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Diets and Stable Isotope Derived Food Web Structure of Fishes from the Inshore Gulf of Maine

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Abstract In the nearshore Gulf of Maine, a combination of factors (overfishing, ecosystem change, and ocean warming) is thought to govern groundfish recovery. We analyzed feeding habits of demersal predatory fish from Midcoast Maine (abundant river herring) and Passamaquoddy Bay (low river herring) in eastern Maine, using stomach content and stable isotope analyses, to determine the prevalence of river herring (alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*) in nearshore (<4.5 km) groundfish diets. Invertebrates dominated all predator diets at all sites. At Midcoast sites, catch-per-unit-effort (CPUE) of Atlantic cod was higher, and fish predators showed a strong seasonal pattern in river herring consumption compared to Passamaqouddy Bay. Cod, pollock (*Pollachius virens*), and sculpins (*Myoxocephalus octodecimspinosus* and *M. scorpius*) from Midcoast sites tended to be enriched in $\delta^{15}N$ relative to Passamaquoddy Bay. Contrasting fast vs. slow turnover tissue (fin vs. muscle) indicated that focal species migrated or food availability changed seasonally and Atlantic mackerel (*Scomber scombrus*) in Passamaquoddy Bay were assimilating into a trophically depleted food web. We posit that lack of forage fish in Passamaquoddy Bay contributed to conditions that encourage an invertebrate based diet. River herring are also an order of magnitude less abundant in Passamaquoddy Bay than at Midcoast sites, limiting the availability of this seasonal food source. River restoration may contribute to recovery of groundfish stocks nearshore by increasing the availability of high lipid, seasonally available prey.

Keywords Cod · *Gadus* · Diet · River herring · Nearshore · Commercial fishing · Alewife · Groundfish

Introduction

Fisheries have had significant impacts on marine food webs worldwide, with the highest impacts in continental shelf and slope regions near human populations (Halpern et al. 2008; Worm et al. 2006). Fishing, as one of many potential anthropogenic drivers, has reduced biodiversity and affected marine food webs (Myers and Worm 2005; Worm et al. 2006) through trophic cascades (Pace et al. 1999), changes in community diversity (Worm et al. 2006), and serial depletion, replacement, and addition of species to the commercial harvest (Essington et al. 2006). Exploitation has increased the amount of energy concentrated in less commercially desirable components of the food web (Auster and Link 2009; Link et al. 2009), even though biomass among trophic guilds appears to remain constant (Link et al. 2009; Lotze and Milewski 2004; Nye et al. 2009).

An understanding of dietary preferences and food web relationships is useful for clarifying species roles and interactions within an ecosystem. The groundfish complex in the Gulf of Maine is a suite of species, including cod, haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes fasciatus*),

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hakes (*Urophycis* sp.), and flounders (Pleuronectidae), that occupy similar habitats and show a high degree of diet overlap. Historically, the most sought after of these fish was cod. We focus on cod here, among other species, because it is an iconic fish that has declined from the core of the US colonial fishery to an overfished commercial and recreational fishery (Department of Commerce 2016).

Cod consume fish and invertebrates, including arthropods, crustaceans, gastropods, and mollusks, feeding in both benthic and pelagic habitats (Collette and Klein-MacPhee 2002; Johannesen et al. 2012; Link and Garrison 2002). Cod undergo an ontogenetic diet shift at roughly 30-cm total length (TL), switching from an invertebrate-heavy juvenile diet to an adult diet with more fish (Garrison and Link 2000; Link and Garrison 2002; Sherwood et al. 2007). Research in the 1960s and 1970s detailed diet habits of cod and other groundfish, noting that consumption of fish prey was relatively rare in Maine bays and coves, even for cod over 30 cm TL (Hacunda 1981; Macdonald and Green 1986; Tyler 1971; Tyler 1972; Willis et al. 2013). These observations were counter to historic publications that made a direct connection between anadromous fish and commercially important marine groundfish (Field 1914). Fish poor groundfish diets of the 1960s and 1970s were likely related to excessive fishing pressure in the Northwest Atlantic by US and foreign fleets at that time (Melvin and Stephenson 2007; Overholtz 2002; Serchuk and Wigley 1992).

Recent studies have explored the connection between river herring, inshore cod spawning aggregations (Ames 2004) and winter grounds (Ames and Lichter 2013), positing that river herring prey was a driver of some groundfish behavior. Stomach content analysis of groundfish from the Gulf of Maine (Garrison and Link 2000; Link et al. 2009; Smith et al. 2007) and nearshore waters of Midcoast Maine (McDermott et al. 2015) have identified river herring as likely important to groundfish feeding behavior. These authors and others (Lake et al. 2012; Saunders et al. 2006) make strong and compelling arguments for restoring anadromous fish spawning habitat, particularly through dam removal, as a means of altering the decline of groundfish species.

Stable isotope analysis (SIA) is a commonly used tool for evaluating nutrient dynamics and food web structure (Boecklen et al. 2011; Michener and Kaufman 2007; Peterson et al. 1985). The method relies on the premise that the stable carbon and nitrogen isotope composition of an organism reflects that of its diet, with some known (or estimated) isotopic fractionation (Caut et al. 2009). The isotopic fractionation, or offset, between diet and animal tissue for ^{13}C and ^{15}N is approximately 1‰ (Sweeting et al. 2007b) and 3.4‰ (Minagawa and Wada 1984; Sweeting et al. 2007a), respectively. ^{13}C is indicative of the basal source of carbon in the food web, and ^{15}N is used to establish trophic position of an organism, provided the isotopic composition of nitrogen at the base of the food web is known.

SIA can integrate days, months, or sometimes years of diet habits into a single measure, depending upon the tissue turnover time of the body part analyzed (Dalerum and Angerbjörn 2005); thus, it is important to analyze the same tissue type when comparing isotopic data across multiple sites and species. Additionally, the temporal and spatial variability in isotope composition of primary producers must be included (Post 2002). In many cases, suspension feeders (e.g., mussels) and algal grazers (e.g., herbivorous snails) are used to estimate δ^{15}N at the base of the food web (Post 2002). SIA can also provide some information regarding habitat use. Carbon sourced from the nearshore benthic habitat tends to be higher (enriched) in ^{13}C compared to carbon sourced from pelagic or offshore habitats (Fredriksen 2003). Researchers have used stable isotope analysis to discern the influence of organic matter derived from terrestrial, phytoplankton, macroalgae, and saltmarsh sources on estuarine food webs in the Gulf of Maine (Deegan and Garritt 1997; Incze et al. 1982; McMahon et al. 2005; Peterson et al. 1986).

Diet item analysis (DIA) is also useful for determining food web structure, but is notorious for its “snapshot-in-time” nature. Different food items last longer in the gut (Davenport and Bax 2002; Hobson et al. 1994) and can bias DIA toward hard shelled prey like large decapods and gastropods. Variability in fish consumption, both temporally and by individual preference, can limit the wider applicability of DIA (Pinnegar and Polunin 2000).

Here, we investigate the relationship between anadromous fish and marine predators in the bays and coves of Maine within 5 km of shore. We assessed food web structure for readily captured demersal fishes (cod, mackerel, pollock, longhorn sculpin, and shorthorn sculpin) adjacent to large (Midcoast) and small (Passamaquoddy Bay) river herring runs. We hypothesized that differences in the availability of fish prey (e.g., anadromous river herring) would be apparent in the diets of predators (e.g., cod). Stomach content and stable isotope analysis were used as complementary and comparative methods to look for differences between sites and among predators. We also located historical diet studies of groundfish from coastal Maine (Hacunda 1981; Macdonald and Green 1986; Wainright et al. 1993; Willis et al. 2013) to provide a longer-term perspective on fish diets and ecosystem change through the last 50 years.

