or is slightly later than *A. aestivalis* (O'Leary & Kynard, 1986). Once in coastal waters, juvenile and adult anadromous fishes are distributed over large geographic areas (Neves, 1981). Therefore, predator–prey interactions involving anadromous fishes can occur over a range of spatial and temporal scales. Adequately interpreting the dietary significance of predation on GOM anadromous fishes requires examining the spatial and temporal overlap of marine predators and their potential anadromous prey.

The present goal was to evaluate the extent of predation on anadromous fishes by quantifying their presence in the diet of potential marine piscivores in the GOM. To meet this goal, sampling was undertaken at different spatial and temporal scales, designed to reflect expected patterns in the overlap of these fishes with potential predators. Specifically, targeted inshore sampling was conducted at the mouths of the Kennebec and Penobscot Rivers, ME (Fig. 1), during periods of expected adult return in spring and juvenile outmigration in late summer and autumn. Data were also analysed from a broad-scale, fishery-independent survey of fish diets on the north-west Atlantic coastal shelf conducted by the U.S. NOAA Northeast Fisheries Science Center (NEFSC). These data sources allowed three specific research hypotheses to be addressed: (1) anadromous fishes comprise a detectable and non-trivial amount of the diets of groundfishes and other marine piscivores in the GOM, (2) the incidence of predation on anadromous prey is highest at more localized spatial scales (in the vicinity of estuaries) rather than widespread throughout the GOM and (3) because of the strong size dependencies in piscivory, predation is highest during outmigration of juvenile alosines in the autumn rather than during the spawning migration of adults in the spring. To broaden the inference of the analyses, parallel analyses were conducted involving consumption of Atlantic herring *Clupea harengus* L. 1758, which have similar morphologies to the alosines that are the focus here, but are more broadly distributed spatially and temporally.

MATERIALS AND METHODS

Quantification of the occurrence of anadromous prey in the diets of marine piscivores was sought throughout the north-west Atlantic Ocean. Based on extant diet studies, the analyses focused on probable predators: *S. acanthias*, *G. morhua*, goosefish *Lophius americanus* Valenciennes 1837, silver hake *Merluccius bilinearis* (Mitchill 1814), red hake *Urophycis chuss* (Walbaum 1792), white hake *Urophycis tenuis* (Mitchill 1814), thorny skate *Amblyraja radiata* (Donovan 1808), winter skate *Leucoraja ocellata* (Mitchill 1815) and sea raven *Hemitripterus*

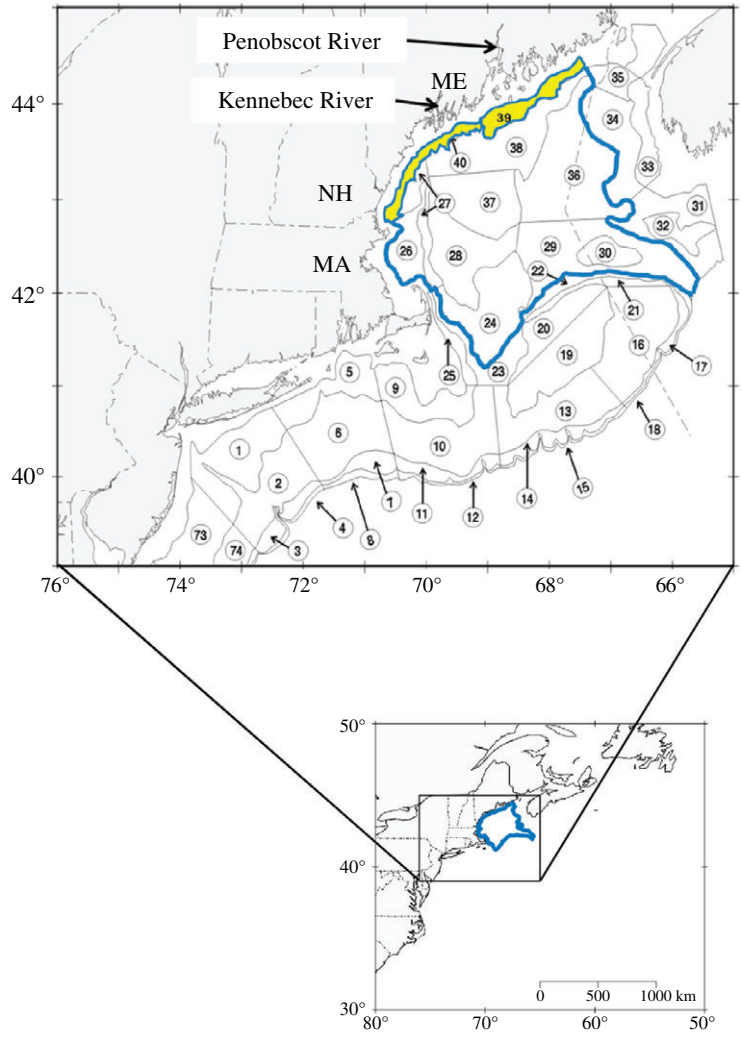

FIG. 1. Map of the north-east U.S.A. and Gulf of Maine (GOM) and neighbouring waters. Shown on the detailed map are the mouths of the Kennebec and Penobscot Rivers, Maine, which were the focus of targeted inshore sampling of marine predators. Geographic boundaries for Massachusetts (MA), New Hampshire (NH) and Maine (ME) are indicated. Also shown are the numbered strata used in the Northeast Fisheries Science Center (NEFSC) fishery-independent survey. The offshore GOM strata are collectively outlined (—). Strata 39 and 40 are highlighted (—) for clarity. Inshore strata are too small to be shown effectively on the map, but they are located between the coastline and the shoreward boundary of strata 39 and 40.

americanus (Gmelin 1789). The diets of these species were quantified over a range of spatial scales.

