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ARTICLE

The influence of forage fish abundance on the aggregation of Gulf of Maine Atlantic cod (*Gadus morhua*) and their catchability in the fishery

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Abstract: Shifts in the distribution and aggregation patterns of exploited fish populations can affect the behavior and success of fishermen and can complicate the interpretation of fisheries-dependent data. Starting in 2006, coinciding with an increase in sand lance (*Ammodytes* spp.) abundance, Gulf of Maine Atlantic cod (*Gadus morhua*) concentrated on Stellwagen Bank, a small (405 km²) underwater plateau located in the southwestern portion of the larger (52 461 km²) stock area. The cod fishery in turn concentrated on Stellwagen Bank. Specifically, the proportion of Gulf of Maine cod landings caught in a single 10-minute square area (260 km²) encompassing the tip of Stellwagen Bank increased from 12% in 2005 to 45% in 2010. An increase in landings per unit effort in the fishery coincided with the concentration of the fleet on Stellwagen Bank. Overall, both fisheries-independent and fisheries-dependent data indicate that an increase in sand lance abundance resulted in cod aggregating in a small and predictable area where they were easily caught by the fishery. More broadly, this work illustrates how changes in the distribution patterns of fish and fisherman can decouple trends in abundance and fisheries catch per unit effort.

Résumé : Des changements des motifs de répartition et de concentration de populations de poissons exploitées peuvent avoir une incidence sur le comportement et le succès des pêcheurs et compliquer l'interprétation des données dépendantes des pêches. Depuis 2006, parallèlement à une augmentation de l'abondance des lançons (*Ammodytes* spp.), les morues (*Gadus morhua*) du golfe du Maine se sont concentrées sur le banc Stellwagen, un petit (405 km²) plateau sous-marin situé dans la partie sud-ouest de l'aire de répartition du stock (52 461 km²). La pêche à la morue s'est du coup axée sur le banc Stellwagen. Plus précisément, la proportion de débarquements de morues du golfe du Maine capturées dans une seule zone de 10 minutes carrées (260 km²) englobant l'extrémité du banc Stellwagen est passée de 12 % en 2005 à 45 % en 2010. Une augmentation des débarquements par unité d'effort dans cette pêche a coïncidé avec la concentration de la flotte sur le banc Stellwagen. Globalement, tant les données indépendantes que dépendantes des pêches indiquent qu'une augmentation de l'abondance des lançons s'est traduite par le regroupement des morues dans une petite zone prévisible où leur prise par les pêcheurs était alors chose facile. De manière plus générale, l'étude illustre comment des changements des motifs de répartition des poissons et des pêcheurs peuvent découpler les tendances de l'abondance et des captures par unité d'effort des pêches. [Traduit par la Rédaction]

Introduction

Catch per unit effort (CPUE) is among the most commonly available time series in fisheries science, but is also one of the most difficult to interpret (Maunder et al. 2006). Much of this difficulty results from the dynamic nature of various factors that affect the efficiency and behavior of the fishing fleet, including regulations, fishing technology, and changes in the price of fish and fuel (Maunder and Punt 2004; Hampton et al. 2005). However, even when these various drivers of CPUE can be standardized, there is still uncertainty in the expected relationship between CPUE and abundance. The simplest proportional relationship between CPUE and abundance appears not to hold in many types of fisheries, largely because of the effect of population abundance on the spatial dynamics of fish populations and fishing effort (Hilborn and Walters 1992). An alternate power relationship between CPUE and abundance has been proposed, with most fish exhibiting hyperstability, whereby CPUE declines at a lower rate than abundance (Harley et al. 2001). Hyperstability assumes that fishing effort is focused on aggregations of fish and that local abundances in these fish aggregations are maintained, even when the abundance of the population as a whole declines. With hyperstability, CPUE still provides information on trends in fish abundance, as an increase in CPUE suggests an increase in fish abundance of at least equal magnitude. However, a hyperstable relationship between CPUE and abundance may break down if the factors that drive fish to aggregate are not stable over the duration of the CPUE time series (Rose et al. 2000).

Both physical and biological factors can drive changes in the degree of aggregation of a fish population and, in turn, their catchability in a fishery. For example, the vulnerability of yellowfin tuna (*Thunnus albacares*) to surface gear is driven by their vertical distribution, which in turn is restricted by the depth of the thermocline. During El Niño years, a shoaling of the thermocline in certain areas increases the catchability of yellowfin tuna, as their level of aggregation in the surface layer increases (Lehodey 2001; Sharp 2001). The collapse of the Newfoundland population of Atlantic cod (*Gadus morhua*) provides another example of

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changes in CPUE being driven by environmental factors rather than abundance (Rose and Kulka 1999). CPUE in this fishery actually increased during the population collapse. This opposing trend in CPUE and the abundance of the population was attributed to a combination of cooling and a decline in capelin (*Mallotus villosus*) in the northern part of the population range (Rose et al. 2000). Suitable habitat for cod was thus restricted to the southern portion of their range, resulting in a hyperaggregation of the population. The fishery in turn tracked the spatial distribution of cod and achieved high catch rates across a very small area, even while the population declined. A failure to account for changes in the spatial patterns of the cod population and the fishery resulted in CPUE being used in the assessment model as an index of abundance. This in turn led to overestimates of population size and the maintenance of quotas that far exceeded sustainable levels (Hutchings and Myers 1999).