Methods

Study Area

Our study area included Passamaquoddy Bay and the Midcoast Maine (Fig. 1). We sampled fish and their prey at

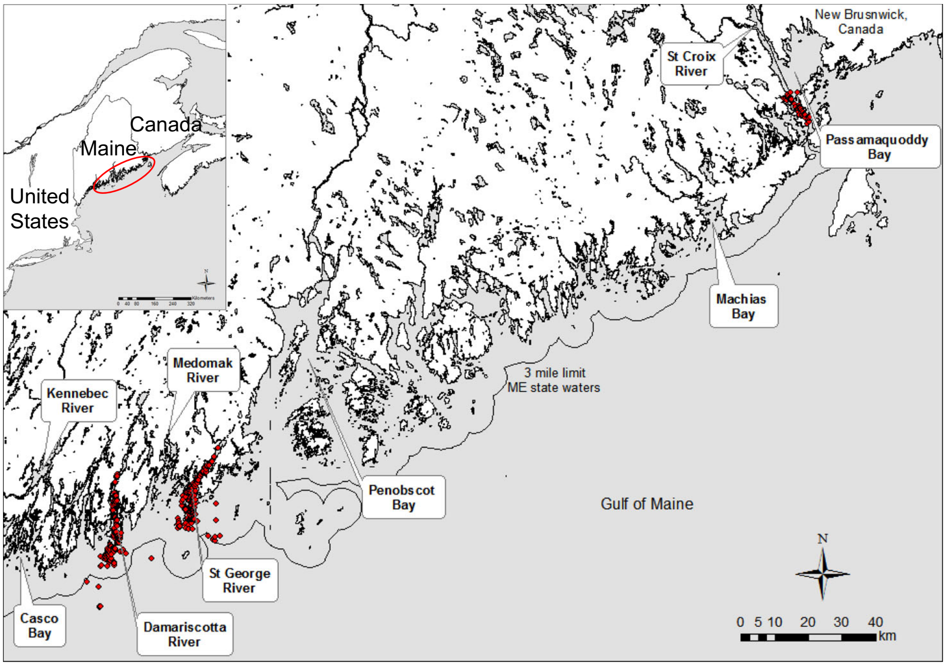

Fig. 1 Map of study areas located in Midcoast Maine and Passamaquoddy Bay on the Maine–New Brunswick border. Fish samples were collected from Damariscotta River, St. George River, and Passamaquoddy Bay between 2005 and 2008. *Points* indicate actual sampling locations. Crab isotope data were collected at Bailey Island, northern Casco Bay

three sites: one to the north (Passamaquoddy Bay) and two in Midcoast Maine, south of Penobscot Bay (St George and Damariscotta). August 2007 water temperature in Harpswell Sound (25 km west of the Damariscotta site) was 16.6 °C (2-m depth), compared to 11.1 °C (1-m depth) in Passamaquoddy Bay's Western Passage during the same period (Northeastern Regional Association of Coastal and Ocean Observing Systems 2014).

Passamaquoddy Bay is a branch of the Bay of Fundy between Maine, USA, and southwestern New Brunswick, Canada. It is delineated by an archipelago of islands (45.00° N, 66.95° W), which define the two principal entrances to the bay. Our sampling occurred in the Western Passage area (Fig. 1), through which tidal flows can reach 4 m $*s^{-1}$ (Trites and Garrett 1983), and the tide is semi-diurnal with a maximum range of 8.3 m (Brooking et al. 2006). Gravel is the most prevalent bottom type at the Passamaquoddy Bay site (49.1%), but rock or hard bottom (33.6%) and sand (17.2%) are also present (Barnhardt et al. 1998).

The Damariscotta River Estuary (Dam; 43.79° N, 69.56° W) and St. George River Estuary (Stg; 43.89° N, 69.29° W) are located within 26 km of each other and are referred to collectively as the Midcoast sites. Each of these sites also features an archipelago of 7–11 islands leading to a narrow drowned river mouth 2–3 km across. Tides are semidiurnal and range from 2.5–3.3 m (Lazzari et al. 2003). Hard (rock) bottom is the dominant bottom type for Damariscotta and St. George (77.3 and 60.8%, respectively) (Barnhardt et al. 1998). Sand (22%) is the second most prevalent bottom type at the Damariscotta site, and mud (37.7%) is the second most prevalent bottom type at the St. George site (Barnhardt et al. 1998). Damariscotta and St. George sites are more similar to each other than either is to Passamaquoddy Bay, as one would expect given their proximity (Fig. 1).

The Passamaquoddy and Midcoast sites differed dramatically in actual productivity (based on river drainages and lake surface area) of river herring runs (Table 1). The St. Croix River was once a rich source of anadromous baitfish for Passamaquoddy Bay, and direct harvests of river herring were substantial (Perley 1852). At the time of our study, the St. Croix River herring run was a fraction of its most recent high of 2.7 million fish in 1987 (Willis 2009) and an estimated carrying capacity of 22.6 million fish (Dill et al. 2010). Little River, a stream in Perry, ME, near our Passamaquoddy sampling site, also contributed some river herring to the bay (Table 1). The 34-km stretch of coast that includes the Midcoast sites encompasses three river systems, Damariscotta, Medomak, and St. George, and the productive (for river herring) Kennebec River lies just to the west. It has been hypothesized that river herring, particularly alewife, stabilized local populations of groundfish until dam construction limited this source of prey (Ames and Lichter 2013; Hall et al. 2010). Historically, the region was called the "Great Fishing Square" and supported the first European fishing camps to exploit the abundance of groundfish accessible within sight of land (Duncan 1992; Snow 1976). Reports from the Damariscotta, St. George, and Kennebec (including the Androscoggin tributary) rivers each showed river herring

Table 1 Estimated spawning runs of river herring (alewife and blueback herring) in the vicinity of sampling sites

Coastal site	River system	Accessible lake spawning area (ha)	Year	Estimated spawning run size	Source
Midcoast	Damariscotta	1918	2007	307,332	DFC
			2008	560,949	DFC
	St. George	1269	2007	516,355	MERHSFP
			2008	770,931	SGFC
	Medomak	164			
	Kennebec	3155	2006	794,020	MERHSFP
			2007	843,076	MERHSFP
			2008	1,011,012	MERHSFP
	Androscoggin	1800	2006	34,239	Maine DMR
			2007	60,662	Maine DMR
			2008	92,359	Maine DMR
Passamaquoddy	St. Croix	577	2005	11,632	SCIWC
			2006	11,829	SCIWC
			2007	1294	SCIWC
			2008	12,261	SCIWC
	Little River	689	2005	8008	MERHSFP
			2006	60,060	MERHSFP
			2007	80,080	MERHSFP
			2008	100,100	MERHSFP

Most spawning adults are 3–4 years in age. Size of spawning runs were used as indicators of the size of the river herring resource in the marine environment adjacent to our sampling sites. Each listing is a single counting location, except for Kennebec which constitutes five. St. Croix River counts are conducted at St. Stephen, New Brunswick, and the Little River is located in Perry, Maine

DFC Damariscotta Fish Committee, *MERHSFP* Maine ASMFC River Herring Sustainable Fishing Plan, *SCIWC* St. Croix International Waterway Commission

returns in excess of 300,000 individuals during our study period (Table 1).

Diet Collection and Analysis

Passamaquoddy Bay was sampled in July 2005, April–September 2006, July–October 2007, and May and July–October 2008. Midcoast estuaries were sampled only from May–September 2007, and May and July–October 2008. All sites were within 5 km of the mainland and within 0.5 km of the most seaward island.

