

# Tracking cod diet preference over a century in the northern Gulf of Maine: historic data and modern analysis

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**ABSTRACT:** Limited information is available regarding long-term compensation in the food webs of exploited ecosystems. We compared the results of 3 studies that assessed the diets of Atlantic cod from Passamaquoddy Bay, Maine, USA, spanning 100 yr, using diet summary statistics to compare historical and modern datasets. We found that 1965 cod consumed fewer invertebrates than cod caught in 1896, but that cod caught in the period 2005 to 2008 ate diet items more similar to the 1896 fish. Large cod caught in the summer of 1965 primarily ate fish, particularly Atlantic herring, whereas few fish were found in the diets of 2005 cod. Documented changes in diet may reflect changes in technology and resource exploitation that altered the prey field available to cod over time. In the 1890s, the herring and finfish fisheries were widespread and landings were large, but other components of the food web, particularly invertebrates, were comparatively unexploited. Impacts on the benthos of Passamaquoddy Bay increased by the 1960s with the widespread use of heavy dredge and trawl gear. By 2005, most fisheries had abandoned Passamaquoddy Bay, and cod and herring were reduced in numbers. Ecosystem resilience can be seen in the return of modern cod to the 1896 diet, but compensatory dynamics in the food web appear to have favored benthic, then pelagic, and finally a 'balance' of diet constituents, but with fewer commercially important finfish in the ecosystem overall. When and where the data exist, 18th and 19th century accounts of fishery activity can be used to put modern trends in perspective.

**KEY WORDS:** Historical ecology · Cod · Clupeid · Diet · Frequency of occurrence · Passamaquoddy Bay · Trophic position

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## INTRODUCTION

According to Francis et al. (2007), characterizing and maintaining ecosystem resilience is one of 10 guiding principles, or 'commandments,' in applying ecosystem-based management to fisheries. In this context, resilience is defined as the extent to which ecosystems can absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states (Hughes et al. 2005, Francis et al. 2007). In

application, resilience refers to qualities of a food web that determine its stability: its spatial and temporal structure, species diversity and scale of interactions, resistance to perturbation, and vulnerability to crossing a threshold into an alternative state (Francis et al. 2007). Operationally, fisheries scientists need to know how food web resilience is created and maintained in exploited systems.

Knowledge of how food webs have changed through time is pertinent because it appears that resilience thresholds already have been crossed for

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most commercially important fish stocks (Pauly et al. 2002, Myers & Worm 2003). There is a global trend towards smaller target species and more fisheries biomass harvested from lower trophic levels (Dulvy et al. 2003, Baum & Worm 2009). Channels of energy flow have changed significantly in the Northwest Atlantic since reliable quantitative data were first collected in the 1960s and 1970s (Auster & Link 2009, Link et al. 2009). Although biomass among trophic guilds has remained constant, the overall community has trended towards higher abundances of commercially unimportant species (Lotze & Milewski 2004, Link et al. 2009, Nye et al. 2009a). However, the data available to gauge temporal change in food webs only captures the period right before widespread fishery collapse prior to establishment of the Exclusive Economic Zone in the Northwest Atlantic.

Quantitative descriptions of marine ecosystems before mechanization of US fishing fleets almost never meet the stringent data requirements of modern mathematical models. Until recently, this has meant that the most dramatic changes in exploited food webs were known only through anecdotes or isolated observations (Pitcher 2001). Certainly, the adoption of ever more sophisticated scientific methods has contributed to the 'shifting baseline' syndrome (Pitcher 2001, Pauly et al. 2002, Pauly & Maclean 2003). Thousands of observations and numerical data buried in old sources, like the US Commission of Fisheries reports, have been overlooked. Fisheries were monitored at the turn of the 19th century and quantitative data do exist, but often catch and effort data are dispersed through decades of reports from state and federal government entities. While many US documents are available online, some state reports are rare and can be difficult to find and expensive to obtain. Units of measurement can also be problematic. Frequently, fishery output was recorded as dressed or processed product rather than pounds or kilograms landed. Units used in the 18th, 19th, and early 20th centuries are uncommon today (e.g. quintal, hogshead, barrel) and frequently varied in weight between and within countries. Finding appropriate conversion factors can be difficult and time consuming. Old fishery records require careful review and digitizing of the data before they can inform modern fishery practices. Consequently, even if managers did look back more than a generation for evidence of dramatic ecosystem change, considerable effort would be required to find data from before the advent of standardized data collection in the 1940s, 1950s, and 1960s.

Historical ecology is a new concentration in ecology actively working to discover historical datasets and translate them for use in modern statistical analyses and models. Purely qualitative data have been used to estimate presence/absence and relative abundance of species (Fortibuoni et al. 2010). Nineteenth-century catch records, catch per unit effort, and first-hand observations of fleet activity have been modeled to yield a biomass estimate (Rosenberg et al. 2005). Economic data from the same period have been used to scale catch records from another 19th century fishery (Alexander et al. 2009). Historical ecology requires painstaking investigation and methodological interpretation. Additional information from disparate sources, such as maps, census records and traditional knowledge preserved in written narrative, frequently becomes the metadata required to utilize historical data fully. In other cases, discontinuities in time series and fine spatial resolution make quantitative data unusable without novel forms of standardization (Alexander et al. 2011).

Historical literature clearly indicates that the number of forage fish present in the inshore Gulf of Maine (GOM) today is a small fraction of the biomass that was present during the pre-colonial era (Duncan 1992, Lotze & Milewski 2004, Alexander et al. 2009, Limburg & Waldman 2009, Hall et al. 2010). Reports from the early days of fishery investigation identified Atlantic herring *Clupea harengus*, menhaden *Brevoortia tyrannus*, and river herring (alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) as extremely abundant seasonal resources in the nearshore GOM (Field 1914, Collette & Klein-MacPhee 2002, Ames 2004, Franklin 2007, Hall et al. 2010). Estimates of river herring abundance during the pre-colonial era are in the hundreds of millions for Maine rivers alone (Hall et al. 2010). Originally used as a subsistence food, fertilizer, and trade item by both Native Americans and early European settlers, the abundant and easily caught fish later became a commercial commodity traded to the Caribbean. Even then, half or more of most alewife catches were consumed locally (Atkins 1887). However, a proliferation of dams prevented spawning and decimated populations by the Civil War. Menhaden supported extensive oil reduction and fertilizer industries that spread from Blue Hill, Maine, in 1848, throughout coastal New England. Hundreds of millions of pounds of GOM menhaden were transformed into machinery lubricant during the next 40 yr, but they were wiped out commercially in the GOM by 1900 (Franklin 2007).