TARGETED INSHORE SAMPLING

Targeted sampling was conducted in coastal areas of the GOM waters near the mouths of the Kennebec and Penobscot Rivers during times when anadromous fishes were suspected to be present. Sampling was carried out aboard NOAA's R.V. *Gloria Michelle* from 12 August

2010 to 27 August 2010 (summer 2010; Fig. 1). Sampling from the R.V. *Gloria Michelle* emulated the NOAA NEFSC's bottom-trawl survey sampling standards for food habits (Reid *et al.*, 1999; Link & Almeida, 2000; Smith & Link, 2010). Tows on the R.V. *Gloria Michelle* used a 15·2 cm mesh net with a 15·2 cm codend and were conducted at 5·5 to 6·0 km h^{-1} and varied from 15 to 30 min in duration.

Additional stomach samples were obtained from the Maine Department of Marine Resources (MDMR) bottom-trawl survey aboard the F.V. *Robert Michael*. Three sampling events spanned the coast of New Hampshire to northern Maine (Fig. 1) from 3 May 2010 to 4 June 2010 (spring 2010), 11 October 2010 to 22 October 2010 (autumn 2010) and 2 May 2011 to 20 May 2011 (spring 2011). Tow times for these surveys were standardized to 20 min with an average tow speed of *c.* 4·6 km h^{-1} (*c.* 2.5 knots). The MDMR survey used a 5 cm mesh net with a 2·5 cm codend. The door spread was slightly wider on the R.V. *Gloria Michelle* than on the F.V. *Robert Michael*.

BROAD-SCALE SAMPLING

Data from the NEFSC's food habits database were obtained to expand the spatial and temporal coverage. The NEFSC has conducted bottom trawl surveys in offshore and inshore strata using a standardized design since 1963. The diets of fishes collected in these surveys have been quantified since 1973. Details of the sampling design can be found in Link & Almeida (2000) and Smith & Link (2010). There are differences with regard to frequency of coverage between offshore and inshore areas. Stations in offshore GOM areas (NEFSC strata 24, 26 through to 30 and 36 through to 40; Fig. 1) have been sampled at a minimum each spring and autumn since 1973 and less uniformly at other times of the year. Inshore GOM stations (NEFSC strata 70 through to 92; Fig. 2) are not regularly sampled by the spring and autumn surveys, but are opportunistically sampled and provide only limited insight into trophic ecology of the coastal area.

To obtain diet data, the food habits database was queried for the presence of anadromous species in diets of marine predators caught within the GOM during 1973 through to 2009. Anadromous fishes in the GOM included in preliminary searches were Atlantic salmon *Salmo salar* L. 1758, *A. pseudoharengus*, *A. aestivalis* and *A. sapidissima*.

STOMACH PROCESSING

Stomach sampling generally followed the same protocols used in the NEFSC bottom trawl survey (Link & Almeida, 2000; Smith & Link, 2010). On the targeted inshore sampling cruises, predators were eviscerated onboard to remove individual stomachs by cutting at the top of the intestine and as high up the oesophagus as possible and then stomachs were preserved in 70% ethanol. This is slightly different from the onboard sampling methods used in the NEFSC surveys of opening stomachs onboard, but follows the onboard quality assurance protocol used for every 25th tow by the NEFSC survey (Smith & Link, 2010). Stomachs evident of trawl feeding were noted and excluded from analysis. In the laboratory, stomach contents were sieved, rinsed with water and prey items were identified to the lowest taxa possible given digestive state. Wet mass and digestive state were recorded, prey lengths measured or estimated when possible and then all samples were re-preserved in 70% ethanol.

DIET QUANTIFICATION AND ANALYSIS

Anadromous prey content of each predator's diet was calculated from the targeted inshore sampling and the NEFSC survey data. To summarize the gut content's data, per cent frequency of occurrence (%*O*) and per cent diet composition by mass (%*W*) were estimated using sampling estimators similar to Link & Almeida (2000). The commonly reported index of relative importance (I_{RI}) was not calculated because of the effect that differences in taxonomic resolution of diet items has on resulting calculations (Cortés, 1997; Hansson, 1998). Marine piscivores were assumed equally available among sampling locations and seasons.

Odds-ratio statistics were used to evaluate the role of spatial scale with anadromous prey consumption given the low frequency of occurrence of these prey in stomachs. The odds of an

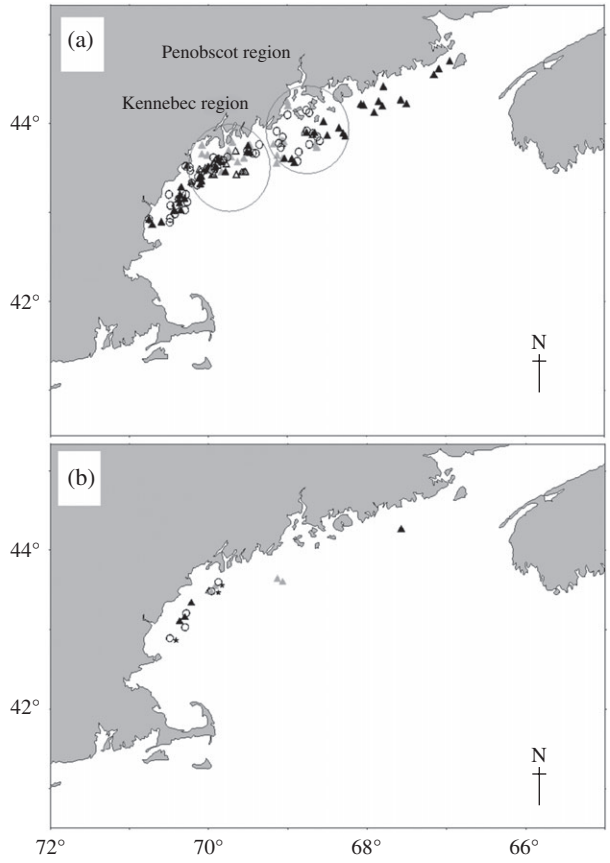

FIG. 2. Map of inshore Maine waters showing (a) locations of targeted inshore sampling stations and (b) locations of inshore targeted stations at which diadromous prey were found in predator stomachs in spring 2010 (▲), summer 2010 (△), autumn 2010 (▲) and spring 2011 (○).