Hook-and-line angling was used as the primary method for capturing focal species (e.g., cod, mackerel, pollock, longhorn sculpin, and shorthorn sculpin) to avoid gear conflicts with lobster traps, buoys, and lines. Choice of angling areas was based on bottom topography. Fish were captured using baited hooks and unbaited jigs within 2 m of the bottom sediment as the boat drifted across humps or bottom features where the sea floor shoaled from 25–36 m to 12–18 m. When bait was used, it was primarily cut fish (mackerel, herring, river herring, menhaden, *Brevoortia tyrannus* in order of use), or occasionally soft shell clam (*Mya arenaria*). Start and end time of the drift and number of hooks used were recorded to calculate catch-per-unit-effort (CPUE = catch × (persons fishing × minutes)$^{-1}$ × 60 min). Fishing relatively shallow areas reduced cases of barotrauma and regurgitation. A fish with obvious signs of barotrauma was counted as having an "empty" stomach, and only tissue was collected from these specimens for stable isotope analysis. See Willis et al. (2013) for a more detailed description of fishing methods, including discussion of hook vs. mobile gear bias. In brief, angling collects a smaller size range of fish than trawl gear but with no difference in diet composition or empty vs. nonempty stomachs.

Captured fish were held in a flow-through live well until processed for stomach contents and SIA. Typically, 30 min or less elapsed between capture and processing. We obtained diet samples from cod, mackerel, pollock, and sculpins >15 cm in TL. We separated cod into two categories (small, <30 cm TL, and large, ≥30 cm TL) based on ontogenetic shifts in cod diet preference and obvious breaks in the size distribution (Link and Garrison 2002). Gastric lavage was used to flush the fish stomachs (Hartleb and Moring 1995). Fish were first placed in a weak solution of MS-222 (2 g to 4 L of seawater) until they displayed loss of equilibrium. A 13-mm outer diameter tygon tube connected to a 4-L garden sprayer filled with seawater was inserted into the fish stomach. The stomach was filled with water and gently squeezed. Regurgitated diet items were captured on a 500-μm sieve. Hard, large objects (e.g., crabs) could be felt through the stomach wall after the first flush, triggering a second flush or manual removal (using 30 cm forceps) of diet items that became lodged in the sphincter at the top of the stomach. Tissue samples (dorsal muscle, scales or fin) for SIA were removed after gastric lavage as well. Most fish were released alive after recovery; there was a >75% survival to release for nondissected fish. Mortalities were used to collect additional tissue samples and to test for gastric lavage efficiency.

Gastric lavage quickly stops digestion because digestive acids are rinsed from the sample, and the diet items come in immediate contact with the preservative, a mixture of alcohols and polyethylene glycol (Warmington et al. 2000). The efficiency of diet collection was tested quantitatively to confirm that gastric lavage was effective in flushing diets from the focal species (cod = 85%, $n = 20$; mackerel = 91%, $n = 23$; pollock = 100%, $n = 20$; sculpins = 85%, $n = 21$). Fish were first lavaged, then euthanized before their stomach was excised to check for additional stomach items. In addition, all technicians were trained in the gastric lavage method by the same PI. When necessary, fish were sacrificed with an overdose of MS-222.

Diet items were identified to the lowest taxonomic level feasible (usually family), counted, and total wet weight for each type of diet item was recorded. Most major diet items were collapsed into large categories for analysis (e.g., crab, amphipod), because, for any given diet, the degree of digestion differed and thus affected the level of taxonomic identification that could be achieved. Proportions of diet contents were expressed as an index of relative importance (%IRI) which accounts for number (N), weight (W), and frequency of occurrence (O) of individual diet items (Garvey and Chipps, 2012; Liao et al., 2002; Willis, 2009):

$$\%\mathrm{IRI} = 100 \times (\%\mathrm{O} \times (\%\mathrm{W} + \%\mathrm{N}))$$

Blue mussels (*Mytilus edulis*) were used to estimate the baseline isotope composition of the pelagic food web at all three sites. The isotopic composition of mussel foot tissue represents an integrated signal of diet spanning several weeks which smooths out the spatial and temporal variability of primary producers consumed by these organisms (Dalerum and Angerbjörn 2005; Post 2002). Mussels and all fish tissues were dried at 60 °C for 48 h and homogenized with a mortar and pestle. Mussels were sampled opportunistically from the same locations where fish were collected.

Several of the dominant prey species (as determined from stomach content analysis) were analyzed for stable isotope content. These included river herring and Atlantic herring from the St. George and Passamaquoddy Bay sites, Caprellidae and other amphipoda from the Passamaquoddy Bay site, and Jonah (*Cancer borealis*), rock (*Cancer irroratos*), and green (*Carcinus maenas*) crabs from Bailey Island (Casco Bay), just west of the Damariscotta sites. Crabs were collected and analyzed for SIA in 2007 and 2008 for another study and are presented here.

For SIA of fish, a portion of the anal fin was removed with scissors. Fin membrane was targeted during sampling; however, fin rays were occasionally incidentally sampled as well. Dorsal muscle was collected from a subset of sacrificed fish by removing a 1-cm cube of tissue from a skinless dorsal filet. Fin and muscle were compared for consistency between tissue types and to see whether fin, which was collected from more fish, could be used to increase sample sizes. Fin tissue also records more recent (weeks) diet data due to its fast tissue turnover properties, whereas muscle represents longer-term diet habits based on tissue turnover at the scale of months or longer (Heady and Moore 2013; Perga and Gerdeaux 2005). Differences in isotopic results of fin and muscle tissues for an individual fish meant that the fish had changed diets in the recent past, due to changes in foraging strategy or food available for consumption. For SIA, whole bodies of Caprillidae and amphipods and leg muscle tissue of crabs were dried or lyophilized and homogenized using a mortar and pestle.

Approximately 0.5 mg of dried and powdered tissue per organism was analyzed for ^{13}C and ^{15}N stable isotope composition at two labs. A DeltaPlus XP isotope ratio mass spectrometer (IRMS) interfaced to a Costech ECS4010 Elemental Analyzer (EA) via a ConFlo III was used at the University of New Hampshire Stable Isotope Laboratory and a Thermo Delta V Advantage coupled to a Costech ECS4010 EA via a ConFlo III combustion interface was used at the Environmental Geochemistry Laboratory, Bates College, Maine. All stable isotope values are reported in delta (δ) notation, in units of permille (‰), where $\delta = [((R)_{\mathrm{sample}}/(R)_{\mathrm{standard}}) - 1) \times 1000]$, and $R = {}^{13}\mathrm{C} \times ({}^{12}\mathrm{C})^{-1}$ or ${}^{15}\mathrm{N} \times ({}^{14}\mathrm{N})^{-1}$, and the standards are Vienna PeeDee Belemnite, and air for carbon and nitrogen, respectively. Ten percent of the samples were run in replicate between the two labs; the mean standard error of cross-lab replicates was 0.07‰ for N and 0.02‰ for C.

C/N values provide information on the type and purity of the tissue analyzed. The C/N value of proteins typically ranges between 3.5 and 4.0 (Graham et al. 2013). Neither hydroxyapatite, a potential contaminant to the fin tissues from fin ray bone, nor lipids, a potential contaminant of muscle, contain any nitrogen. The presence of these components might elevate the C/N of the bulk tissue significantly, and bias the isotopic results. We excluded samples with C/N greater than 4.0 from our data analyses to ensure that isotopic comparisons were made solely between muscle and fin proteins.

Data Analysis and Statistics

Principal component analysis (PCA) was used to compare fish diet data (%IRI) among sites and years using Primer 6 (v.6.1.13) and Systat 12 (v.12.00.08). Diet data (%IRI) were cube root transformed to achieve multivariate normality. Analysis of covariance (ANCOVA) was performed to assess the influence of location and fish size on δ^{15}N and δ^{13}C content of muscle or fin tissue. The ANCOVA determines whether the dependent variable (here δ^{15}N or δ^{13}C) is different among the locations sampled despite differences in length of fish sampled at each site (covariate). A homogenous SIA vs. length slope means that SI can be evaluated without confounding variance between length and location.

Results

Catches and Diet Data

CPUE differed among the three sites for different species. Cod and pollock were rare in Passamaquoddy Bay and abundant at Midcoast sites (Table 2). Mackerel were abundant in all locations, particularly in Passamaquoddy Bay. Conversely, shorthorn and longhorn sculpins were prolific at the Passamaquoddy Bay site, but rare at the Midcoast sites (Damariscotta and St. George).