Inshore Atlantic herring schools likely outnumbered both alewives and menhaden, as they made up the bulk of the weir and pound net catch. Atlantic herring were observed spawning along the entire GOM coast in the late 1800s, but they were especially prized and heavily harvested in the Bay of Fundy. Eastport and Lubec, Maine, were the capitals of herring harvest and sardine processing for nearly a century (Goode 1884, Moore 1896, International Passamaquoddy Fisheries Board 1960). The last of the large herring were fished out of Passamaquoddy Bay, an inland sea on the border of New Brunswick, Canada, and Maine, USA, by the 1880s (Lotze & Milewski 2004). In 1927, there were 519 weir sets in Passamaquoddy Bay, but almost all focused on small herring for the sardine canneries, consisting of ages 1 to 3 juvenile herring moving in tight aggregations. In 2005, only 2 weirs were left in the US waters of Passamaquoddy Bay and 89 in all of coastal New Brunswick (Power et al. 2011). Market forces and, eventually, regulations influenced the fishing effort on sardines, such that abundance and catch were not perfectly correlated through time; however, effort, catch, and abundance have been generally accepted as strongly correlated since the later 20th century.

Not surprisingly, with such a large forage base available, predatory fish were also abundant in Passamaquoddy Bay. This large, productive, protected bay had been the site of many forms of fisheries exploitation, especially after Europeans settled in the area circa 1730 (Harnedy & Harnedy 2003, Lotze & Milewski 2004). Signs of stock decline were already visible between 1825 and 1850. By 2000, groundfish catch in the Bay of Fundy was 3 to 37% of what it had been a century before (Lotze & Milewski 2004).

In this study, we hypothesized that present-day conditions of low quantities of prey fish, as evidenced by low river herring returns and low weir landings of Atlantic herring, would be evident in present-day cod diets relative to diets of cod in the late 19th and mid-20th centuries. Modern cod would have a less fish-based, less energetically rich diet, and a lower trophic position in the food web. We compared diets collected between 2005 and 2008 in Passamaquoddy Bay with 2 studies of the feeding habits of Atlantic cod *Gadus morhua*: one conducted in 1896 and a second in 1965.

## MATERIALS AND METHODS

### Study area

Passamaquoddy Bay is an inlet of the Bay of Fundy between Maine, USA, and southwestern New Brunswick, Canada. The Bay is delineated by an archipelago of islands (45° 05' N, 67° 00' W) which define the 2 principal entrances to Passamaquoddy Bay, the Letete Passage and the Western Passage, through which tidal flows can reach 4 m s<sup>-1</sup> (Trites & Garrett 1983). The maximum water depth in the passages is approximately 130 m, and the tide is semi-diurnal with a maximum range of 8.3 m (Brooking et al. 2006).

All cod diet studies were conducted in or near the Western Passage, Passamaquoddy Bay (Fig. 1). Average August 2007 water temperature was 11.1°C (1 m depth). The water column is well mixed (Trites & Garrett 1983), with annual average water temperature of 7°C (range 0 to 12°C).

### 1896 diet study

During the summer and fall of 1896, the US Fish Commission conducted a study in Eastport, Maine, that examined the stomach contents of cod, haddock, hake, and pollock (Kendall 1898). Many of the fish examined were brought to the Eastport Fish Market

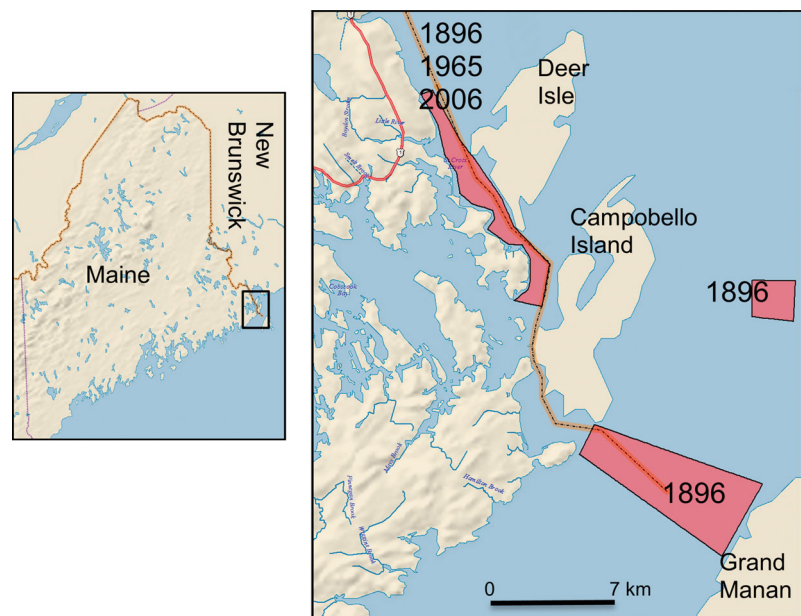


Fig. 1. Maine coast. Polygons demarcate areas fished, and dates correspond to which study sampled in that area. The Western Passage is located to the southwest of Deer Isle and Campobello Island

and had their stomachs removed for analysis during the cleaning process. Most were caught in Quoddy (Passamaquoddy) Bay, West Quoddy (Passamaquoddy) Bay, between Campobello and Grand Manan Islands, and Cochran Ledge in Eastport Harbor. Fish commission scientists also fished in the Eastport area and examined the stomach contents of freshly caught cod. Although gear type was not mentioned explicitly in the document, gear type was assumed to be either bottom long line or hand line. Trawls were not used in the area until 1933 when 1 otter trawl was recorded in Washington County, Maine, by the US Fish Commission (W. B. Leavenworth unpubl.).