In 2011, the stock assessment for Gulf of Maine Atlantic cod concluded that the stock was overfished and that rebuilding had been limited since the 1990s (NEFSC 2012*a*). These conclusions were broadly questioned, in part because the commercial fishery was reporting increased ease in catching cod in the years leading up to the assessment. The assessment model was further criticized for its failure to use CPUE data as an index of abundance. Here we evaluate whether the reported ease in catching cod in the Gulf of Maine commercial fishery was driven in part by the increasing abundance of sand lance (*Ammodytes* spp.) and decreasing abundance of Atlantic herring (*Clupea harengus*) in the region. These two dominant prey items for Atlantic cod in the Gulf of Maine have different habitat associations that are expected to affect the spatial distribution of their predators. Atlantic herring is a migratory, small pelagic species that shifts distribution in response to changing oceanographic conditions. Sand lance also feed in the water column, but are restricted to locations proximate to shallow sandy bottom habitat where they bury each night for protection (Winslade 1974). We hypothesize that (*i*) Atlantic cod shift distribution to reflect the distribution of the most abundant prey species, (*ii*) cod become more aggregated when sand lance are abundant because of the limited amount of sand habitat available to sand lance in the Gulf of Maine, and (*iii*) CPUE and the distribution of the fishing fleet are affected by the composition of the forage fish community.

Description of the Gulf of Maine cod fishery

Off the Northeast United States, Atlantic cod are assessed as two different stocks, one in the Gulf of Maine and the other on Georges Bank (Fig. 1A). These stock boundaries simplify a more complex and finer-scale population structure in the region (Ames 2004; Kovach et al. 2010). The commercial exploitation of Atlantic cod in the Gulf of Maine extends to precolonial times (Kurlansky 1998). Since 1977 commercial landings have ranged from 2000 to 18 000 metric tonnes (t) (NEFSC 2013), though in the mid-1800s landings may have exceeded 60 000 t (Alexander et al. 2009). Commercial landings have declined since the early 1990s, averaging approximately 4300 t over the past decade (Fig. 2; NEFSC 2013). Since 2002, commercial landings have comprised about 67% of the total fishery catches of Gulf of Maine cod; commercial discards and recreational catches make up the remaining removals. Currently, commercial landings are split about equally between the otter trawl and sink gillnet fleet, which combined, account for 95% of the total commercial landings.

Rich (1929) and Ames (2004) provide in-depth descriptions of historical fishing grounds for Atlantic cod in the Gulf of Maine. These reports, based in large part on interviews with fishermen, document over 200 different locations throughout the Gulf of Maine that historically supported cod fishing. In recent decades, cod fishing has contracted to the western Gulf of Maine, matching a contraction in cod distribution evident in fisheries-independent survey data (NEFSC 2013). Currently, the eastern Gulf of Maine does not support an economically viable cod fishery. The ports of Portland, Maine, and Gloucester, Massachusetts, have long been the major offloading ports for Gulf of Maine cod, though from 2007 to 2010 Gloucester accounted for >60% of the total Gulf of Maine cod landings (NEFSC 2013). Among the features targeted by fishermen, particularly out of Gloucester, is Stellwagen Bank, a shallow plateau in the southwestern Gulf of Maine that contains a mixture of sand and hard bottom habitat (Fig. 1A).

Management measures for Gulf of Maine cod have changed numerous times over the past three decades (Table 1). Prior to 1982, cod was primarily managed through annual total allowable catches and minimum mesh sizes (Serchuk et al. 1994). In 1982, management measures were implemented that utilized input controls such as mesh sizes and minimum retention sizes to restrict catch. Beginning in 1994, there was an attempt to reduce fishing effort through limits on the number of days at sea vessels were allowed to fish. Further reductions in days at sea occurred in 1996, 2002, and 2004, and beginning in 2006, vessels fishing in the western Gulf of Maine were charged 2 days at sea for every 1 day fished. Additional effort restrictions included daily possession limits (landings per day at sea), which ranged from 30 lbs (13 kg) to 1000 lbs (453 kg) between 1997 and 2010 (Table 1). Various seasonal and year-round closed areas were also instituted between 1998 and 2004, with most still currently in effect (Fig. 1A; Table 1). In 2010, annual catch limits were introduced in addition to a new sector management system. The overwhelming majority of the groundfish fleet formed industry sectors or fishing collaboratives. The sectors were given a share of the total commercial groundfish annual catch limit and were exempted from days-at-sea restrictions and trip and day landing limits. A limited number of groundfish vessels did not join sectors, and these vessels remained under days-at-sea and possession limit input controls.