Diet of the five focal species showed considerable overlap in %IRI within sites but also showed some common themes between locations (Table 3). Amphipods in the families Caprellidae and Aoridae were the most prevalent items in fish diets across sites and fish species. At the Passamaquoddy Bay site, amphipods were dominant in the diets of all five focal species with IRIs over 50% (Table 3). Lobster ranked second and fourth in importance for shorthorn sculpin from Damariscotta and St. George, respectively, but no lobster were found in the diets of any fish species from Passamaquoddy Bay. Crab was the top ranked diet item for both sculpin species from St. George and Damariscotta and for cod caught at the St. George site. Fish was not statistically significant in the diet item of any species at any location (Fig. 2), but was a “top three” diet item for Damariscotta large cod (IRI score 33%) and for St. George pollock (IRI score 33% [Table 3]).

Cod and mackerel CPUE was lowest in the spring and increased in the summer and fall (Fig. 3a, c). Fish were more prevalent in diets in the fall of 2007 for cod, mackerel, and pollock (Table 4). However, on average, fish were found in about 40% (frequency of occurrence) of the cod collected from Damariscotta and St. George, regardless of season; frequency of occurrence of fish was higher for Passamaquoddy Bay cod, though CPUE for cod was lower (Fig. 3b). Clupeid fishes (Atlantic herring and river herring) were positively identified in diets in the fall of 2007; the majority of those clupeids were juveniles found in diets of mackerel and pollock.

Ordination of IRI scores grouped combinations of species and sites into three loose clusters based on diet content. PCA groups sites into clusters based on the similarity in species composition found at those sites. Sites with more similar species lists in more similar proportions are placed closer together in n-dimensional space. Here, sites are the species location combinations (e.g., Stgcod = St. George small cod) and diet contents are the equivalent of species lists. The PCA explained 38 and 32% of the variation in diet among combinations of species and sites on principal components axis 1 (PC1) and axis 2 (PC2), respectively (Fig. 2); an additional 11% of the variation in diet was explained on principal components axis 3 (not shown). Mackerel from all three sites grouped together based on a high occurrence of zooplankton in the diets. Passamaquoddy Bay large and small cod, pollock, and both species of sculpin grouped together based on a high occurrence of amphipods. Small Damariscotta cod also had amphipods as a large component of their diets. Sculpins and large cod from the Midcoast sites grouped together based on a high occurrence of decapod crustaceans in the diets, crab being more prevalent than lobster. Lobster only made up 3–6% of the diet for Midcoast cod. St. George and Damariscotta pollock did not cluster with other species, emblematic of their varied diet (Table 3). Fish were not a statistically significant vector in the PCA ($p > 0.05$).

Isotope Data

Blue mussel isotope values were similar across sites and with other reported mussel data from the Gulf of Maine (Lesser et al. 2010), suggesting similar baseline conditions that facilitated direct comparison of δ^{15}N data, in particular, across sites. The average δ^{15}N from all three sites was 8.3‰ (±0.2 SD). Mean δ^{13}C values for all three sites was −18.8‰ (±0.6 SD).

Muscle and fin samples were compared in two ways: muscle vs. fin by site and species; only matching muscle vs. fin tissue from the same individual fish. Fin and muscle tissue differed by site only for Passamaquoddy Bay mackerel (^{15}N) and Passamaquoddy longhorn sculpin (^{13}C) (Table 5). Mackerel fins were significantly depleted in ^{15}N and pollock fins were significantly enriched in ^{13}C (Table 6) compared to muscle for tissues from the same fish. Except for these instances, muscle and fin values were interchangeable indicating that most species were consuming isotopically similar diets over timescales of months (recorded in muscle) to weeks (recorded in fins). Most analyses going forward were conducted on fin tissue

Table 2 Sample size and other collection statistics for the five focal species from the three sample sites

Species	Location	*N*	CPUE	*n* stomachs	Empty %
Atlantic cod	Damariscotta	179	1.6	174	3.9%
	St. George	109	1.1	106	2.8%
	Passamaquoddy	25	0.3	25	0.0%
Atlantic mackerel	Damariscotta	285	2.5	183	5.3%
	St. George	298	3.1	195	2.3%
	Passamaquoddy	403	4.3	212	6.5%
Pollock	Damariscotta	262	2.3	76	1.5%
	St. George	136	1.4	24	0.7%
	Passamaquoddy	33	0.4	33	0.0%
Sculpin, longhorn	Damariscotta	51	0.5	36	15.7%
	St. George	22	0.2	17	4.5%
	Passamaquoddy	215	2.3	128	11.2%
Sculpin, shorthorn	Damariscotta	27	0.2	7	3.7%
	St. George	16	0.2	5	6.3%
	Passamaquoddy	215	2.3	89	21.9%

Catch-per-unit-effort (CPUE) is expressed as number of fish collected per hour of angling

N total number of fish caught, *n stomachs* total number of stomachs sampled, *Empty %* percent of empty stomachs

because of the larger number of fins collected, the exception being mackerel in which case muscle tissue was used.

The δ^{15}N values for fish from the Midcoast sites were consistently enriched relative to fish from Passamaquoddy Bay (Table 7; Fig. 4), despite similarities in baseline mussel SI values. Slopes of length vs. δ^{15}N relationships were homogenous allowing influence of length to be accounted for in all comparisons except cod. Length was a significant covariate in explaining δ^{15}N of all species, as expected with ontogenetic shifts in fish size and size of prey. The strong effect of site vs. δ^{15}N for cod was confounded by the steep, positive, nonhomogenous slope of the length vs. δ^{15}N regression for Passamaquoddy Bay cod (Fig. 4; Table 7). The shorthorn sculpin ANCOVA was statistically significant for δ^{13}C between sites, but Tukey's post hoc test did not indicate what sites were statistically different.

Corroborating Diet Analysis Methods

Stable isotope data from predatory fish in our study corroborated well with observed stomach contents (DIA). For example, the δ^{15}N values were lower in fish from Passamaquoddy Bay than those from the Midcoast, corresponding to low trophic level prey in fish diets. The average longhorn sculpin diet from Passamaquoddy Bay contained 89% amphipods (δ^{15}N = 6.4), compared to that from Damariscotta, which contained 80% crab (δ^{15}N ranged between 9.5 and 12.2‰; Table 5). The difference in carbon source also agreed between diets and SIA values. Crab and amphipod were heavily represented in sculpin diets compared to cod diets (Table 3), and δ^{13}C SIA values reflected more benthic energy sources in sculpin tissue and more pelagic energy sources in cod tissue (Table 5). For example, the contribution of pelagic sourced carbon was apparent in Passamaquoddy Bay when compared between cod (55% amphipods, δ^{13}C = −17.7‰) and shorthorn sculpin (60% amphipods, δ^{13}C = −15.9‰).

Discussion

We noted an increase of predator presence in the nearshore in the fall, concurrent with more (juvenile) fish, including river herring, appearing in predator diets. We expected adult river herring to be prevalent in the diet of cod from the Midcoast because of the large spawning migration that occurs there, but this was not the case. Fish (as a broadly defined diet item) was a top three diet item for large Atlantic cod from Damariscotta and pollock from St. George. Juvenile river herring comprised up to 41% of the fish in the diets of all fishes collected in the Damariscotta region of the Midcoast in fall 2007. In other years, the river herring pulse, seasonal outmigration of juveniles from freshwater habitat to the ocean, was overwhelmed by decapods in the diets of Midcoast fish, and amphipods in the diets of Passamaquoddy Bay fish. McDermott et al. (2015) used trawl gear in 2010–2011 in the Midcoast region to address similar questions regarding river herring as groundfish prey, finding that the odds of encountering river herring in groundfish stomachs was highest closest to the rivers where river herring spawn. Smith et al. (2007) noted a similar seasonal pulse pattern of fish prey in cod diets.