Cod diet content was reported taxonomically in 1896, that is, by diet category, date caught, then fish species (Fig. 2). Because the original 1896 document did not report occurrence of diet items by individual fish, we assumed that each reported sampling location on a sample date was equivalent to 1 sample fish. For example, diet items listed for 1 July from the Wolves were considered items from a 1 July Wolves 'fish,' regardless of how many fish were actually collected (data that were not available). Ironically, the more ubiquitous a diet item, the less detail the authors

reported. In particular, skeleton shrimp *Caprella* sp. were 'found in both cod and haddock from various localities' (Kendall 1898, p. 182) with no additional information. We assumed that caprellids occurred in a plurality of fishes collected and assigned caprellids to 51 % of the samples to reflect this in our analysis.

#### 1965 diet study

From March 1965 to June 1966, a series of Canada Department of Fisheries and Oceans research cruises surveyed Passamaquoddy Bay and sampled cod stomach contents. Trawl samples were taken monthly between 10 March 1965 and 27 June 1966 from an area near Perry, Maine, and Deer Island, New Brunswick, just on the Canadian side of the US–Canada International boundary (approximately 45° 1' 9.35" N, 67° 2' 46.71" W), in the Western Passage. Otter trawl tows were used on 20 cruises, each cruise sampling 1 of 5 substations in a 3.2 × 1.6 km sample area (Tyler 1971b, 1972).

A companion Canadian Department of Fisheries and Oceans report (Tyler 1971a) contained diet data

#### *Eupagurus bernhardus*. Hermit crab.

Sept. 1, cod, Cochran Ledge.

5, cod, Cochran Ledge.

Oct. 18, cod, Quoddy Reef.

This species is not rare in this region, but only a few were found in fish stomachs.

#### *Eupagurus kröyeri*. Hermit crab.

Aug. 3, haddock, between the Wolves and Grand Manan.

Aug. 17, haddock, Eastport.

Sept. 23, cod, market.

Not uncommon.

#### *Hyas coarctatus*. Spider crab.

Aug. 3, cod, between the Wolves and Grand Manan.

Aug. 17, cod, Eastport.

21, cod, Yellow Rock.

23, cod, West Quoddy.

28, haddock, market.

Sept. 5, cod, Cochran Ledge.

12, cod, market.

Oct. 6, cod, Cochran Ledge.

19, cod, Quoddy Bay.

20, cod, Head Harbor.

Quite plentiful, especially in hako stomachs.

Another prawn, which could not be identified, was found in a cod stomach.

#### *Pycnogonum littorale*,

Aug. 17, haddock, Eastport.

Oct. 24, haddock, Head Harbor.

Oct. 25, haddock, Storer Ledge.

Very few specimens found.

#### Fishes.

##### *Acanthocottus*, sp. Sculpin.

Sept. 5, cod, Cochran Ledge.

Too much digested for identification.

##### *Acanthocottus scorpius granlandicus*.

Sculpin.

Oct. 18, cod, Quoddy Reef.

##### *Acanthocottus* or *Hemitripterus*. Sculpin or sea raven.

Oct. 6–11, cod (fragments), Cochran Ledge.

##### *Liparis liparis*. Sea slug.

Oct. 21, cod, Yellow Rock.

##### *Muraenoides gunnellus*. Rock-cod; butter-fish.

Fig. 2. Scanned excerpt of diet data as reported by Kendall (1898). Data are arranged by diet item, under which is listed the date, fish species, and the origin of the fish in which the diet item was found



from the study in nearly raw form: diet contents were reported as the total number of stomachs collected, along with the items found, the number of stomachs containing each item, and the total weight of that diet item summed across all stomachs (Fig. 3). Neither diet items by fish, nor weight of individual items per fish, were listed by Tyler (1971a). The catch was grouped into 10 cm length bins from 10 through 69 cm. We broke the fish into 2 categories (large:  $\geq 30$  cm and small:  $\leq 29$  cm) based on ontogenetic shifts in cod diet preference (Link & Garrison 2002). Diet items were collapsed into large taxonomic groups matching those used for the contemporary (2005–2008) diet study (below). Diet item codes were published by Losier & Waite (1989). The data were split into winter (November to March) and summer (April to October) samples.

#### 2005 diet study

From 2005 to 2008 (2005 study), the University of Southern Maine (USM) conducted a diet study of groundfish in nearshore Maine waters (<5 km from land). Passamaquoddy Bay was sampled in July 2005, April to September 2006, July to October 2007, and May and July to October 2008. We used hook-and-line angling as the primary method for capturing fish to avoid gear conflicts with lobster traps and to accommodate strong currents in the Western Passage. Each trip consisted of 2 to 5 people, usually 3 including the ship captain. Each crewmember used a deep sea jigging rod with 1 to 5 hooks. Hook size varied from small (2.2 cm length, 0.8 cm gape, 1.5 cm front) to large (5.3 cm length, 2.2 cm gape, 2.8 cm front). A given fishing rig consisted of 2 to 3 small hooks and a large hook at the bottom. Hooks were either baited, were a tinselled or feathered jig without bait, or both. Jig selection depended upon angler preference or what type of jig was catching fish that day. All rigs were actively jigged.

CRUISE 3 MAR 18/65					
COD	10-19 CM				
PREY	NO.	FREQ	TOT WT	AV WT	2*STE
	STOM	O/O	GM	GM	
2000	11	55	2.80	.14	.08
2819	7	35	1.70	.09	.05
3200	1	5	.50	.03	.05
2611	1	5	.30	.02	.03
NUM STOM W IDENTIFIABLE CONTENTS					20

Fig. 3. Scanned excerpt of diet data as reported by Tyler (1971a), listing prey items, number of cod diets containing those items, frequency of occurrence, total weight (g), average weight (g), and 2× standard error

Choice of angling areas was based on bottom topography: we targeted humps or bottom features where the sea floor shoaled from 25–36 m up to 12–18 m and fished to 'adrift.' A 'drift' began on the up-current or up-wind side of the feature (depending upon which was stronger) and carried the boat over the top of the feature. Fish tended to be caught on both incline and decline slopes. If no fish was caught after 2 to 3 passes, a new topographical feature was selected. If fish were caught, the drift path was repeated until no fish were caught during 1 to 2 additional passes over the feature. Start and end time of the drift and number of hooks used were recorded. Increasing hook size was not necessarily associated with increasing fish size; in some cases, the largest fish were caught on the smallest hooks.