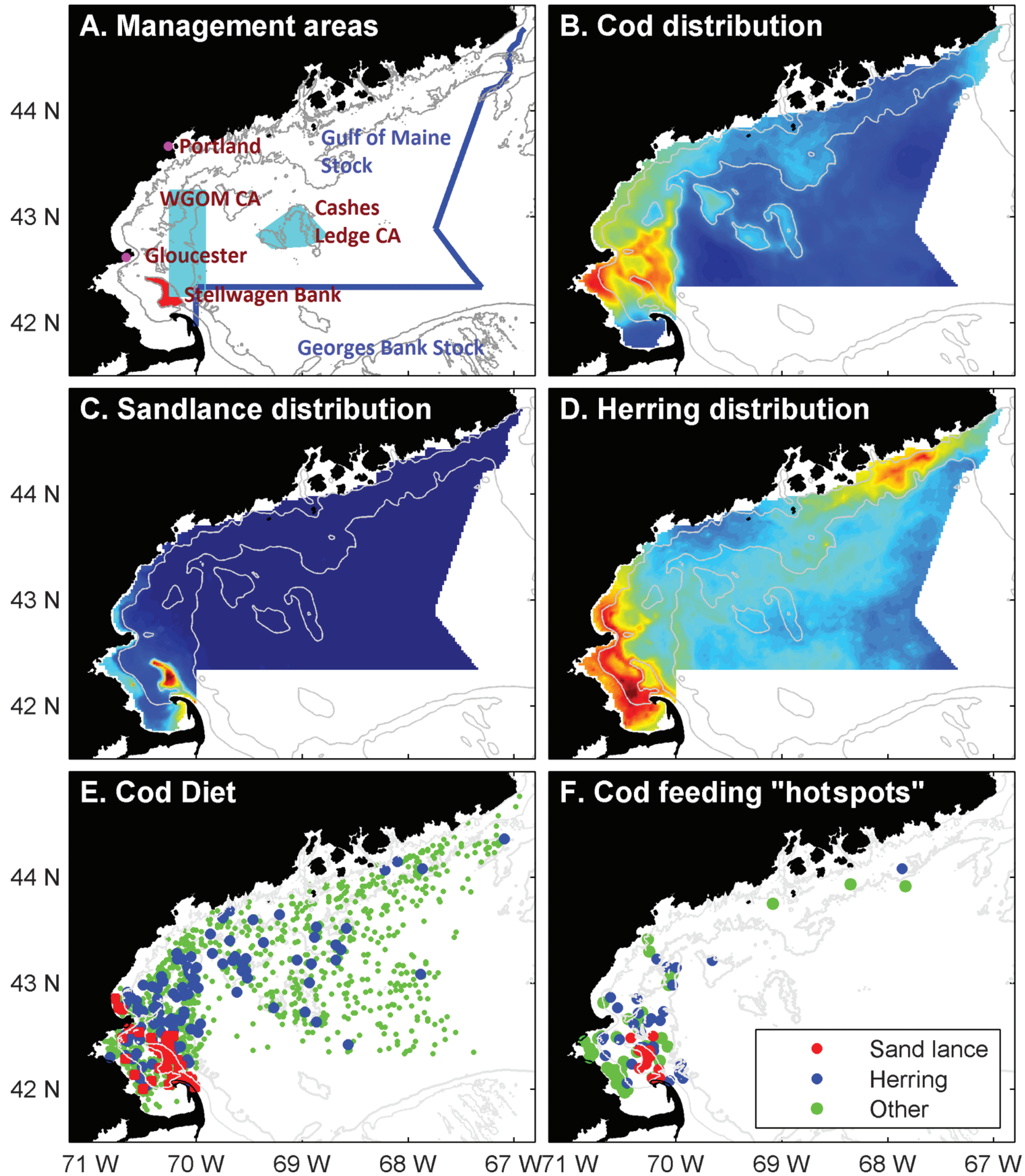
The 2011 Gulf of Maine cod stock assessment was conducted using the statistical catch-at-age model, the Age Structured Assessment Program (ASAP; Legault and Restrepo 1998; Legault 2012). The tuning indices were constructed from fisheries-independent indices of abundance from federal and state trawl surveys (NEFSC 2012*a*). In assessments prior to 2011, a fisheries-dependent landings per unit effort (LPUE) index spanning from 1982 to 1994 was also included in the assessment model as an index of abundance (Mayo et al. 1994). This LPUE index was not updated past 1994 because of concerns about how frequent regulatory changes in the form of effort controls affected the relationship between LPUE and abundance. Subsequent to the 2011 assessment, there was a renewed interest in calculating a LPUE time series because of the perceived inconsistency between the reported ease in catching cod in the Gulf of Maine and the limited rebuilding estimated in the assessment (Fig. 2).

Materials and methods

Data sources

The primary fisheries-independent data we used comes from the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) annual fall (September–November) and spring (March–May) bottom trawl surveys. Full details of the surveys and sampling gear can be found in Smith (2002) and NEFSC (2012*a*). Briefly, 300–400 stations are sampled in a random stratified design twice annually on the northeast US continental shelf extending from Cape Hatteras, North Carolina, to the Western Scotian Shelf, Canada. At each station, all fish species are identified and weighed, and all individuals are measured, with some subsampling of length measurements when species-specific catches are exceptionally large. Calibration coefficients derived from dedicated calibration surveys were used to standardize catch rates of Atlantic cod for changes in vessel and sampling protocol (Brooks et al. 2010).