event can be formally defined as the probability of an event occurring (such as tossing a heads in a coin toss) divided by the probability of it not occurring (*i.e.* tossing a tail in a coin toss; Fleiss *et al.*, 2003). Because the odds is a fraction of two probabilities, it can vary ($0 < \text{odds} < \infty$). Thinking about the coin toss example, the odds is an expression of how much more likely tossing a heads is than tossing a tails. If odds = 1, the two events are equally likely. If odds > 1, the first event is more likely than the second, and conversely if odds < 1 the first event is less likely than the second. In the present application, the ratio of two odds, or the odds ratio (ω), the odds of finding an alosine in the diet of a predator were calculated when sampled at one scale to the odds of finding an alosine in the diet of a predator when sampled as a different scale. The odds ratio (ω) is calculated as: $\omega_{1,2} = [(p_1)(1-p_1)^{-1}][(p_2)(1-p_2)^{-1}]^{-1}$, where p_i is the probability that an event occurs in group i, where i represents the different spatio-temporal sampling regime (Fleiss *et al.*, 2003). Because ω is a ratio of odds, it can also vary ($0 < \omega < \infty$). Values of $\omega > 1$ indicate that the likelihood of alosine consumption is greater at the first scale than at the second, and values of $\omega < 1$ indicate that the likelihood of alosine consumption is lower at the first scale than at the second. For this application, the probability that an alosine is observed in diet at one scale i is calculated as $n_i N_i^{-1}$, where n is the number of stomachs with anadromous prey and N is the total number of stomachs examined. Substituting as appropriate and rearranging yields: $\omega_{1,2} = [n_1(N_2 - n_2)][n_2(N_1 - n_1)]^{-1}$.

TABLE I. Definition of geographic strata used in hierarchical comparisons of consumption of diadromous prey at different spatial scales

Name	NEFSC strata	Approximate area (km^2)	Description
Entire	All	293 000	Entire north-west Atlantic coastal shelf survey area
GOM Offshore	24, 26–30, 36–38	19 153	GOM strata, outlined in blue on Fig. 1
GOM+	GOM+ 39, 40	20 461	GOM strata plus nearshore strata
Western GOM	28, 37 and 38	6917	Western GOM strata
Nearshore GOM	39, 40	1308	Nearshore GOM stations, regularly sampled since 1973
Inshore GOM	70–92	2870	Inshore strata (not shown on Fig. 1), sampled irregularly since 1973

GOM, Gulf of Maine; NEFSC, Northeast Fisheries Science Center.

To test the hypotheses regarding the spatial distribution of predation on anadromous prey, odds ratios were calculated for each predator species that compared the targeted sampling with the NEFSC sampling aggregated at a range of spatial scales as described below. The 95% C.I. were calculated for each odds ratio using an asymptotic approximation, with small sample corrections (Fleiss *et al.*, 2003). Instances where the 95% C.I. does not include 1 are statistically significant.

Odds ratios were used to compare the targeted inshore sampling data from the spring, summer and autumn to data collected during the same seasons at six separate spatial scales (Table I) to explore the likelihood of detecting predation on anadromous fishes as the sampling focused upon the Kennebec and Penobscot Rivers. Data over this spatial hierarchy were analysed for each predator–season combination, as appropriate, starting from the entire shelf ecosystem and gradually focusing down to increasingly smaller regions. The broadest scale of comparison, termed entire, compared the targeted inshore sampling data to the entire data from the NEFSC survey (Fig. 1 and Table I). At the next smaller scale, the targeted inshore sampling data were compared with data from the GOM Offshore by including data from NEFSC strata 24, 26 through to 30 and 36 through to 38 (Fig. 1 and Table I). A second analysis at this same approximate scale, termed GOM +, added inshore GOM waters in strata 39 and 40 to the comparison set (Fig. 1 and Table I). At the next smallest scale, termed western GOM Basin, the targeted inshore sampling data were compared only with data from strata 28, 37 and 38 (Fig. 1 and Table I). These waters represent the regularly sampled offshore strata. At a smaller scale, the targeted inshore sampling data were compared only with data from the nearshore GOM (NEFSC strata 39 and 40). These two strata are the most inshore of the regularly sampled NEFSC strata (Fig. 1). Finally, the targeted inshore sampling data were compared with data from the NEFSC inshore samples (strata 70 through to 92) that overlap spatially with the targeted inshore sampling, but are not regularly sampled in the NEFSC survey.

To evaluate whether the patterns with anadromous prey were reflective of overall feeding or something specific to consumption of anadromous prey, a parallel set of analyses were conducted with *C. harengus* as prey to provide contrast to the river herring.