Captured fish were held in a flow-through live well until processed, usually within 30 min or less of capture. We obtained diet samples from fish >150 mm in length using gastric lavage to flush the fish's stomach (Hartleb & Moring 1995). Fish were anesthetized by immersion into a 5 gallon (~18.9 l) bucket (1/3 to 1/2 full) of sea water and MS-222 or another approved anesthetic until the fish lost equilibrium. Regurgitated diet items were captured on a 500  $\mu$ m sieve. Fish were then fin-clipped, allowed to recover in a live well of fresh seawater, and released alive. Diet contents were stored in polyethylene bottles with an 85% ethyl alcohol, 5% ethylene glycol, 10% water mixture (Warmington et al. 2000). Gastric lavage produced a high-quality diet sample because it stopped the digestive process immediately. It also minimized the number of fish euthanized to make diet collections.

For each fish, diet items were identified to the lowest taxonomic level possible, ranging from species to 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, etc.). Because diet summary statistics are sensitive to the number of taxa used in the analysis, diet item data are frequently collapsed into functional or large taxonomic groups. Also, the degree of digestion can inhibit identification of diet items past a certain taxonomic specificity.

#### Calculations and assumptions

Three datasets were generated from the diet data: frequency of occurrence (FO), percent weight (weight%), and

trophic position (Bowen 1996, Willis 2009). The 1965 data included seasonal (winter vs. summer) and small ( $\leq 29$  cm) and large ( $\geq 30$  cm) fish (see above); fish caught in the 2005 study were all grouped into a  $>30$  cm size category; 2 were  $<30$  cm at 27 and 29.8 cm. No length data were available for cod collected in 1896; we assumed these fish were large because of anecdotal evidence regarding average cod length 100 yr ago vs. today. Thus we compared diets from 6 groups of fish: large fish from 1896, winter 1965, summer 1965, and 2005–2008, and small fish from winter 1965 and summer 1965.

The authors of the historic cod diet data used standards for taxonomic specificity and grouping appropriate for their times. Our goal was to retain as much historical data as possible for the analysis, which required making assumptions about what taxa were found in composite groups based on functional ecology. For example, 'crustacean' was a diet category not uniformly defined. Organisms in the 'crustacean' category of the 1896 study were identified to family, genera, or species. The USM study defined 'crustacean' as unidentified Malacostraca, barnacles, and ostracods. The 1965 study did not define 'crustacean' within any of the associated documents; however, other small members of the subphylum Crustacea were identified to species so we concluded that, like the USM definition, 'crustacean' was a catch-all for small/larval decapods that could not be readily identified.

### Frequency of occurrence

FO is a measure of the number of individuals that consumed a particular diet item in a population. The total number of individuals that consumed an item is divided by the total number of individuals that were sampled. In other words, FO is a semi-quantitative estimate of the 'popularity' of a diet item for a sub-population of fish (see Hyslop 1980 for discussion).

Diet data for 1896 and 1965 were not presented as items in individual fish; therefore, there was a limit to the diet statistics that could be calculated. Calculating FO was possible for all 3 studies. FO calculations for 1896 study were based on diet items found on 1 d from 1 sample site; the total number of cod caught was not reported. Thus the calculations represent total number of days in which an item was found divided by the total number of days sampled at a given site. FO calculations from the 1965 study required a slightly different aggregation method. In

this case, the data were summarized by size class (large vs. small) and season (summer vs. winter). For the 2005 study, FO calculations were made by aggregating across all years and combining all cod into a single size class (large =  $\geq 30$  cm). FO was converted to FO% by dividing the FO score for each diet item by the FO total from each study subcategory (1896, 1965 winter large, 1965 winter small, 1965 summer large, 1965 summer small, 2005).

### Percent weight

Traditionally, weight% was calculated as total weight of a diet item (i.e. amphipod, fish, etc.) divided by the total weight of all diet items in that fish's diet. Because the 1896 study was not presented as individual fish, we were unable to calculate weight%. For the 1965 study, we aggregated total weight per item and total weight of all items by size class (large versus small) and season (winter versus summer). For the 2005 study, weight% calculations were made by aggregating across all years and combining all cod into a single size class (large =  $\geq 30$  cm).

### Trophic position

Trophic position was calculated using diet constituents or  $\delta^{15}\text{N}$  values derived from stable isotope analysis that describe the position of an organism in a food web, e.g. top predator vs. primary consumer. Because historic (1965 and 1896) stable isotope data were not available, we assumed that modern  $\delta^{15}\text{N}$  values of cod prey species gave a reasonable approximation of historic values for the GOM. Prey  $\delta^{15}\text{N}$  values were taken from published diet and unpublished stable isotope data sets for estuaries in and near the GOM, including Massachusetts Bay (Tucker et al. 1999), Georges Bank (Fry 1988), Cape Cod Bay (Carmichael 2004), Plum Island Sound (Deegan & Garritt 1997), and Newfoundland (Sherwood & Rose 2005). Trophic position was calculated for the fish and prey organisms in each study assuming a 3.4  $\delta^{15}\text{N}$  difference between trophic levels; bivalves were used to set a common baseline according to Vander Zanden et al. (1997). The trophic position calculations followed Vander Zanden et al. (1997), such that percent composition of each diet item was multiplied by average (literature derived) trophic position of each diet item category. The resulting values were summed, +1, to arrive at trophic position.

### Other analyses

Non-metric multidimensional scaling (MDS) was used to facilitate comparison of cod diets among years. Data were square-root transformed to improve multivariate normality. Cluster analysis (complete linkage) calculated from a Bray-Curtis similarity matrix was used to determine levels of diet similarity between years. Primer 6 (v.6.1.13) and Systat 12 (v.12.00.08) were used for statistical analysis.

### RESULTS

Cod were caught in every month of the 1965 survey, but were only caught in June to October of the 2005 study. The 1896 study was conducted in the summer and fall of 1893 (Kendall 1898). The 1965 survey was trawl based, in contrast to the 2005 and 1896 studies, which were hook and line or long line based. Five times as many fish were caught in 1965 as in 2005–2008. The size distribution of fish in 1965 ranged from 10 to 69 cm (Fig. 4); in 2005–2008, fish ranged in size from 29 to 49 cm, with the majority of fish in the 30–39 cm size class. All cod were caught in either 2005 or 2007. No size data were available for the 1896 study.