Fig. 1. Maps of the Gulf of Maine study area, including (A) the Gulf of Maine Atlantic cod (*Gadus morhua*) management and assessment area, noting the Western Gulf of Maine Closed Area (WGOM CA), Cashes Ledge Closed Area, Stellwagen Bank, and the two primary fishing ports Portland, Maine, and Gloucester, Massachusetts. Distribution on the spring and fall bottom trawl surveys of (B) Atlantic cod, (C) sand lance (*Ammodytes* spp.), and (D) Atlantic herring (*Clupea harengus*). Stomach sampling data was used to show (E) the locations in which cod were found to have consumed sand lance (red), Atlantic herring (blue), and other (green) prey items, as well as (F) feeding "hotspots" for each prey item, defined as locations at which the abundance and stomach fullness of cod were simultaneously high.



Stomach sampling of Atlantic cod and other fishes has been part of the NEFSC trawl survey protocol since 1973. Over this period the allocation of sampling effort within and among species has changed as the Food Web Dynamics Program has shifted its focus from species-level questions to broader food-web analyses (details in Smith and Link 2010). Since 2000, stomach samples have been analyzed from at least one cod in each 10 cm length bin at each station, resulting in a mean of 160.0 (σ = 26.5) cod stomachs analyzed per year in the Gulf of Maine. From 1992 to 1999, narrower length bins were used, which led to a higher number of cod sampled per year (μ = 321.1, σ = 70.2 stomachs per year). Prior to 1992, the number of stomachs analyzed varied much more year-to-year (μ = 182.7, σ = 133.7 stomachs per year), and a targeted sampling effort was designated for each 12 h watch rather than for each station, leading to a lack of stomach sampling at some stations. Stomachs were primarily analyzed shipboard, with the stomach volume and taxonomic composition of prey proportions recorded. Proportions of prey volumes were converted to mass following the methods described in Link and Almeida (2000).

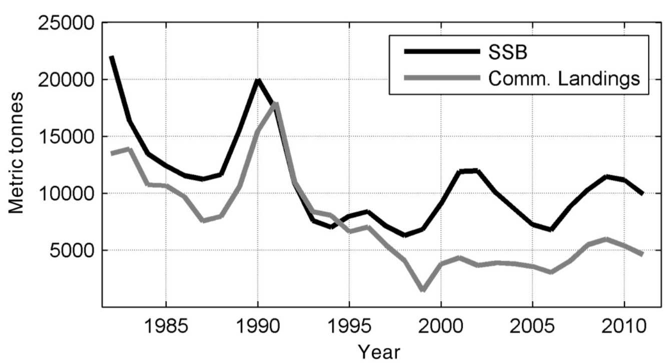
We used a composite index of abundance developed using 17 and 15 fisheries-independent indices to track long-term trends in abundance of sand lance and Atlantic herring, respectively (Table 2). For both taxa, long-term population trends are not clearly resolved using NEFSC trawl survey indices alone. Both taxa have high coefficients of variation of survey catches on the bottom trawl survey. For sand lance, the 2008 to 2009 change in the trawl survey net, and in particular the increase in the mesh size of the net liner from 1.27 to 2.54 cm (½ to 1 inch), resulted in a substan-

Table 1. Summary of major regulatory actions that have affected the Gulf of Maine Atlantic cod fishery since 1982.

Date	Regulatory action	Minimum mesh size (in)	Minimum fish size (in)	Day–trip limit	Closures	Days at sea (DAS) restrictions
1 Jan. 1982			17			
1 Jan. 1983		5.5				
1 Jan. 1989			19			
1 May 1994	Amendment 5	6.0				DAS monitoring with reduced schedule, mandatory reporting
1 May 1994	Amendment 7					Accelerated DAS reduction
1 May 1997	Framework 20			1000 lbs·day^{-1}		
1 May 1998	Framework 25			700 lbs·day^{-1}	WGOM, year-round	
25 June 1998				400 lbs·day^{-1}		
1 Feb. 1999	Framework 26				Additional seasonal closures	
1 May 1999	Framework 27	6.5 square; 6.0 diamond		200 lbs·day^{-1}		
28 May 1999				30 lbs·day^{-1}		
3 Aug. 1999	Interim rule			100 lbs·day^{-1}; 500 lbs·trip^{-1}		
5 Jan. 2000	Framework 31			400 lbs·day^{-1}; 4000 lbs·trip^{-1}	Additional seasonal closures	
1 June 2000	Framework 33	6.5 square; 6.5 diamond				
1 Nov. 2000					Cashes Ledge: 1 month	
1 May 2002	Interim rule		22	500 lbs·day^{-1}; 4000 lbs·trip^{-1}	Additional seasonal closures; Cashes Ledge: year-round	20% reduction in DAS
1 May 2004	Amendment 13			800 lbs·day^{-1}; 4000 lbs·trip^{-1}		Further reduction in DAS
1 May 2006	Emergency rule			600 lbs·day^{-1}; 4000 lbs·trip^{-1}		
22 Nov. 2006	Framework 42			800 lbs·day^{-1}; 4000 lbs·trip^{-1}		DAS counted 2:1 in inshore GOM
1 May 2010	Amendment 16			No day and trip limits except for a small fraction of the fleet in common pool	Some changes to rolling closures for sector vessels	DAS counted in 24 h blocks; no differential DAS counting except as amendments
1 May 2011	Framework 45				Whaleback seasonal closure	