The pulse-like nature of river herring as prey may play an important role in the recovery of cod stocks. Sherwood and

Table 3 Proportional diet composition of focal species based on index of relative importance (%IRI, presented as a fraction) for Damariscotta (Dam), St. George (Stg), and Passamaquoddy (Pas) sites

	Amph	Biva	Crab	Fish	Gast	Kr-my	Lobs	Poly	Shri	Zoop	Other
Atlantic cod, all sizes											
Dam	*0.193*	0.011	0.173	*0.243*	0.001	–	0.034	0.100	*0.185*	0.001	0.059
Stg	*0.184*	0.007	*0.345*	0.079	–	0.001	0.027	0.066	*0.231*	0.001	0.059
Pas	*0.580*	0.057	0.038	*0.176*	–	*0.068*	–	0.041	0.036	–	0.005
Atlantic cod, large											
Dam	0.045	0.005	*0.197*	0.331	–	–	0.062	0.034	*0.244*	–	0.082
Stg	*0.124*	0.007	*0.405*	0.111	–	–	0.038	0.027	*0.233*	–	0.055
Pas	*0.553*	0.048	0.032	*0.209*	–	*0.081*	–	0.040	0.033	–	0.005
Atlantic cod, small											
Dam	*0.421*	0.030	*0.102*	0.082	0.002	–	0.001	*0.226*	0.101	0.001	0.033
Stg	*0.200*	0.008	0.042	0.003	–	0.003	–	*0.176*	*0.149*	0.002	0.068
Pas	*0.650*	*0.145*	*0.115*	–	–	–	–	0.020	0.062	0.004	0.004
Atlantic mackerel											
Dam	0.001	0.004	–	*0.256*	0.001	–	–	0.001	0.001	*0.729*	*0.007*
Stg	–	–	–	*0.076*	–	0.004	–	–	0.003	*0.885*	*0.031*
Pas	*0.100*	–	–	0.058	–	0.110	–	0.001	0.001	*0.725*	*0.005*
Pollock											
Dam	*0.338*	*0.121*	–	0.120	0.088	–	–	–	–	*0.321*	0.010
Stg	*0.327*	0.034	–	*0.332*	*0.259*	0.001	–	0.011	0.002	0.024	0.010
Pas	*0.683*	*0.305*	–	–	0.001	–	–	–	–	*0.009*	0.001
Sculpin, longhorn											
Dam	–	0.003	*0.798*	0.007	–	–	*0.118*	0.001	–	–	*0.071*
Stg	0.003	*0.035*	*0.925*	0.003	–	0.002	0.007	0.001	0.003	0.001	*0.022*
Pas	*0.894*	0.002	0.002	*0.057*	–	–	–	*0.037*	0.001	–	0.007
Sculpin, shorthorn											
Dam	0.010	0.013	*0.538*	–	–	–	*0.336*	–	–	0.019	*0.084*
Stg	*0.334*	0.008	*0.377*	0.013	–	–	*0.246*	–	–	0.003	0.019
Pas	*0.602*	0.004	*0.118*	0.031	–	0.003	–	*0.206*	0.001	–	0.034

Atlantic cod were split into small (fish <30 cm TL) and large (≥30 cm TL) categories to account for ontogenetic shifts in feeding preference. The top three prey items by %IRI score for each species-site combination are in italics. Column headers are diet items: *Amph* = amphipod, *Biva* = bivalve, *Crab* = crab, *Fish* = fish, *Gast* = gastropod, *Kr-my* = krill-mysid, *Lobs* = lobster, *Poly* = polychaete, *Shri* = shrimp, *Zoop* = zooplankton

Rose (2005) argued that seasonally available high protein, high lipid prey is important for the reproductive cycle of cod. Yearling river herring are present in the nearshore Gulf of Maine in the fall, along with the predators that consume them. Because benthic organisms (e.g., crabs and amphipods) are less nutritious than fish (Mullowney and Rose 2014, Sherwood and Rose 2005, Lawson et al. 1998), we posit that lower quality diet items currently being consumed by cod might be contributing to limited recruitment and a small cod population in the nearshore Gulf of Maine.

Fin vs. Muscle (Short-Term vs. Long-Term Feeding Strategies)

Stable isotope values of different tissues often vary depending on their carbon and nitrogen turnover rate (Ankjærø et al. 2012; Sweeting et al. 2007a; Sweeting et al. 2007b). Differences in muscle vs. fin tissue turnover can be interpreted as a recent diet or habitat change. White dorsal muscle tissue, which is most frequently used for SIA, has a turnover time of between 60 and 86 days (Ankjærø et al. 2012). Fin, particularly at the end or tip where new growth occurs, has a shorter turnover time (days to weeks) and reflects the current diet (Boecklen et al. 2011; Dalerum and Angerbjörn 2005; Heady and Moore 2013). The cod we sampled had very similar stable isotope values for fin and muscle, indicating stability in diet and habitat use. In contrast, mackerel from Passamaquoddy Bay showed fin SIA values that were significantly depleted in δ^{15}N compared to muscle, suggesting a more recent shift toward lower trophic level feeding. SIA may be reflecting the ability of mackerel to switch from consuming fish to zooplankton depending upon, we presume, prey availability; a phenomenon we observed in the field (K. Wilson, personal observation). Another hypothesis is that mackerel were "new arrivals" to Passamaquoddy Bay where fish, or some other high trophic level prey, was not as abundant as in a previous habitat. Evidence of the shift was stored in the fast turnover tissue. We interpret this difference in mackerel tissue vs. fin δ^{15}N as indicating the pattern from Passamaquoddy Bay of depleted δ^{15}N is endemic to the food web found in that region.

Benthic vs. Pelagic Organic Matter Sources in the Nearshore Food Web

Carbon isotope values of cod, pollock, and sculpins from Passamaquoddy Bay aligned most closely with Caprellidae

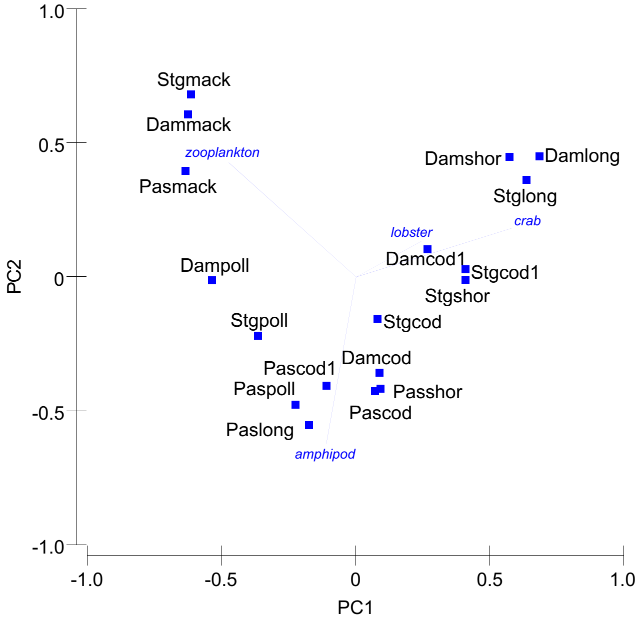

Fig. 2 Results of principal components analysis depicted with joint plot of diet contents. Rays displayed have significant Pearson correlation of $p < 0.05$. PC axes 1 and 2 correspond to diet items that defined differences among species diets. Ray length is proportional to the importance of the diet item. The farther from the origin a point is on a ray axis, the stronger the association of that diet item with diets of that species-site combination. Pas = Passamaquoddy, Dam = Damariscotta, Stg = St. George; cod = Atlantic cod <30 cm, Atlantic cod1 = cod ≥30 cm, mack = Atlantic mackerel, poll = Pollock, long = Longhorn sculpin, shor = Shorthorn sculpin

($\delta^{13}C = -17.6‰$) and other amphipoda ($\delta^{13}C = -16.7‰$), providing a link between microphytobenthos production and upper trophic levels (Thiel 1999). Aoridae made up the largest proportion of amphipods in fish diets from Passamaquoddy Bay, in particular the species *Leptocheirus pinguis*, a burrowing amphipod with documented parental care behavior (Thiel et al. 1997). Previous work in Passamaquoddy Bay demonstrated that not only are *L. pinguis* and *Unicola* spp. abundant, but they are chosen as prey more frequently than their abundance would indicate for simple opportunistic predation (Macdonald and Green 1986). *L. pinguis* and *Unicola* spp. are also present at Midcoast sites, but other prey was either more plentiful or preferred by demersal predators.