### Diet data

Cod diets were more diverse in 2005 than in either of the 2 previous studies. We identified organisms

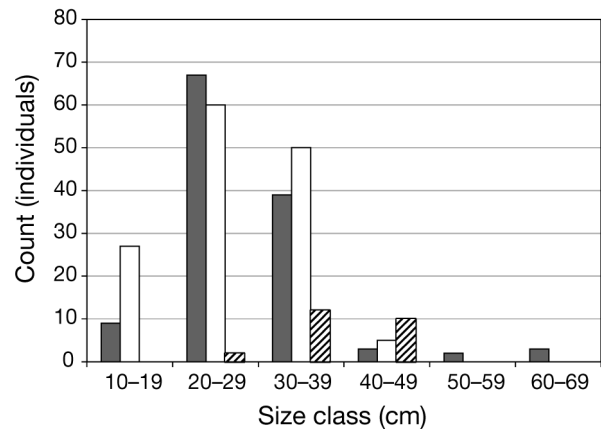


Fig. 4. *Gadus morhua*. Catch frequency by size class of cod from the 1965 and 2005 studies. Summer 1965 encompasses the months of April through October, inclusive. The Winter 1965 period encompasses the months November through March, inclusive. Sampling for the 2005 study occurred between April and October of 2005 to 2008. Solid bars correspond to summer 1965, open bars are winter 1965, and hatched bars are 2005 data

that represented 14 taxonomic categories, compared to 10 each in 1896 and 1965 (Table 1). In 1965, the summer and winter catch of small cod had 6 to 8 identified diet categories. Calculation of the Shannon diversity index also demonstrated that modern cod had the most diverse diet and small summer 1965 cod had the least diverse diet.

Cod collected in all 3 studies consumed fish as one of the top 4 diet items, particularly for large summer cod. Fish were found in 38 to 55% of cod caught

Table 1. *Gadus morhua*. Frequency of occurrence of prey taxa in historical and modern cod diets. Superscript letters (a–d) indicate top 4 diet items. Small: cod  $\leq 29$  cm in length. n: number of diets collected (2006, 1965 study) or number of sampling days (1896 study); Shannon: Shannon diversity index

Item	2005	Summer		Winter		1896
		Large 1965	Small 1965	Large 1965	Small 1965	
n	19	47	76	55	87	24
Shannon	2.56	2.18	1.63	1.93	1.65	2.20
Bivalvia	0.21	0.04	0	0	0	0.26
Gastropoda	0	0.02	0	0	0	0.26
Polychaeta	0.54 <sup>b</sup>	0.15 <sup>d</sup>	0.09 <sup>d</sup>	0.13 <sup>d</sup>	0.06	0.05
Cnidaria	0.17	0	0	0	0	0.05
Annelida (worms)	0.08	0	0	0	0	0
Decapoda	0.04	0.11	0.11 <sup>c</sup>	0.18 <sup>c</sup>	0.41 <sup>b</sup>	0
Brachyura (crabs)	0.25	0.13	0	0.04	0	0.95 <sup>a</sup>
Nephropidae (lobster)	0	0	0	0	0	0
Caridea (shrimp)	0.38 <sup>d</sup>	0.47 <sup>a</sup>	0.04	0.22 <sup>c</sup>	0.17 <sup>d</sup>	0.26
Euphausiacea/Mysida (krill-mysids)	0.29	0.13	0.82 <sup>a</sup>	0.73 <sup>a</sup>	0.59 <sup>a</sup>	0
Copepoda	0.08	0	0	0	0	0
Eggs	0.08	0.01	0	0.02	0	0
Amphipoda	0.63 <sup>a</sup>	0.17 <sup>c</sup>	0.26 <sup>b</sup>	0.25 <sup>b</sup>	0.25 <sup>c</sup>	0.53 <sup>c</sup>
Isopoda	0.08	0	0	0	0	0.053
Echinodermata	0.13	0	0	0	0	0.47 <sup>d</sup>
Teleostei (fish)	0.54 <sup>b</sup>	0.38 <sup>b</sup>	0.04	0.04	0.01	0.58 <sup>b</sup>

(Table 1). Cod from the 2005 study consumed fish from the families Clupeidae, Cottidae, and Ammodytidae, in addition to a majority of unidentified fish remains. Clupeids included positively identified Atlantic herring. Fish food items from summer 1965 samples included the families Clupeidae, Gadidae, Labrisomidae, and Lumpenidae, with over 70 % of the fish prey identified as Atlantic herring. Fish food items from the 1896 study included *Acanthocottus*, *Hermitripteris*, Pholidae, Clupeidae, Cottidae, and Liparidae. Kendall (1898) reported that herring were frequently found in all fish, though some were obviously bait.

By weight, fish made up 29 % of cod diets from the 2005 study. Overall, diets from large summer 1965 cod contained 69 % fish, and diets from small summer cod contained 14 % fish by weight (Table 2). Fish all but disappeared from small and large cod diets in winter 1965, making up 7 % or less of the total diet weight. No diet weight data were available for the 1896 study.

Invertebrates showed the greatest change between studies, or, in the 1965 data, between seasons. Crabs were found in 95 % of the samples collected in 1896, but were only present in 25 and 13 % of the 2005 and 1965 large summer cod, respectively (Table 1). Echinoderms were also present in 47 % of the cod

Table 2. *Gadus morhua*. Proportion of prey taxa in historical and modern cod diets. Superscript letters (a–d) indicate top 4 diet items. n: number of diets collected; Shannon: Shannon diversity index