Note: 1 in = 2.54 cm; 1 lb = 0.453 kg. WGOM, western Gulf of Maine.

Fig. 2. Time series of Gulf of Maine Atlantic cod estimated spawning stock biomass (SSB) and commercial landings from the 2012 assessment (NEFSC 2013).



tial reduction in catchability (Miller et al. 2010). During both the spring and fall calibration study, fewer than half of the stations that caught sand lance with the ½ inch liner also caught sand lance with the 1 inch liner. For Atlantic herring, a substantial uncalibrated change in catchability in the mid-1980s, generally attributed to a change in the trawl doors used by the surveys, has led to a consistent splitting of the survey time series in the stock assessments (NEFSC 2012*b*).

To develop the composite indices, we used fisheries-independent indices from state and federal bottom trawl surveys, an acoustic survey for Atlantic herring, larval surveys for sand lance, and stomach content analyses of the predators of both species. Larval surveys have a long history of use in tracking population trends of sand lance (Sherman et al. 1981). Previous studies have shown the utility of using prey proportions from stomach content surveys for tracking the abundance of taxa, such as sand lance, that are poorly sampled by trawl surveys (e.g., Cook and Bundy 2012). Indices of the proportion of sand lance or Atlantic herring in the diet of a predator species were included in the composite index if the diet database contained more than 100 instances of that predatory interaction within a season across all years of that survey. The composite index for each species is representative of abundance patterns across the northeast US continental shelf (Cape Hatteras to Canada) rather than in the specific areas inhabited by Gulf of Maine cod. Atlantic herring on the northeast shelf are considered a single stock complex that undergoes seasonal alongshelf migrations, and thus a shelf-wide index should approximate trends specifically in the Gulf of Maine. For sand lance, the available data are too limited to resolve Gulf of Maine specific trends in abundance, as sand lance only occupy a small area of the Gulf of Maine, and this area is not sampled each year by any one survey. Overall, about 5% of the area occupied by sand lance on the entire northeast shelf occurs in the Gulf of Maine.

The most extensive fisheries-dependent data available comes from self-reported vessel trip reports (VTRs) submitted by fishermen. Since 1994, all vessels permitted to fish for groundfish, including cod, have been required to submit VTRs, which include information on the vessel permit, date of sailing, gear fished, gear configuration (gear size, mesh size), fishing duration, average fishing location, species caught, and the date of landing. Vessel operators are required by federal regulations to report both the retained and discarded quantities of catch, but discard amounts are seldom reported on VTRs. The self-reported nature of VTR data has led to questions about its accuracy. However, recent evaluations of the accuracy of both the reported retained catch (Palmer et al. 2007) and fishing locations (Palmer and Wigley 2009) using independent data suggest that for cod, the VTRs represent a reliable data source for the purposes of characterizing the spatial composition of fleet activity and fishery landings. Since 2001, greater than 90% of VTRs that reported fishing in the Gulf of Maine contained detailed fishing locations. Between 1994 and 2000, the percentages exceeded 60% and were generally greater than 80%. All VTR positional data were converted to 10-minute squares (each square is 10 minutes of longitude by 10 minutes of latitude) for analyses. Aggregating VTR positional data to spatial bins smaller than 10-minute squares is questionable given the underlying accuracy and precision of VTR data. Three notable shortcomings of VTR data are (*i*) the data are self-reported and

Table 2. Time series used in developing the composite index of sand lance and Atlantic herring abundances.