RESULTS

A total of 1505 stomachs collected from 150 hauls [Fig. 2(a)] during the targeted inshore sampling were examined from 11 fish predator species. Of this total, 1128 stomachs contained prey (Table II). Seventeen stomachs contained anadromous fish prey (Table II). Observed consumption of anadromous fishes was concentrated spatially around the two river systems that were the focus of sampling [Fig. 2(b)]. Predators with

TABLE II. Summary of stomachs examined by species and season with and without diadromous prey in the targeted inshore sampling

	Spring 2010		Summer 2010		Autumn 2010		Spring 2011		
Species	With	With out	With	With out	With	With out	With	With out	Total
Squalus acanthias		4	1	108	5	28		2	148
Leucoraja ocellata		1		0		0		1	2
Amblyraja radiata		14		23		2		6	45
Gadus morhua	2	29		56		5	1	28	121
Merluccius bilinearis		47		69		72	4	82	274
Pollachius virens		2		3		1		0	6
Urophycis tenuis		18		93		57		47	215
Urophycis chuss		27		1		35		12	75
Myoxocephalus octodicemspinosus		0		5		17		0	22
Hemitripterus americanus	1	26		4		0		6	37
Lophius americanus	1	25		116	1	26	1	14	184
Total	4		1		6		6		17

anadromous prey in their stomachs included *S. acanthias*, *G. morhua*, *M. bilinearis*, *L. americanus and H. americanus*. Although other predators (*U. tenuis*, *U. chuss* and *A. radiata*) demonstrated some degree of piscivory, anadromous fishes were not detected in their diets. At this aggregate level, these data indicated a low occurrence of anadromous prey, expressed as $\%O = 1{\cdot}5$. The largest per cent frequencies of occurrence of alosine prey were observed in *S. acanthias* [$\%O = 17{\cdot}9$ during autumn 2010; Fig. 3(a)], *L. americanus* [$\%O = 7{\cdot}1$ during spring 2011; Fig. 3(a)] and *G. morhua* [$\%O = 6{\cdot}9\%$ during spring 2010; Fig. 3(a)]. For other predators or seasons, alosines occurred in the diet at $\%O$ from 0 to 5 (Table II).

Only *A. pseudoharengus* and *A. aestivalis* were positively identified from the targeted inshore sampling. Three prey items could only be identified in the *Alosa* genus. Thus, when anadromous prey are referred to hereafter, it is to *A. pseudoharengus* and *A. aestivalis*. Sufficient non-empty stomachs were collected to support statistical analyses of diets for *S. acanthias*, *G. morhua*, *M. bilinearis* and *L. americanus*. Accordingly, data for other species are not included in subsequent analyses. For the four predatory species considered, the NEFSC food habits database contained information for 111 928 stomachs. Of this total, 103 contained anadromous prey. This is equivalent to $\%O = 0{\cdot}1$. The highest observed $\%O$ from the food habits database were at least one order of magnitude lower than those observed in the targeted inshore sampling [Fig. 3(b)].

Consumption of anadromous prey by the four species with sufficient data was more likely to occur in the spring or autumn than in summer months (Fig. 3). Anadromous prey were common in *L. americanus* diets in spring and in autumn sampling and were only present in the diets of *G. morhua* and *M. bilinearis* during spring months (Fig. 3). It is notable that *S. acanthias* consumption of anadromous prey was particularly high during autumn months in 2010 in targeted nearshore sampling, but this pattern was not evident in the broader sampling (Fig. 3).

Odds ratios were calculated comparing the presence of anadromous prey in targeted inshore sampling to the presence of anadromous prey in four marine piscivores during