Item	2005	— Summer —		— Winter —	
		Large 1965	Small 1965	Large 1965	Small 1965
n	19	47	76	55	87
Shannon	2.21	1.91	1.54	1.93	1.56
Bivalvia	0.21 <sup>b</sup>	0.01	0/–	0/–	0/–
Gastropoda	0/–	0.01	0/–	0/–	0/–
Polychaeta	0.05	0.04 <sup>d</sup>	0.02	0.03	0.02
Cnidaria	0.01	0/–	0/–	0/–	0/–
Annelida (worms)	<0.001	0/–	0/–	0/–	0/–
Decapoda	0/–	0.02	0.02	0.08 <sup>c</sup>	0.13 <sup>c</sup>
Brachyura (crabs)	0.13 <sup>d</sup>	0.06 <sup>c</sup>	0/–	0.07 <sup>d</sup>	0/–
Nephropidae (lobster)	0/–	0/–	0/–	0/–	0/–
Caridea (shrimp)	0.07	0.12 <sup>b</sup>	0.04 <sup>d</sup>	0.22 <sup>b</sup>	0.18 <sup>b</sup>
Euphausiacea/Mysida (krill-mysids)	0.15 <sup>c</sup>	0.02	0.74 <sup>a</sup>	0.48 <sup>a</sup>	0.62 <sup>a</sup>
Eggs	<0.001	0/–	0/–	0.04	0/–
Amphipoda	0.07	0.02	0.05 <sup>c</sup>	0.02	0.05 <sup>d</sup>
Isopoda	<0.001	0/–	0/–	0/–	0/–
Echinodermata	0.01	0/–	0/–	0/–	0/–
Teleostei (fish)	0.29 <sup>a</sup>	0.69 <sup>a</sup>	0.14 <sup>b</sup>	0.07 <sup>d</sup>	0.01
Unknown	0.02	0/–	0/–	0/–	0/–

Table 3. *Gadus morhua*. Trophic position of cod, calculated using cod diet compositions from each study and baseline-adjusted modern  $\delta^{15}\text{N}$  values from the Gulf of Maine. Weight data were not reported for the 1896 study. FO: frequency of occurrence

Sample	Weight%	FO%
2005	3.7	3.61
Summer large 1965	4.11	4.02
Summer small 1965	3.62	3.22
Winter large 1965	3.84	3.74
Winter small 1965	3.74	3.49
1896		3.74

samples from 1896, but only in 13 % of 2005 cod, and were absent from 1965 cod entirely, regardless of time of year collected or size of cod. Amphipods were a common diet item across all times and size categories. Amphipods were found in 63 % of cod captured in the 2005 study, and we estimated that amphipods were found in 53 % of the samples from 1896. However, amphipods were only present in 17 % of large summer cod sampled in 1965.

Seasonal differences in invertebrate consumption were evident in 1965. Krill and mysids (hereafter krill-mysids) were a significant portion of the diet of small cod in 1965, making up 74 % (summer) and 62 % (winter) of the diet by weight (Table 2). Krill-mysids were also found in many of the cod sampled: 82 % (summer) and 59 % (winter) of the small cod caught (Table 1). For large winter cod, 73 % of fish caught contained krill-mysids, which made up 48 % of the diet weight. Krill-mysids were much less important to large summer cod than winter cod in 1965 and 2005 (Table 1). Krill-mysids were absent in 1896, although this may have been an artifact of taxonomic detail reported by the authors.

Trophic position of cod through time peaked in 1965. Trophic position ranged from 3.2 to 4.1 (Table 3).

#### Multivariate analysis

We used multivariate bi-plots with similarity ellipses derived from cluster analysis to illustrate commonalities and differences in cod diets. Results of MDS analysis for FO of diet item occurrence grouped 1965 large sum-



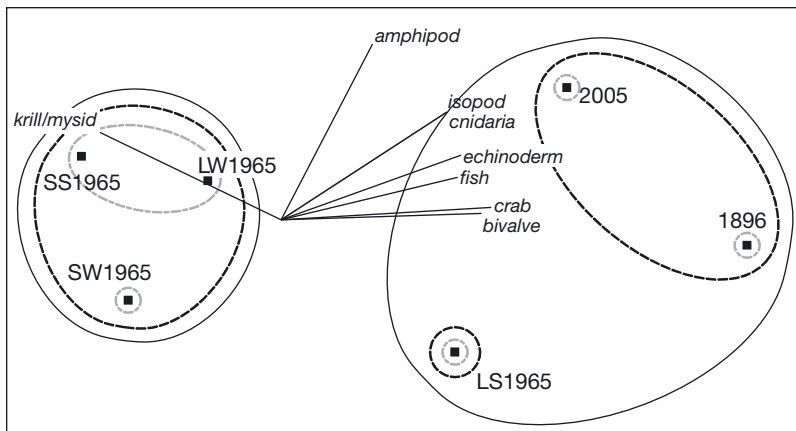


Fig. 5. Nonmetric dimensional scaling analysis of frequency of occurrence (FO) data. Ellipses are based on cluster analysis of Bray-Curtis similarity matrix (complete linkage). Points are 25% (gray dashed), 50% (black dashed), or 75% (solid) similar in diet composition, based on FO diet data. Biplot elements (diet categories) were significantly correlated with first 2 PC axes at  $p < 0.05$  based on Spearman rank correlation. LS: large ( $\geq 30$  cm), summer; LW: large, winter; SS: small ( $\geq 29$  cm), summer; SW: small, winter. 2D stress = 0.001

mer cod and small and large winter cod close together in the ordination, all with at least a 50% similarity in the proportion of cod eating similar food items (Fig. 5). This grouping was driven by the presence of krill-mysids in samples. The 2005 and 1896 diet samples were grouped together with at least a 50% similarity, based on cod eating echinoderms, crabs, and bivalves. Large cod sampled in summer 1965 were intermediate between these 2 groupings, showing preference for more shrimp than any other diet category, but intermediate preference for other defining food items like crab or krill-mysids. There was a 25% similarity between large summer 1965 cod in diet preferences and 2005 and 1896 cod.

## DISCUSSION

One of the primary questions of this study was whether the diet of nearshore cod has changed significantly based on data from 1896, 1965, and 2000s. Can the 1896 diet study be used as an accurate indicator of diet preference? A number of assumptions were used to adapt qualitative data collected by Kendall (1898) into semi-quantitative data comparable to data collected 59 and 110 yr later. We were fortunate that enough information was included to make calculating a modified FO possible. FO is the least powerful of the summary tools used for diet data, but it does provide a snapshot of population level prey preference over long durations; i.e. X per-

centage of all the fish sampled consumed a given diet item (Hyslop 1980). Ordinarily, data from individual fish stomachs are used to calculate FO; here we used daily aggregations of diet data for 1896 and 1965. The modified FO may misrepresent the occurrence of some diet items; however, weight% and count% can also bias diet results, the former towards infrequent but heavy items, and the latter towards ubiquitous but small diet items like zooplankton, or, in this case, amphipods.