Time series	Duration	Sand lance	Herring	Citation
NEFSC autumn trawl survey	1963–2008	×	×	Smith 2002
NEFSC spring trawl survey	1968–2008	×	×	Smith 2002
NEFSC winter trawl survey	1992–2007		×	Smith 2002
NEFSC Gulf of Maine summer shrimp trawl	1984–2010		×	Clark 1989
NEFSC summer scallop dredge survey	2001–2010	×		Serchuk and Wigley 1986
Massachusetts autumn trawl survey	1978–2010	×	×	Howe 1989
Massachusetts spring trawl survey	1978–2010	×	×	Howe 1989
New Jersey trawl survey	1988–2010	×	×	Byrne 1994
University of Rhode Island Graduate School of Oceanography trawl survey	1959–2010		×	Collie et al. 2008
NEFSC ichthyoplankton survey — Georges Bank	1977–2010	×		Richardson et al. 2010
NEFSC ichthyoplankton survey — southern New England	1977–1987; 2000–2010	×		Richardson et al. 2010
Georges Bank herring acoustic survey	1999–2010		×	Overholtz et al. 2006
Winter skate (*Leucoraja ocellata*) diet composition: NEFSC spring trawl survey	1977–2010	×		Smith and Link 2010
Winter skate (*L. ocellata*) diet composition: NEFSC autumn trawl survey	1977–2010	×		Smith and Link 2010
Spiny dogfish (*Squalus acanthias*) diet composition: NEFSC spring trawl survey	1977–2010	×	×	Smith and Link 2010
Spiny dogfish (*S. acanthias*) diet composition: NEFSC autumn trawl survey	1977–2010	×	×	Smith and Link 2010
Silver hake (*Merluccius bilinearis*) diet composition: NEFSC spring trawl survey	1973–2010	×		Smith and Link 2010
Silver hake (*M. bilinearis*) diet composition: NEFSC autumn trawl survey	1973–2010	×	×	Smith and Link 2010
Cod (*Gadus morhua*) diet composition: NEFSC spring trawl survey	1973–2010	×	×	Smith and Link 2010
Cod (*G. morhua*) diet composition: NEFSC autumn trawl survey	1973–2010	×	×	Smith and Link 2010
White hake (*Urophycis tenuis*) diet composition: NEFSC autumn survey	1973–2010		×	Smith and Link 2010
Longhorn sculpin (*Myoxocephalus octodecemspinosus*) diet composition: NEFSC spring survey	1985–2010	×		Smith and Link 2010
Total		17	15	

Note: NEFSC, Northeast Fisheries Science Center.

the catch amounts and location require accurate reporting by the vessel operator; (*ii*) for a trip fishing in a single statistical area, the report only contains a single geographical position when fishing may have occurred over a broad area; and (*iii*) VTRs seldom contain information on the discarded catch.

We used a combination of vessel monitoring system (VMS) and fisheries observer data to validate trends evident from the analyses of the VTR data. VMSs report fishing boat locations at set time intervals. By using VMS data, we can estimate the location of fishing activity and reallocate the VTR-reported catch to the estimated fishing areas (methods documented in Palmer and Wigley 2009). Unfortunately, for the groundfish fishery, VMS data are only available back to 2004.

The data collected by at-sea observers represents perhaps the most accurate fisheries-dependent information, but the data are only available for a small fraction of groundfish trips. For the majority of the observer time series (1989–present), the fraction of trips observed is <10%, though in 2010 and 2011 the fraction was much larger (>30%) owing to the at-sea monitoring requirements of sector management. Unlike VTRs, observer data contains accurate information on both the retained and discarded catch.

Using both VMS and observer data, we could address two important questions: (1) can area-specific landings trends apparent in the VTR data be verified with VMS and observer data; and (2) are the trends observed in cod landings also apparent in the discarded fraction of the catch?

Fisheries-independent data analysis

Distribution maps for Atlantic cod, Atlantic herring, and sand lance were produced based on the entire trawl survey dataset to allow broad comparisons among species. The mapping used an inverse-distance weight interpolation procedure on cube-root-transformed abundance data from the NEFSC bottom trawl survey. These three taxa are strongly tied to bathymetric features, and thus bottom-depth differences between the interpolated grid point and the sampled station were incorporated into the interpolation technique as an additional penalty on the distance measurement. A depth change of 50 to 100 m was set equivalent to a distance difference of 30 km in this interpolation procedure; this value was based on a quantitative analysis the interpolation procedure using bottom temperature.

We sought to define foraging hotspots for Atlantic cod because of the tendency for fisheries to target aggregations of fish. A foraging hotspot was defined as a trawl survey location in which the abundance of cod and the relative volume of their stomach contents within a tow were simultaneously high. The use of stomach content data was intended to distinguish an aggregation that may have been driven by foraging versus other factors such as spawning. Only cod >25 cm were considered in this analysis, corresponding to the approximate size of the onset of piscivory (Link and Garrison 2002; Smith et al. 2007), but less than the size limit used in the fishery (≈55 cm). The relative volume of stomach contents in individual fish was standardized based on the mass of the fish. As the weighing of individual fish only started in 1992, we used time series mean season-specific length–mass relationships ($M = aL^b$; fall survey: $a = 6.17 \times 10^{-6}$, $b = 3.13$; spring survey: $a = 4.71 \times 10^{-6}$, $b = 3.17$) to assign masses to all fish with stomach samples. Stations that were simultaneously in the top 20% of both abundance and relative stomach volume across all years were considered foraging hotspots. These foraging hotspots were classified based on the prey taxa that were the dominant stomach content at that station.