Interestingly, blue mussel $\delta^{13}C$ and $\delta^{15}N$ signals were similar across all sites, indicating that the base production in the Midcoast and Passamaquoddy food webs was similar. Thus, the observed enriched Midcoast $\delta^{15}N$ signal in decapods and decapod predators would have to originate from some pathway other than local pelagic primary production, suggesting that we may have seen an effect of lobster fishing related to higher trap densities in Midcoast Maine. Baited lobster traps introduce hundreds of metric tons of pelagic zooplanktivorous fish (e.g., Atlantic herring) to the benthos along the Maine coast, and the Midcoast region is one of the most heavily trapped areas in Maine. Lobster have a significantly enriched $\delta^{15}N$ value that is correlated with trap density (Grabowski et al. 2010; Grabowski et al. 2009), i.e., correlated with access to a fish-based diet. Thus, lobsters, crabs, and predators of the ^{15}N-enriched species that visit lobsters traps would be expected to show relatively enriched $\delta^{15}N$ values. Although lobsters were not prevalent diet items in this study, crabs are frequently encountered as bycatch in lobster traps and crabs were common diet items.

Fishing as an Ecosystem Driver

It is important to put the results we found in the context of overall changes to nearshore ecosystems in the Gulf of Maine

Fig. 3 Catch rate (CPUE) of Atlantic cod (**a**) and Atlantic mackerel (**c**) by site and season. The average proportion of fish in Atlantic cod (**b**) and Atlantic mackerel (**d**) diets by site and season are also presented. CPUE and diet proportions were averaged over 2007 and 2008, years when all three areas were fished concurrently. *Error bars* are ±1 SD. See Table 4 for dates corresponding to seasons. Black = Damariscotta, white = St. George, gray = Passamaquoddy

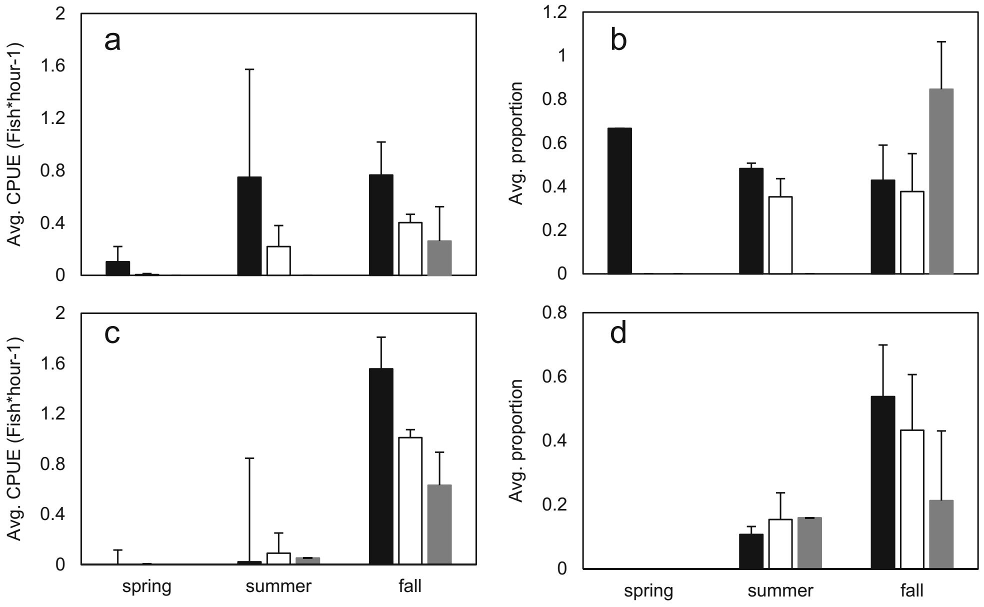

Table 4 Seasonal catch of predators with fish in diets

		2007			2008		
Species	Site	Spring	Summer	Fall	Spring	Summer	Fall
Atlantic cod ≥30 cm	Dam	3/3/2/0	16/16/9/0	31/31/18/2	3/3/2/0	22/22/13/0	41/41/15/0
	Stg	1/1/1/0	14/14/7/0	14/14/9/0	0/–/–/–	4/4/3/0	40/40/14/0
	Pas	-	0/–/–/–	12/12/9/0	0/–/–/–	0/–/–/–	3/3/3/0
Atlantic mackerel	Dam	0/–/–/–	15/14/3/0	71/60/39/20	0/–/–/–	58/0/–/–	149/108/46/0
	Stg	0/–/–/–	39/39/12/0	41/35/17/6	0/–/–/–	0/–/–/–	165/121/46/2
	Pas	–	59/22/7/3	79/46/10/0	0/–/–/–	102/0/–/–	174/144/30/1
Pollock	Dam	0/–/–/–	30/20/5/0	59/55/33/4	14/0/–/–	21/0/–/–	145/1/1/0
	Stg	0/–/–/–	13/4/2/0	20/20/16/0	32/–/–/–	0/–/–/–	77/–/–/–
	Pas	-	1/–/–/–	4/3/1/1	0/–/–/–	1/0/–/–	27/0/–/–

Numbers correspond to: total collected/number examined/number eating fish/number eating fish identified as Clupeidae (Atlantic herring or river herring). No sampling trips were taken at the Passamaquoddy site in spring of 2007. Seasons roughly correspond to dates of spring = May 15–June 9; summer = July 23–August 30; fall = September 14–October 25

– no data

over time. We attempted to focus on cod, but this species was relatively rare compared to other noncommercial groundfish. Previous studies of Passamaquoddy Bay in the 1960s and Midcoast sites in the 1970s revealed that cod food webs were dominated by small bodied prey, such as amphipods, carideans, euphausiids, and mysids (Hacunda 1981; Macdonald and Green 1986; Tyler 1971; Tyler 1972; Willis et al. 2013). Indeed, for locations over 250 km apart with different temperature regimes and substrate types, the diets of cod in this study looked remarkably similar for that time period. The results of this study indicate a divergence in diets, where Midcoast diets had more fish than reported in the 1970s, but Passamaquoddy Bay diets were essentially the same. How has Midcoast Maine changed?

The proliferation of lobster fishing in Maine has changed accessibility to fishing grounds for mobile gear fishermen. Groundfish rebuilding efforts associated with the Magnuson-Stevens Fishery Act of 1976 effectively reduced nearshore fishing effort that had increased steadily since the 1940s (Ames 2004; Serchuk and Wigley 1992). Many day-boat fishermen (~10 m vessels) switched to lobstering in the 1990s (Acheson 2006; Acheson 2013; Steneck et al. 2011), with a resultant increase in stationary fishing gear that interfered with trawls and dredges. Landing trawl-caught lobster is illegal in Maine (Sec. 2. 12 MRSA §6432, sub-§1), which also helped displace bottom trawl gear from state waters. Stationary gear is comparatively less dense in Passamaquoddy Bay (T. Willis, personal observation) and mobile gear trawl fisheries include scallop in winter, sea cucumber and groundfish in summer, and urchin in the fall. In addition, most of Passamaquoddy Bay is in Canada, which has different fishing seasons and effort than Maine fisheries, e.g., additional scallop season in summer.