Other authors have dealt with the difficulties of adapting early scientific and naturalist observations to modern statistical methods by assigning order of magnitude relative abundances based on changes in descriptions over time (Rosenberg et al. 2005, Fortibuoni et al. 2010). Others developed new

metrics that attempted to bridge modern and past data reporting conventions with metrics that consider per capita effort (Alexander et al. 2009, 2011). In general, detailed diet data from before the 1940s are rare. Of the 3 historical diet lists that we know of, 2 (Linsley 1845, Cheney 1871) merely record appearance, without the number of occurrences. These efforts are important because they can provide critical information about the depth of ecosystem change that has occurred, i.e. dampen the human predisposition towards a shifting baseline (Pauly & Maclean 2003).

Cod diets reflect changes in the prey field of the ecosystem. That is, cod are generalist predators, serving as effective samplers of a wide variety of prey from fish to crustaceans, mollusks, and bivalves (Collette & Klein-MacPhee 2002). For example, diet items from Georges Bank peaked and declined as a reflection of major ecosystem changes also seen in cod diets (Link & Garrison 2002, Link et al. 2009). Bivalves, crabs, and echinoderms were essentially absent from the diets of large cod in 1965, yet these items were present and important in the diets of cod collected in 1896 and 2005. Our hypothesis is that other fishing activity, especially scalloping, negatively impacted the abundance of benthos in Passamaquoddy Bay, and this change was reflected in cod diets.

Several changes in fishing effort over time in the Passamaquoddy Bay region may have impacted the prevalence of benthos in cod diets. In 1896, there was little to no dredge activity in Passamaquoddy Bay.

The fishing fleet was sail powered at the time without capacity to drag multi-ton dredge gear in the swift currents of the bay. However, by 1919, half of the Washington County, Maine, fleet was motorized, up from 5% in 1905 (Department of Commerce and Labor 1906, 1921). Peak harvests of scallops *Placopecten magellanicus* in Passamaquoddy Bay occurred in 1914 (219 t), 1933 (371 t), and 1934 (700 t), with a long-term average of 29 t (1896 to 1940). Scallop dredges disturb bottom sediments, break shellfish, and displace mobile crustaceans like crabs and lobster that are not damaged by dredge activity (Thrush et al. 1995, Collie et al. 2000, Robinson et al. 2001). By 1950, there was 'sporadic fishing by a few Digby Scallopers' (Caddy & Chandler 1976). Clam fishing was equally depressed in the 1950s; a green crab invasion dramatically reduced soft-shell clam *Mya arenaria* populations in the Passamaquoddy Bay region (Trott 2004, Beal 2006). Pollution also negatively affected clams and clam harvesting in the 1950s (Caddy & Chandler 1976).

Atlantic herring, and forage fish in general, may have been at record low abundances in Passamaquoddy Bay during the most recent cod diet study. Herring were mentioned as frequently found in 1896 diets. In 1965, 69% of the fish found in cod diets were identified as Atlantic herring, but we found few identifiable fish remains (and, in fact few fish at all) in cod diets in the 2005 study. Modern records of Atlantic herring landings (adult and sardines) in the Bay of Fundy, SW New Brunswick, region, started in 1963 at 36 000 t and climbed to 75 000 t by 1968, then declined to 8500 t by 2009 (Power et al. 2010, 2011). The presence of Atlantic herring in cod diets in 1965 would indicate that the herring resource was capable of supporting the high levels of exploitation and biological demand for at least a short period of time. Landings in 2005 and 2006 were the second and third lowest landings from the region in the 46 yr duration of the herring time series, followed by 2008 and 2009 as the lowest landings in the time series (Power et al. 2010). That we found no Atlantic herring in cod, and in fact caught no cod in 2006 and 2008, demonstrates that the current herring resource may not be sufficient to support both exploitation and biological demand.

Our difficulty catching cod in Passamaquoddy Bay may be related to the scarcity of herring prey. Evidence and lore point to migratory cod as followers of fish prey on their seasonal migration (Field 1914, Rose 1993, Ames 2004). As recently as 1981, adult cod sampled from the same area as the 1965 and the 2005 studies were classified as common in summer (Mac-

donald et al. 1984). Although method may have contributed to the low catch rate in the 2005 study, other diet studies conducted in the southern GOM employed hook and line with success (Smith et al. 2007, Sherwood & Grabowski 2010). No cod were caught during spring sampling in the 2005 study (end of April to mid-June), even though this time frame overlapped with the peak period for catching cod (using hook and line) historically (Bigelow & Schroeder 1925, Duncan 1992, Kurlansky 1997, Ames 2004). In contrast, July and August 2005 and 2007 were successful fishing periods, suggesting that fish were moving inshore with warming waters or with prey items such as Atlantic herring. Ames (2004) reported that spring catches of cod were traditionally low in March, April, and May, presumably because cod were spawning during the early spring and did not readily take a hook until the spawning season ended. Lower catch rates may also be a result of changing cod distribution. Observations from the National Marine Fisheries Service spring and fall trawl surveys indicate that the range of cod in the GOM was contracting south and to deeper cooler water (Nye et al. 2009b). The 2005 study catch rate may simply reflect the declining cod abundance in the ratio of commercial groundfish to non-commercial groundfish that started in the late 1980s (Blackwell et al. 1995, Lotze & Milewski 2004, Nye et al. 2009a).

These observations beg the question of whether hook data and trawl data can be compared directly. This is an area where additional research is required. Studies that used both hook and trawl methods to capture groundfish, including cod, found that hooks produced a more narrow size range of groundfish compared to trawls (Halliday 2002, Ford et al. 2008). We found no studies for gadids that addressed whether hook sampling biased diet analysis results towards more hungry fish more willing to take a hook; however, a study of lanternshark *Etmopterus pusillus* found no statistical difference, controlling for size, in the diets of trawl or long line caught sharks (Xavier et al. 2012). Our observations were that fish which appeared literally stuffed to the gills with food still took our hooks if the tidal conditions were correct to facilitate feeding. Many of the sites fished were chosen based on local knowledge and were described as being best at particular tide stages that lasted for only a short period of time. Our hypothesis is that under the extreme tidal conditions present in Passamaquoddy Bay, if a target fish like cod is present at a location during favorable conditions, it will eat beyond satiation, provided its predators and physiology facilitate feeding.