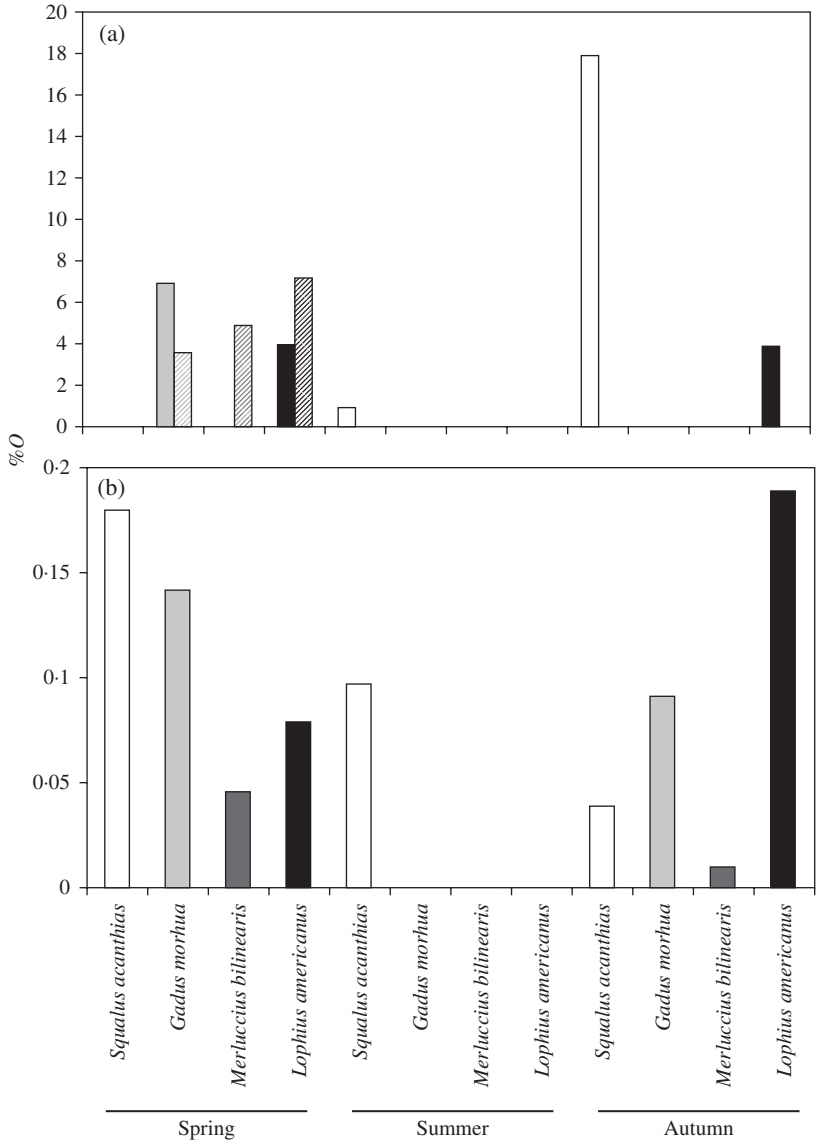

FIG. 3. Per cent occurrence (*%O*) of diadromous prey in *Squalus acanthias*, *Gadus morhua*, *Merluccius bilinearis* and *Lophius americanus* collected during spring, summer and autumn. Data are shown for (a) targeted inshore sampling in 2010 (■, ■, ■, □) and 2011 (▨, ▨, ▨) and (b) the Northeast Fisheries Science Center sampling for the 'Entire' region, as defined in Table I. Note the differences in scale between (a) and (b).

three seasons from sampling conducted at a hierarchy of six different spatial scales. Data were available to calculate odds ratios for 27 of these four predators × three seasons × six spatial scales (=72) possible combinations. Two-thirds (18) of the calculated odds ratios were significantly >1 (Fig. 4). The odds-ratio analyses generally indicate that anadromous prey are more common in targeted inshore sampling than in NEFSC sampling when the NEFSC data are aggregated at broader scales than at smaller scales

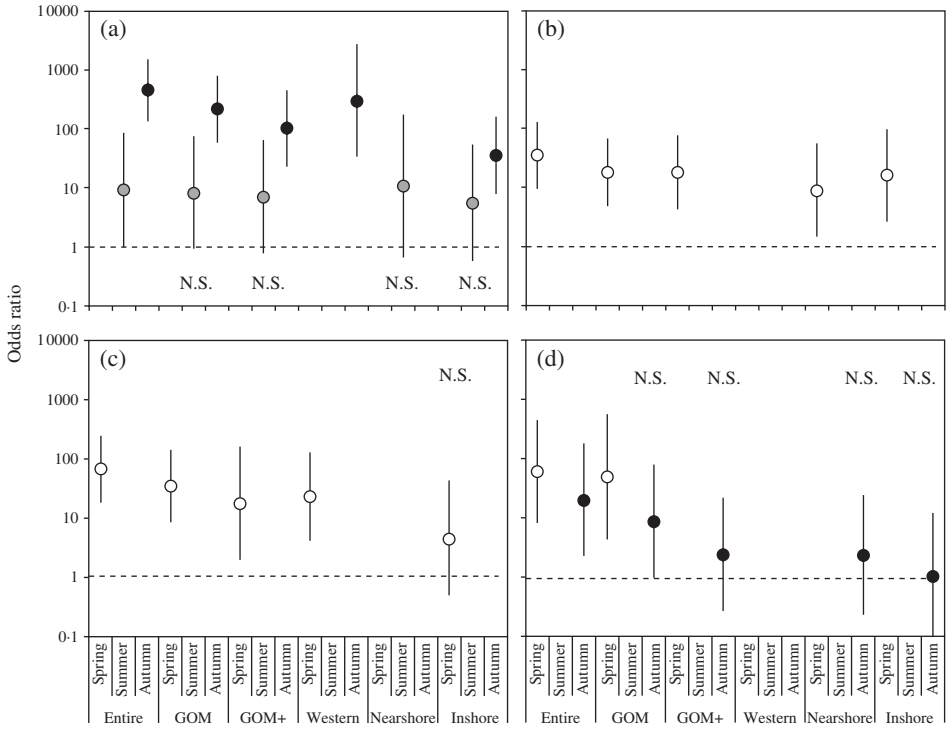

FIG. 4. Odds ratios (±95% C.I.) for consumption of diadromous prey for (a) *Squalus acanthias*, (b) *Gadus morhua*, (c) *Merluccius bilinearis* and (d) *Lophius americanus*. Each panel shows the odds ratio comparing the targeted sampling with Northeast Fisheries Science Center (NEFSC) data stratified at different scales from largest to smallest for three seasons: spring (○), summer (●) and autumn (●). Odds ratios for combinations of region and season where no diadromous prey were consumed cannot be defined. Note odds ratios with 95% C.I. that do not include 1 indicate that diadromous prey are significantly more common than in the NEFSC survey at the scale specified. Comparisons where odds ratios were not significantly different are indicated by N.S. GOM, Gulf of Maine.

(*i.e.* odds ratio, $\omega > 1$; Fig. 4). For example, analyses of the occurrence of anadromous prey in autumn *S. acanthias* diets indicate that the mean odds ratio decreased from 461·8 when the comparison is made at the broadest scale to 36·07 when targeted data were compared with inshore strata in the NEFSC database [Fig. 4(a)]. Similar decreasing patterns were evident for *M. bilinearis* [Fig. 4(c)] and *L. americanus* [Fig. 4(d)]. The pattern was less clear for *S. acanthias* diets in the summer [Fig. 4(a)] and for *G. morhua* in spring months [Fig. 4(b)]. Also, although the pattern of a decline in odds ratio with spatial scale was observed in *L. americanus* [Fig. 4(d)], many of the comparisons for this species were not statistically significant.