Fishing activity could explain the food web differences we found between Damariscotta and the Midcoast, either through lobster trap bait, as discussed above, mobile gear habitat disturbance, or "competition" between fish predators and fishermen for midtrophic level prey. Commercial fishing, particularly mobile gear, has a measureable effect on food webs and predator stable isotope values, i.e., low diversity, bottom disturbance, and reduced trophic position of predators (Badalamenti et al. 2002; Fanelli et al. 2010; Robinson et al. 2001; Shephard et al. 2014; Wainright et al. 1993). Some of these negative effects were documented in the Passamaquoddy Bay region (Robinson et al. 2001). Researchers have also documented lower δ^{15}N values for predatory fishes whose fish prey become less abundant. For example, Gomez-Campos et al. (2011) documented lower δ^{15}N values for adult striped dolphin (*Stenella coeruleoalbaa*) because of commercial exploitation of sardine. Wainright et al. (1993) documented a decline in George's Bank haddock (*Melanogramus aeglefinus*) δ^{15}N which, they commented, could have been indicative of a change in haddock feeding ecology related to pelagic prey availability or injection of δ^{15}N depleted material into the food web through bottom disturbance. This statement referred, at least in part, to the overfishing of George's Bank Atlantic herring prior to the stock collapse of 1977 (Melvin and Stephenson 2007; Overholtz 2002). In nearshore Maine, we did not see evidence of depleted material injection in the δ^{15}N signature of blue mussels (Table 5), but we did document filter feeding and detritivorous amphipods depleted by 1.3 to 1.9 ‰ relative to blue mussels in Passamaquoddy Bay. This indicates that ^{15}N depleted nitrogen may be important for detritivores in the Passamaquoddy Bay system and begs for additional study.

Table 5 Mean isotope values for all food web constituents analyzed, reported in ‰ (±1 SD)

Species	Location	*n* muscle/*n* fin	δ^{15}N muscle	δ^{15}N fin	δ^{13}C muscle	δ^{13}C fin
Atlantic cod large	Dam	12/45	14.7 (0.5)	14.9 (0.6)	−17.1 (0.4)	−17.23 (0.6)
	Stg	12/43	14.8 (0.5)	14.9 (0.7)	−16.6 (0.3)	−16.6 (0.6)
	Pas	2/15	12.3 (0.6)	12.3 (1.0)	−17.8 (0.4)	−17.7 (0.6)
Atlantic cod small	Dam	14/22	13.5 (0.6)	13.9 (0.7)	−17.3 (0.5)	−17.1 (0.9)
	Stg	6/16	14.2 (0.4)	14.0 (0.7)	−16.8 (0.2)	−17.0 (0.6)
	Pas	0/1		11.6		−18.1
Atlantic mackerel	Dam	11/1	12.6 (0.6)	12.6	−19.6 (0.4)	−19.8
	Stg	11/1	12.9 (0.4)	11.3	−19.7 (0.7)	−19.9
	Pas	25/15	12.9 (0.4)*	11.6 (0.4)*	−19.9 (0.6)	−19.4 (0.5)
Pollock	Dam	7/6	12.5 (0.6)	12.9 (0.3)	−18.7 (0.7)	−18.1 (0.3)
	Stg	10/6	12.7 (0.3)	12.9 (0.6)	−18.3 (0.4)	−17.6 (0.5)
	Pas	3/6	11.7 (0.5)	11.6 (0.7)	−17.6 (0.5)	−17.1 (0.6)
Longhorn sculpin	Dam	0/31		14.1 (0.5)		−15.8 (0.4)
	Stg	0/15		14.4 (0.4)		−15.5 (0.5)
	Pas	5/36	12.6 (0.7)	12.0 (0.8)	−17.2 (0.5)*	−16.3 (0.7)*
Shorthorn sculpin	Dam	0/22		14.3 (0.5)		−15.3 (0.7)
	Stg	0/11		13.8 (0.5)		−15.4 (0.7)
	Pas	17/44	13.0 (0.9)	12.5 (0.9)	−15.9 (1.2)	−15.9 (0.9)
River herring	Stg	14/1	11.4 (0.2)	10.3	−19.6 (0.5)	−18.3
Atlantic herring	Stg	5/4	11.3 (0.5)	10.5 (0.8)	−19.4 (0.9)	−18.2 (1.3)
	Pas	4/1	12.4 (0.2)	11.5	−18.4 (0.3)	−16.2
Blue mussel	Dam	2	8.6 (0.8)		−18.6 (0.3)	
	Stg	1	8.1		−19.4	
	Pas	4	8.2 (0.6)		−18.3 (0.6)	
Rock crab	BI	3	12.0 (0.5)		−17.1 (0.6)	
Jonah crab	BI	3	11.8 (0.8)		−17.3 (0.3	
Green crab	BI	2	9.5 (0.8)		−16.0 (0.8)	
Amphipods	Pas	comp	6.4		−16.7	
Krill	Pas	comp	7.7		−20.2	
Caprellidae	Pas	comp	7.0		−17.6	
Tunicate	Pas	5	7.4 (0.6)		−22.3 (0.8)	

SIA sample size is represented by the number of muscle and fin tissue samples, *n* muscle/*n* fin. "Comp" indicates composite (pooled) samples of invertebrates

BI Bailey Island, Maine (43.7099 N, −70.0036 W)

*Muscle-fin comparisons that were statistically different using a Bonferroni-corrected *t* test

River Restoration and Nearshore Food Webs

Restoring river herring has been touted as a panacea for restoring the nearshore food web in the Gulf of Maine. Recent restoration efforts have led to differences in river herring abundance in bays of the Maine coast. There was an order of magnitude difference in river herring run size between Passamaquoddy Bay and Midcoast Maine (Table 1), and those numbers likely underestimate the total number of adults because fishways do not pass all the fish that return to spawn (Brown et al. 2013). Where the biggest river herring restoration gains have been made we found evidence of more fish in cod diets, higher cod CPUE and more diverse cod diets. River herring were prevalent in seasonal pulse events as juveniles, dropping into the coastal zone in the later summer and fall (K. Wilson, personal observation). We directly observed juvenile river herring being consumed by cod, mackerel, and pollock in the Midcoast, confirming the assertions of Field (1914): "the value of the alewife [is] as a food for the larger fish which frequent the Massachusetts waters." However, recovery of spawning aggregations of groundfish (Ames 2004; Ames and Lichter 2013) may be many years into the future, as illustrated by cod fishing being deemed unsustainable in the Gulf of Maine in the 1990s (Acheson 2006; Hennessey and Healey 2000) and again in the 2010s (Department of Commerce, National Oceanic and Atmospheric Administration, D.O.C.,

Table 6 Comparison of mean δ^{15}N and δ^{13}C values for muscle vs. fin tissue limited to individuals that contributed both types of tissue

Species	Number	Muscle	Fin	*p* value
Atlantic herring δ^{15}N	5	11.4 (0.7)	10.7 (0.8)	0.2
δ^{13}C		−19.2 (1.1)	−17.8 (1.4)	0.1
Atl. cod lrg δ^{15}N	18	14.5 (1.0)	14.5 (0.9)	1.0
δ^{13}C		−16.9 (0.5)	−16.7 (0.9)	0.7
Atl. cod sml δ^{15}N	18	13.7 (0.6)	14.0 (0.6)	0.2
δ^{13}C		−17.2 (0.4)	−17.1 (0.8)	0.8
Atl. mackerel δ^{15}N	23	13.0 (0.4)	11.7 (0.4)	<0.001*
δ^{13}C		−20.0 (0.8)	−19.7 (0.6)	0.3
Pollock δ^{15}N	14	12.4 (0.6)	12.6 (0.7)	0.6
δ^{13}C		−18.3 (0.6)	−17.7 (0.6)	<0.05

Samples were pooled across sites. A Bonferroni-corrected *t* test was used at the $p < 0.05$ level to test for significant differences in mean values (±1 SD)

*Statistical significance at the Bonferroni-corrected $\alpha = 0.005$

2016). Changes in the physical habitat of the Gulf of Maine (Fogarty et al. 2008; Pershing et al. 2015) and alterations in the ecosystem may produce ecological bottle necks for once abundant predatory fishes (Swain and Sinclair 2000; Walters and Kitchell 2001). Indeed, increasing amounts of energy has been concentrated in less commercially desirable components of the food web (Auster and Link 2009; Link et al. 2009; Lotze and Milewski 2004). That imbalance, fewer and smaller cod and pollock, and more sculpins, is apparent in Passamaquoddy Bay.