The 1896 cod diet data do not reflect a pristine ecosystem, but rather an ecosystem that was at the center of the US canned and smoked herring industry (Duncan 1992, Kurlansky 1997, Lotze & Milewski 2004). In 1895, 23 198 t of herring were used in the herring industries of Eastport and Lubec (Moore 1896); in 1883, 457 872 t of adult herring were landed at Canadian ports in Passamaquoddy Bay, roughly 1 billion fish (Department of Marine and Fisheries 1884). Cod were 'taken in abundance' from Passamaquoddy Bay and off Eastport from the 1820s to 1840s, but by the 1870s, 'only stragglers' were caught (Baird 1873). The prevalence of crabs, amphipods, and echinoderms in cod diets from that time could be interpreted as evidence of an ecosystem lightly impacted by commercial ground gear (Robinson et al. 2001), but we also know that prey fish populations as a whole (alewives, menhaden, and Atlantic herring) were dramatically reduced by 1890 (Lotze & Milewski 2004, W. B. Leavenworth unpubl.). In contemporary diets, dependence upon invertebrate prey is a sign of depauperate prey fields in exploited ecosystems (Link & Garrison 2002, Sherwood et al. 2007, Link et al. 2009), and that may be the case here as well. Winter diets also tend to have more invertebrate prey (Tyler 1971a), but the 1896 study was conducted in later summer and early fall.

Despite what appeared to be a taxed ecosystem in 1965, the trophic position of cod was higher than in 1896 or the 2000s. Trophic position values for large summer cod for 1965 (4.1) were similar to those calculated for Georges Bank cod (3.8; Fry 1988) and Newfoundland cod (4.0; Sherwood & Rose 2005). We were surprised that the modern trophic position of cod from Passamaquoddy Bay (3.6) was considerably lower because cod progress through a strong ontogeny of diet preference with size. A 'juvenile' diet consists of mainly invertebrates and some small fish and lasts until 30 to 40 cm in length (Sherwood et al. 2007, Link et al. 2009). At that point, fish become a dominant diet item, at least in cod populations presumed to be healthy and where forage fish are present. Consuming fish prey assists with gonad formation, tissue repair, and recovery after spawning (Smith et al. 2007).

Modern Passamaquoddy Bay cod could be primarily focused on a lipid-poor invertebrate diet because fish were sporadic prey items. Alternatively, the cod sampled may have not completed their ontogenetic diet shift and were still selecting food items common to juvenile cod. Another explanation is that the 2005 study sample size was too small to accurately encapsulate the feeding preference and trophic position of

cod. In the latter case, the 24 cod captured as part of the 2005 study represented our best efforts in the Western Passage. An average 4 h of angling were required for each cod caught, or about 0.08 cod man-hour<sup>-1</sup>, as compared with 2.7 cod man-hour<sup>-1</sup> caught near Grand Manan in 1861, a change of 2 orders of magnitude (K. Alexander unpubl.). This in itself is a statement about change in the Passamaquoddy Bay ecosystem.

We propose that sequential prey depletion over the past 110 yr, along with direct harvest of cod, has resulted in a new equilibrium of supportable biomass in Passamaquoddy Bay, and arguably in the Bay of Fundy region. The food web in 1965 was likely weighted heavily towards pelagic production after the scallop dredge, pollution, and invasive species (green crab) effects of the preceding decades. Benthic diet constituents were largely absent in large summer 1965 cod, and although fish, including Atlantic herring, dominated cod diet by weight, herring occurred infrequently. Atlantic herring in Passamaquoddy Bay were migratory; local stocks were fished out nearly a century earlier, and thus not available in winter. Diet choice of large winter cod reflects this in the strong resemblance to a juvenile cod diet, heavy in krill and mysids. We speculate that by 2005, both cod and Atlantic herring were seasonal migratory stocks. Cod were eating a diet more similar to that of 1896 cod in 2005–2008, but with a much wider range of benthic food items than in 1896. Many of those items would not be as energetically advantageous as a diet consisting mostly of Atlantic herring (Mateo 2007).

Exploited populations go through a period of increased production in the early stages of harvesting (Pauly et al. 2002, Pauly & Maclean 2003), a phenomenon that may extend to inter-specific interactions as well if there is enough niche overlap between species (Walters et al. 2000). Atlantic herring are not the only forage fish species once documented as abundant in the nearshore GOM that are now largely absent. River herring (alewife and blueback herring) were once harvested by coastal and river weirs in the tens of millions. The St. Croix River, the largest tributary to Passamaquoddy Bay, can support over 2 million adults yr<sup>-1</sup> (590 t), but hovered around 10 000 or fewer spawning adult fish between 2000 and 2009. However, prior to 1825, just 1 of the many packing companies in the Calais–St. Stephen region exported 225 t of alewife annually (Perley 1852), and production estimates were as high as 32 million fish (14 515 t) for the Quoddy region (Lotze & Milewski 2004). Menhaden,

a forage fish known for traveling in large schools and being a favorite of fish predators (Walter et al. 2003, Franklin 2007), were once annual visitors to Passamaquoddy Bay, but disappeared from the Bay of Fundy region in the 1860s (Goode & Atwater 1880). The harvests of Atlantic herring have occurred farther and farther from shore through time, such that no significant herring tonnage has been landed commercially from Passamaquoddy Bay in over a decade (Power et al. 2011).

Arguably, each human generation since the Civil War has experienced a shadow of the Passamaquoddy Bay ecosystem experienced by their forebears. The cod we caught may be descendants of those best able to adapt to a diet of invertebrates. What we see today, throughout the GOM, are historic lows in forage fish abundance that have resulted in a virtual fish desert in nearshore areas, where fish were caught in abundance less than 10 miles (16 km) from the mainland just a century before.

Historical data provide insights into the structure and function of ecosystems that, today, are impaired in their function. The results from our analysis comparing modern survey data with data from 1896 and 1965 point to significant, long-term changes in the coastal GOM marine food web with important implications for the recovery of cod and other groundfish, and the resilience of an ecosystem now dominated by invertebrates. Restoring alewives, menhaden, and Atlantic herring may be essential in bringing back coastal cod populations and rebuilding complexity in an impoverished ecosystem. Finally, this historical perspective challenges notions of sustainability by reminding us what a truly productive, diverse, and resilient ecosystem looked like and how the public perspective has drifted to accept remnant populations as the new normal.

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