We characterized the large-scale trends of cod distribution over the duration of the trawl survey using two metrics. First, we characterized the degree of spatial concentration by applying the Lorenz curve to spatial bins to estimate a scalar metric of spatial distribution known as the Gini index (Wigley 1996). The larger the Gini index, the more aggregated a resource. We used a calculation of the Gini index that accounts for the random stratified sampling of the trawl survey and the uneven and varying allocation of samples among strata (Swenson 1978). Only NEFSC trawl strata within the Gulf of Maine stock boundaries were used for this calculation. Second, we sought to characterize whether there was a shift in the catch-weighted center of abundance of cod on the survey through time. In the Gulf of Maine, the proportional allocation of stations among strata has changed over time, and shallower strata are typically allocated a higher density of stations. We accounted for this by first interpolating cod abundances on the survey across the Gulf of Maine cod stock boundary using a nearest-neighbor approach. We then calculated the abundance-weighted mean latitude and longitude (centroid) of cod across this area. A shortcoming of using centroids is that they can be located in areas with low fish abundances; their utility is thus limited to describing general directional trends in distribution.

To calculate the annual diet composition of Gulf of Maine Atlantic cod, prey mass per stomach was weighted by the number of cod at length per tow and the total number of cod per tow as part of a two-stage cluster design (Link and Almeida 2000; Latour et al. 2008). Diet composition for each season was the weighted mean of prey mass taken as a proportion of the sum of all prey per season. Annual diet composition of Gulf of Maine cod was based on the mean of the diet compositions from the fall and spring trawl survey. Only the trawl survey strata corresponding to the Gulf of Maine cod stock boundaries in the assessment were used in the calculations of percent diet composition for cod. Years in which <25 cod stomachs were sampled in the Gulf of Maine during either the fall or spring survey were not included in the analysis.

Two steps were involved in calculating composite indices of abundance for sand lance and Atlantic herring. First, standardized anomalies (z scores) were calculated for each time series (Richardson et al. 2011). Second, a nonlinear least-square optimization procedure was implemented to derive a composite time series that best fit all of the individual time series. This procedure involved minimizing the square of the difference between the observed anomalies across the sampled years of a survey and a predicted anomaly for those specific years. Time series were equally weighted in this procedure. The overall result of this procedure is a combined index that merges individual surveys of different duration and time periods of sampling. This procedure does not require that the entire time period of the composite index is covered entirely by any one survey. The composite index represents the estimated standardized anomaly (z score) of abundance over the 1968–2010 period. Negative anomalies indicate below average abundances, while positive anomalies indicate above average abundances. An evaluation of this approach using simulated data indicated that it can accurately merge together multiple noisy time series when no individual time series covers the entire time period. Furthermore, the simulations revealed that the use of multiple time series minimizes the influence of any one time series that exhibited an uncalibrated change in catchability (i.e., biased time series).

Two other analyses were performed using the NEFSC fisheries-independent data to evaluate the aggregation and distribution patterns of cod relative to individual forage fish taxa. First, we evaluated the abundance of cod across stations in which sand lance, Atlantic herring, or other prey items were present in the stomach content sampling. A Kruskal–Wallis test was used to compare differences in the abundance of cod at a station given the three prey categories (sand lance, Atlantic herring, other). Similarities in the temporal trends of cod and any one of their prey items could potentially confound this analysis. For that reason we further tested the significance of any differences by resampling the abundance data 1000 times, maintaining the temporal makeup of the original analysis (i.e., for sand lance four stations in 2009, five stations in 2010) but selecting random stations within those years. Second, we compared the abundance of cod on Stellwagen Bank (defined by the 50 m isobath) versus the surrounding area during periods of high sand lance abundance and periods of low sand lance abundance. Stellwagen Bank is consistently identified as the area of highest sand lance abundance in the Gulf of Maine (Weinrich et al. 1997; Hazen et al. 2009). We defined the surrounding area as NEFSC trawl stratum-26 exclusive of Stellwagen Bank. Stellwagen Bank (405 km^2) is only 12% of the area of stratum-26 (3369 km^2) within which stations are randomly assigned; stratum-26 generally has the highest cod abundances in the Gulf of Maine. The trawl survey does not sample Stellwagen Bank every year, and thus it was not possible to calculate annual indices of the abundance of cod on Stellwagen Bank. Instead, we defined four periods in this analysis based on whether sand lance was above or below mean population levels, an early and late low sand lance period (1968–1975, 1992–2005) and an early and late high sand lance period (1976–1991, 2006–2010). A Kruskal–Wallis test was used to compare cod abundances (number·tow^{-1}) between Stellwagen Bank and the surrounding area in each time period.