Per cent composition by mass (*%M*) estimates indicated that anadromous prey can comprise a notable proportion of the diet of marine piscivores, dependent on sampling area (Fig. 5). The mean per cent diet by mass (*%W*) of anadromous prey increased for *S. acanthias*, *G. morhua* and *M. bilinearis* as the sampling scale decreased from the NEFSC 'Entire' region to the NEFSC 'Nearshore' to the targeted inshore sample (Fig. 5). With targeted inshore sampling, the mean anadromous prey compositions

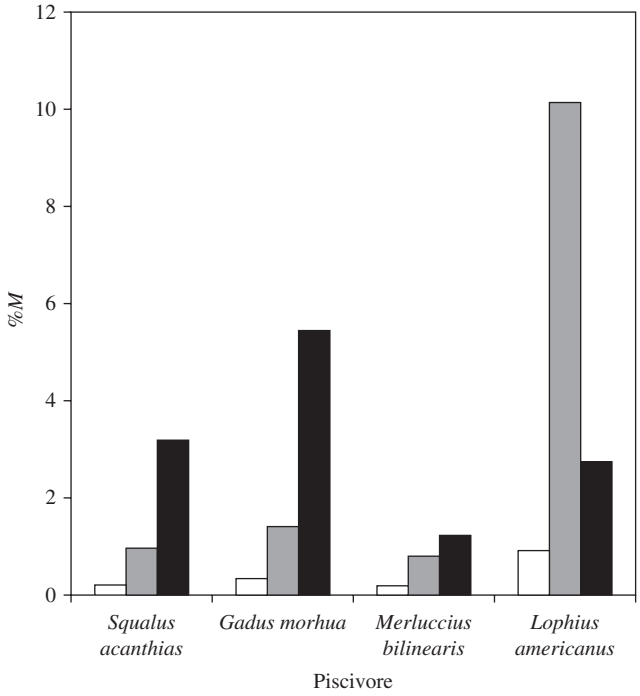

FIG. 5. Per cent by mass (%*M*) contribution of diadromous prey to marine predator diets in targeted and Northeast Fisheries Science Center sampling: Gulf of Maine (□), inshore (■) and targeted (■).

were 3·2, 5·4, 1·2 and 2·7% of the diets of *S. acanthias*, *G. morhua*, *M. bilinearis* and *L. americanus*, respectively. During specific seasons, the contribution of anadromous prey to the diet of marine piscivores at the targeted scale was substantially higher, 8·4% for *S. acanthias* in autumn 2010, 11·2% for *G. morhua* in spring 2010 and 6% for *L. americanus* in autumn 2010.

Observations of consumption of *C. harengus* were also broadly distributed within the targeted sampling area (Fig. 6). There were 153 such occurrences over 62 stations; almost half of the total number of stations sampled. Seventy-seven per cent (40/52) of the calculated odds ratios from the possible combinations of predator, season and spatial scale for which data were available was significantly >1 (Fig. 7). The distribution of significant findings varied among species. Approximately two-thirds of the *S. acanthias* comparisons, almost all of the *G. morhua* comparisons, all of the *M. bilinearis* comparisons and *c*. one-third of the *L. americanus* comparisons, were significantly >1. There was a much less obvious effect of spatial scaling on the likelihood that herring will be found in the diets of the four marine piscivores compared with anadromous prey (Figs 4 and 7).

DISCUSSION

Spatial scale and grain and temporal patterns are important considerations for understanding ecological processes such as trophic interactions (Wiens, 1989; Carroll &

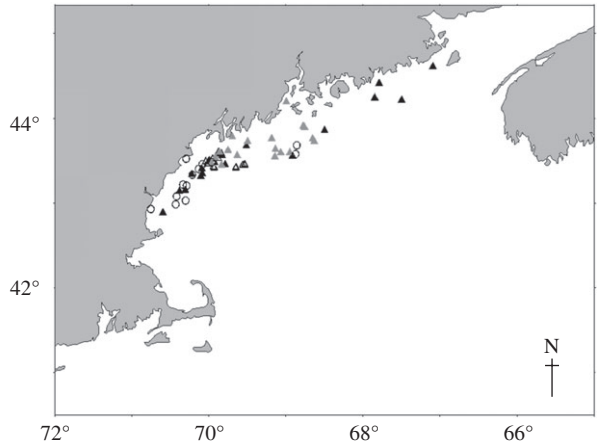

FIG. 6. Map showing geographic locations of presence of *Clupea harengus* in the diets of the four predators analysed for consumption of diadromous fishes within the targeted sampling in spring 2010 (▲), summer 2010 (△), autumn 2010 (▲) and spring 2011 (○).

Pearson, 2000; Block *et al.*, 2001). Nye *et al.* (2011) showed how fine-scale temporal sampling revealed a higher incidence of piscivory in Atlantic croaker *Micropogonias undulatus* (L. 1766) than had been reported previously. The authors demonstrated that piscivory by this species occurred during crepuscular feeding. Previous studies had sampled their diets principally during daylight hours. In a comparative review of the literature, anadromous prey were not commonly noted in diets of various marine predators (Montevecchi *et al.*, 1988; Juanes *et al.*, 1993; Hall & Kress, 2008), but were an important prey item when sampling was conducted at relevant seasonal and spatial scales (Merrick *et al.*, 1997; Orsi *et al.*, 2000; Willette *et al.*, 2001). As demonstrated here, when studies are conducted at appropriate spatial and temporal scales, alosine prey can be important in the diets of marine piscivores in the GOM.

The present analyses of marine piscivore diets in the GOM indicate that alosine prey were detectable and at times a non-trivial component of the diets of marine piscivores. Moreover, inferences regarding the importance of alosine prey were spatially and temporally dependent. When considered at the broadest spatial scales (*i.e.* NEFSC 'Entire' region), consumption of alosine prey by common marine piscivores appears to be detectable, but relatively small. In contrast, when evaluated at spatial and temporal scales relevant to periods of overlapping migration or movement patterns (*i.e.* targeted inshore sampling), these prey may comprise >10% of their diets by mass, and based on odds ratios, be as much as 10–460 times greater in fish diets from near the mouths of local rivers *v.* the greater offshore shelf regions examined here.