Recovery of fish populations does not necessarily follow the same trajectory as decline. Atlantic herring, an important pelagic prey species, has recovered in locations where cod were once economically and ecologically important (Melvin and Stephenson 2007), but demersal fish populations have not (Swain and Sinclair 2000), hinting that Atlantic herring may be limiting recruitment of herring predators (Walters and Kitchell 2001). Whether river herring also can reach abundances where their predation on plankton causes high mortality for the larval stage of their predators is an open question worthy of further study.

Removing barriers to migration appears to increase the number of river herring in a river system, as evidenced by increasing river herring counts in the Kennebec and Penobscot Rivers (Maine Dept. of Marine Resources, unpublished data), and increases the availability of lipid-rich

Table 7 Analysis of covariance (ANCOVA) results for δ^{15}N and δ^{13}C values of focal fish species showing *p* value (F-stat) at $\alpha < 0.05$ level

Species	Isotope	Number	Interaction: slope test	Covariate: length	Factor: location	Tukey's post hoc
Atlantic cod	δ^{15}N	104	<0.001 (7.7)[a]	<0.001 (127.1)	<0.001 (147.9)	NA
	δ^{13}C		>0.05 (0.03)	<0.05 (4.4)	<0.001 (17.1)	Dam ≠ Stg Stg ≠ Pas Dam ≠ Pas
Atlantic mackerel	δ^{15}N	39	>0.05 (2.5)	<0.001 (14.7)	<0.01 (6.5)	Pas ≠ Stg
	δ^{13}C		>0.05 (1.1)	<0.05 (6.1)	>0.05 (0.8)[c]	NA
Pollock	δ^{15}N	18	>0.05 (0.2)	<0.001 (18.3)	<0.001 (36.6)	Dam ≠ Pas Pas ≠ Stg
	δ^{13}C		>0.05 (1.2)	>0.05 (2.1)[b]	<0.01 (6.6)	Dam ≠ Pas Pas ≠ Stg
Longhorn sculpin	δ^{15}N	82	>0.05 (0.03)	<0.001 (27.2)	<0.001 (138.2)	Dam ≠ Pas Pas ≠ Stg
	δ^{13}C		>0.05 (2.1)	>0.05 (0.8)[b]	<0.001 (14.4)	Dam ≠ Pas Pas ≠ Stg
Shorthorn sculpin	δ^{15}N	77	>0.05 (1.3)	<0.001 (17.8)	<0.001 (40.3)	Dam ≠ Pas Pas ≠ Stg
	δ^{13}C		>0.05 (0.02)	>0.05 (3.2)[b]	<0.05 (3.9)	No sig. differences

Fin tissue was used for all species except Atlantic mackerel. Tukey's post hoc test ($\alpha < 0.05$) was used to determine significant differences between sites. Only Atlantic cod ≥30 cm TL were used in this analysis

NA not applicable

[a] Failed homogeneity of slopes test

[b] Length covariate not statistically significant

[c] No difference by location

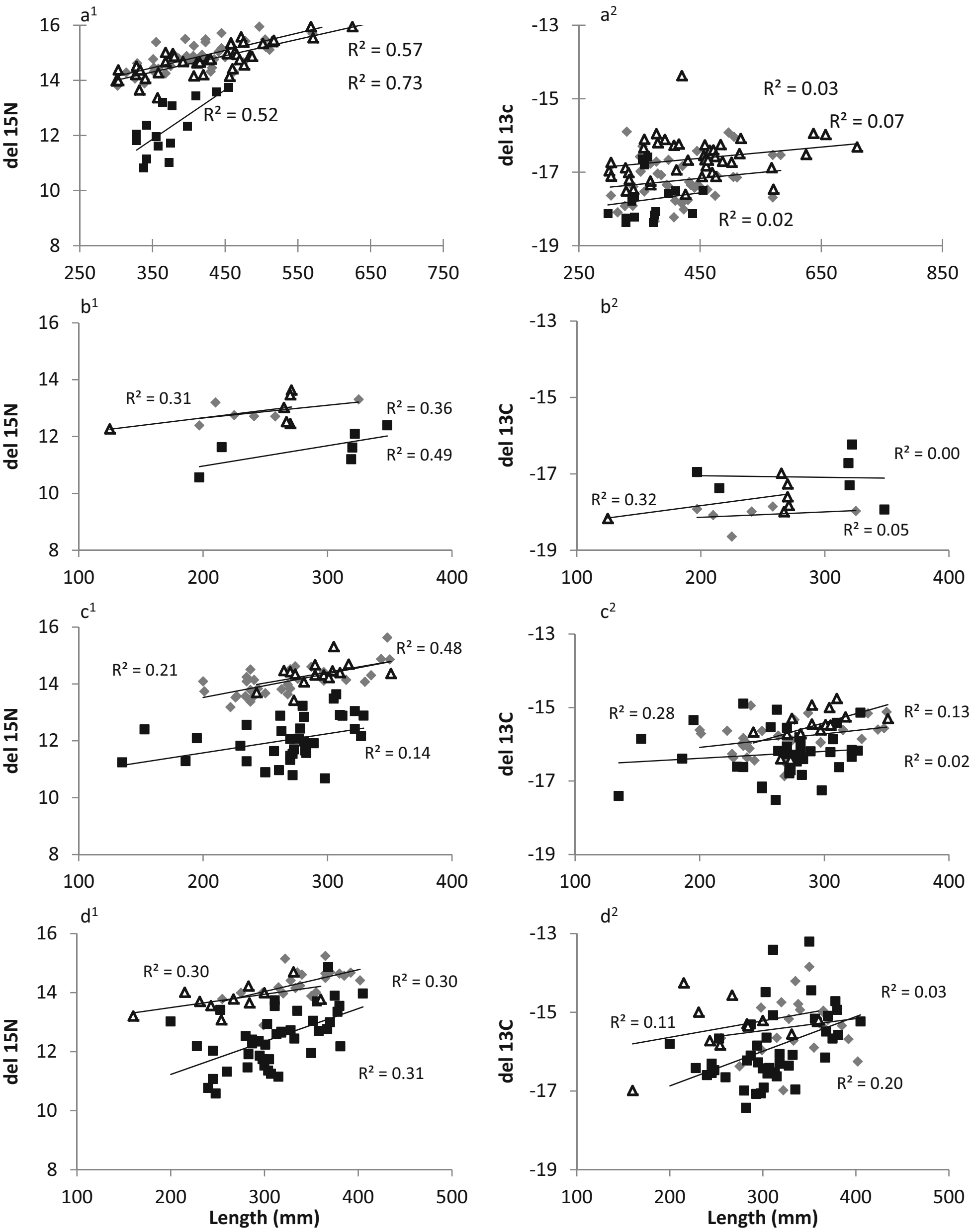

Fig. 4 $\delta^{15}N$ and $\delta^{13}C$ vs. fish TL for four focal species. In each case Passamaquoddy (*square*) fish had significantly ($p < 0.05$) lower $\delta^{15}N$ values (Table 5) than Damariscotta (*diamond*) or St. George (*triangle*) fish. (*a*) Cod ≥30 cm, (*b*) pollock, (*c*) longhorn sculpin, and (*d*) shorthorn sculpin; *superscript number 1* = del^{15}N, *superscript number 2* = del^{13}C. Atlantic mackerel values are not plotted because there was no clear separation in del^{15}N and del^{13}C values among sites

seasonal prey items for marine fishes. Here, we present evidence that physical improvements to coastal freshwater habitats can be beneficial up the food chain to populations of marine predators, and make a case for monitoring the marine effects of these large-scale manipulations closely.

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