The present analysis was dependent on the assumption of equal opportunity of trophic interaction for the piscivores sampled. Diurnal fluctuation in vertical distribution, nocturnal or crepuscular feeding, and other circadian behaviours have the potential to affect these results. *Alosa pseudoharengus* and *A. aestivalis* exhibit species-specific and diurnal variations in vertical distribution (Loesch *et al.*, 1982; Loesch, 1987). Likewise, common marine piscivores display differing circadian feeding behaviour. *Merluccius bilinearis* are nocturnal feeders whose vertical distribution may be governed by hunting behaviour; *G. morhua* and *S. acanthias* are opportunistic with no clear diurnal

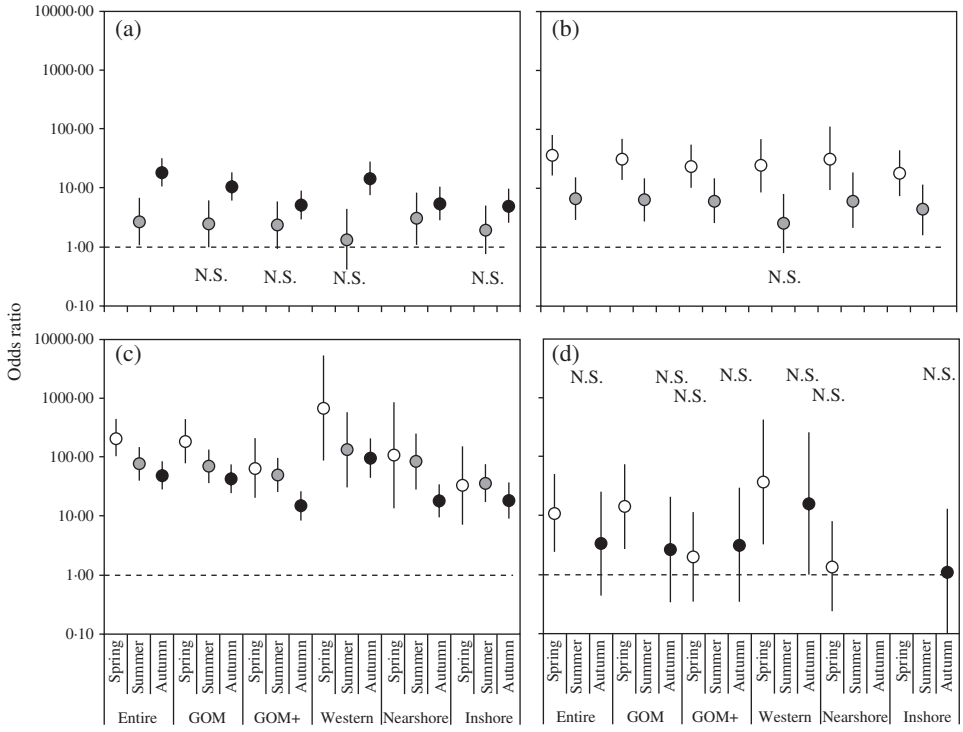

FIG. 7. Odds ratios (±95% C.I.) for consumption of *Clupea harengus* prey for (a) *Squalus acanthias*, (b) *Gadus morhua*, (c) *Merluccius bilinearis* and (d) *Lophius americanus*. Each panel shows the odds ratio comparing the targeted sampling to Northeast Fisheries Science Center (NEFSC) data stratified at different scales from largest to smallest for three seasons: spring (○), summer (●) and autumn (●). Odds ratios for combinations of region and season where no diadromous prey were consumed cannot be defined. Note odds ratios with 95% C.I. that do not include 1 indicate that diadromous prey are significantly more common than in the NEFSC survey at the scale specified. Comparisons where odds ratios were not significantly different are indicated by N.S. GOM, Gulf of Maine.

feeding or vertical distribution pattern (Collette & Klein-MacPhee, 2002). The natural behaviour of these predators to find prey may offset effects of differing vertical distribution associated with alosine behaviour.

Alosine prey were detected in *S. acanthias*, *G. morhua*, *M. bilinearis*, *L. americanus* and *H. americanus*. Each of these species are known to be opportunistic and generalist predators (Smith & Link, 2010). Based on >60 000 stomachs examined, *S. acanthias* consumed mainly teleosts, but had more than 400 different prey items (Link & Almeida, 2000; Smith & Link, 2010). Other principal prey consumed by *S. acanthias* included ctenophores, bivalves and cephalopods (Link & Almeida, 2000; Smith & Link, 2010). The diet of *G. morhua* has been shown to include 400–500 categories based on an examination of >15 000 individual stomachs (Link & Almeida, 2000; Link & Garrison, 2002; Smith & Link, 2010). Fishes dominated the diets, representing more than half of all items examined. The remainder of the diet included bivalves, polychaetes, decapods and other crustaceans. *Merluccius bilinearis* diets are somewhat less diverse. Approximately 200 prey items were identified from >25 000 *M. bilinearis*

stomachs with fish making up more than half of the diet. Similarly, *L. americanus* had *c*. 200 unique prey items from >8000 stomachs with nearly the entire diet composed of fishes. Overall, clupeids, including alosines, comprise *c*. 10–20% of the diets by mass of these four species.

Large migrations are known to change the trophic structure of terrestrial and aquatic ecosystems. Predator migration patterns, fecundity, feeding behaviour and other biological variables are affected by regular and erratic pulses of prey (Botton *et al.*, 1994; Scheel & Packer, 1995; Angerbjörn *et al.*, 1999; Tsipoura & Burger, 1999). Given the migratory pattern of alosines and the diverse diets of piscivore species surveyed here, it could be anticipated that there would be a feeding behavioural response to pulses of increased prey availability in the environment. Hedger *et al.* (2011) have shown that *G. morhua* adapt their movement to pulses of *S. salar* smolt outmigration to occupy areas near the head of the fjord, thereby maximizing the spatial overlap with their prey. Although the present analysis assumed that marine piscivores were equally available throughout the sampling, the data suggest that predators of outmigrating juvenile alosines in the GOM might exhibit similar behavioural flexibility. Indeed, it is likely that the historically greater abundances of alosines would have induced a predatory response in a wider diversity of fishes. A similar argument has been made by Ames (2004) in light of historical data and from surveys of fishermen, Wilson *et al.* (2009) evaluating the ecological role of anadromous fishes as forage, Ames & Lichter (2013) connecting *G. morhua* migration and residency behaviour to young-of-the-year *A. pseudoharengus* availability and Willis *et al.* (2013) based on historic *G. morhua* diet preference. A similar opportunistic predatory response will probably reoccur should alosines be restored in the GOM.

Most recovery plans for anadromous species assume that restoring access to spawning habitat provides the opportunity for establishment of these species. For example, Hall *et al.* (2011) propose that quantifying the amount of virgin spawning habitat restored is the best guide to recovery trajectories for *A. pseudoharengus*, but this presupposes that an increase in juvenile production derived from this newly restored habitat is not entirely consumed as it enters the marine ecosystem. Yet, marine piscivores respond positively to pulses of prey by altering their movements and distributions. As mentioned above, Hedger *et al.* (2011) demonstrated that *G. morhua* in Norwegian fjords change their behaviour during periods of outmigration *S. salar* juveniles. Similarly, marine piscivores have a seasonal dietary preference for Pacific salmon *Oncorhynchus* spp. smolts in the Columbia River (Poe *et al.*, 1991). The evidence presented here suggests that marine piscivores in the GOM probably exhibit similar flexibility in their feeding behaviour and may respond to substantially increased abundances of juvenile anadromous fishes by increasing their consumption of these prey. How this adaptive predation will affect levels of mortality for anadromous populations that are restored remains an important question.

It would be possible to estimate the consumption of anadromous fishes by marine piscivores given the potential increase in production of these prey. Estimating the potential trophic demand of marine piscivores requires estimates of the spatial and temporal overlap of the outmigrating juvenile anadromous fishes with potential marine piscivores, their relative abundances, the daily ration of each potential piscivorous species and their diet selectivity. Strong size dependencies in many of these parameters are likely, such that knowledge of the size structure of both the anadromous prey and the

potential predators would also be helpful. Size (or age)-structured bioenergetics models of each predator could be used to estimate their trophic demand (Hartman & Brandt, 1995). Yet, an integrated understanding can only come from a full ecosystem model. As demonstrated here, it is likely that any such ecosystem model needs to include at least two spatial domains to fully account for the spatially and temporally dynamic interactions between anadromous prey and marine piscivores. Ecosystem models for the GOM (Link *et al.*, 2011) have been and continue to be developed and may provide a platform from which to explore interactions between restored anadromous populations and marine piscivores.

Of the river herring in the GOM, only *A. pseudoharengus* and *A. aestivalis* were notable in the targeted inshore samples; *A. sapidissima* was absent. The lack of observed *A. sapidissima* may be related to the current state of restoration in the GOM. The documented numbers of adult *A. sapidissima* are far fewer than adult *A. pseudoharengus* which number in the millions within the Kennebec River. Potential factors affecting the presence of *A. sapidissima* include timing and method of sampling, feeding behaviour and overall distribution of prey and predators. Future studies may be designed to address the influence of these behavioural factors on the predator–prey interaction and its implications on the trophic significance of anadromous fishes.

Restoration of anadromous species to the GOM may involve significant ecological trade-offs. Anadromous species may provide important ecosystem services including acting as important vectors of energy and nutrient exchange between marine and freshwater ecosystems and as important forage for marine piscivores. Historical information is inadequate to understand how the current marine and freshwater ecosystems will respond to the increases in anadromous production, and the regional landscape has changed dramatically over the past 300 years. One consideration is that adult abundances of anadromous fishes may not increase substantially if much of the juvenile production is consumed as it enters the marine system by marine piscivores that adapt their distribution or life histories to take advantage of the biomass flux of juvenile anadromous fishes. Indeed, empirical evidence from freshwater systems suggests that predator populations may be limited by local production and receive a large portion of their energy from outside of their systems (Pace *et al.*, 2004; Weidel *et al.*, 2008). Under this scenario, the benefit of restoring anadromous species could be the export of excess nutrients from freshwater systems and increased biomasses of marine piscivores. Alternatively, if the increased anadromous production resulted in increased abundance of the anadromous species themselves, an increased fraction of marine production may be transferred to freshwater and terrestrial ecosystems. Given that the most common fate of fishes is consumption by natural predators, it is possible that restoration efforts may not result in a rebound of anadromous spawners to historical levels, but rather the anadromous forage population may become stuck in a 'predator pit' (Bakun, 2006), where the predator population gleans the increase in productivity, but the prey species is unable to rebound. Analysing these and other potential trade-offs is a fruitful area for investigation, and using ecosystem models may provide the context in which to explore such questions. Understanding how the marine, freshwater and terrestrial ecosystems respond to increased anadromous fish stocks will help inform the outcome of restoration efforts and lead to a more robust approach for the management of these species.

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