Fisheries-dependent data analysis

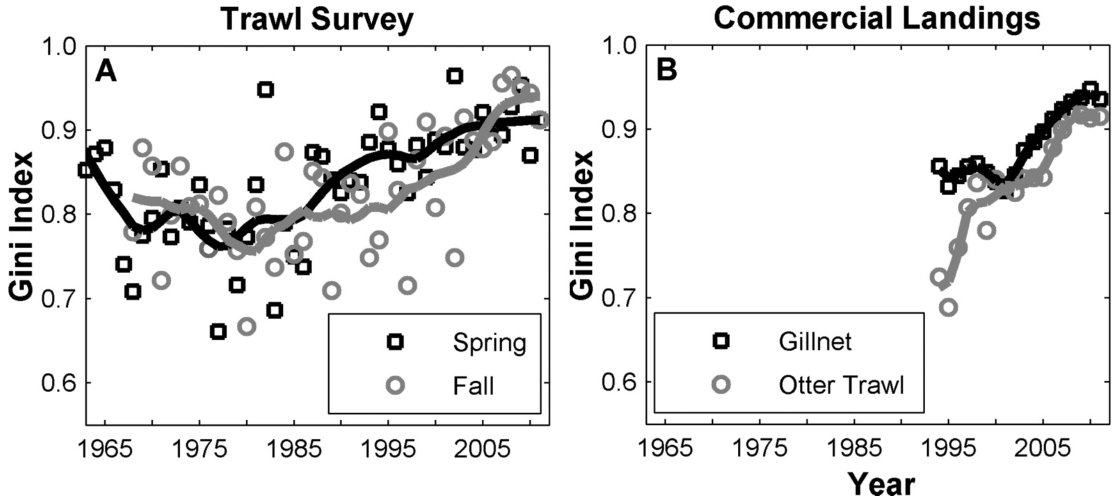
We characterized the large-scale spatial and temporal trends of the commercial fishery in a similar manner to our analysis of fisheries-independent distribution data. First we characterized the degree of spatial concentration of the fishery by calculating the Gini index (Wigley 1996). To apply this technique to VTR data requires that the positional information reported on the VTRs be converted to 10-minute squares (each square is 10 minutes of longitude by 10 minutes of latitude). Next we sought to characterize the directional movement of any detected spatial contraction by evaluating whether the landings-weighted center (centroid) of fishing activity changed over time. In each of these analyses, the commercial fleet was broken into trawl and gillnet sectors.

Our analyses next focused on the finer-scale spatial dynamics of the fleet. A “utilization” index was developed by examining the landings contribution of each 10-minute square within the Gulf of Maine to the total annual Gulf of Maine cod commercial landings. The top five most important 10-minute squares throughout the VTR time series (1994–2011) were then identified based on the time series mean of its utilization index. These five 10-minute squares were then evaluated to determine if particular regions within the Gulf of Maine exhibit unique properties in terms of cod removals (i.e., fishery hotspots) and whether there are temporal trends in the use of these hotspots.

A nominal CPUE was estimated for areas inside and outside the fishery hotspots to understand how fishery efficiency varies by area. Since the CPUE estimates were based solely on VTR, they are in effect LPUE indices. Typically, nominal CPUE (or LPUE) indices require standardization before they can be incorporated into stock assessments. Our intent in this analysis was not to develop fully standardized indices, which would require consideration of many more variables (Mayo et al. 1994), but rather to obtain a general understanding of the impacts of fishery hotspots on CPUE estimates.

Simple linear regression models were used to evaluate possible explanations for the temporal trends in the utilization by the

Fig. 3. Gini index of (A) Atlantic cod sampled on the spring and fall fisheries-independent trawl surveys within the Gulf of Maine and (B) the cod fishery broken down into gillnet and otter trawl gear. Higher values of the Gini index indicate increased concentration of the resource or fishery.



fishery of a "fishery hotspot" on Stellwagen Bank, as well as LPUE by the trawl fishery in that area. Spawning stock biomass (SSB) from the 2012 assessment, total landings, and the composite sand lance index were all considered as independent variables explaining LPUE and the utilization of the fishery hotspot. We used SSB values from the 2012 assessment (NEFSC 2013). Assumptions about biological processes (e.g., natural mortality) and uncertainty in the input data will both affect the SSB time series that is output from an assessment model. To address these issues, regressions were also run with 1000 bootstraped SSB time series and with an alternate assessment model that included a ramp in the natural mortality rate from 0.2 to 0.4 over the 1989–2002 time period.

Results

Atlantic cod distribution and diet

Atlantic cod is widely distributed throughout the Gulf of Maine, with notable concentrations closer to shore and particularly in the southwestern portions of the Gulf of Maine (Fig. 1B). Sand lance distributions are highly restricted in the Gulf of Maine, with high abundances on Stellwagen Bank and more limited abundances in Cape Cod Bay, Ipswich Bay, and the backside of Cape Cod (Fig. 1C). In contrast with sand lance, Atlantic herring are widespread throughout the Gulf of Maine with two areas of concentration, one in the southwestern Gulf of Maine and the other in northeastern Gulf of Maine (Fig. 1D). Atlantic herring are in low abundance in the shallow areas on the top of Stellwagen Bank. The distribution of sand lance and Atlantic herring in the stomach contents of Atlantic cod reflects the distribution of both prey species. A large majority of the instances in which sand lance were sampled in the stomach contents of cod occurred on Stellwagen Bank. Atlantic herring in the stomach contents of cod were much more widespread. Atlantic herring were sampled in the stomach of cod around the edges of Stellwagen Bank but were not found in the stomach contents of cod collected in the shallow areas on the top of the Bank (Fig. 1E).

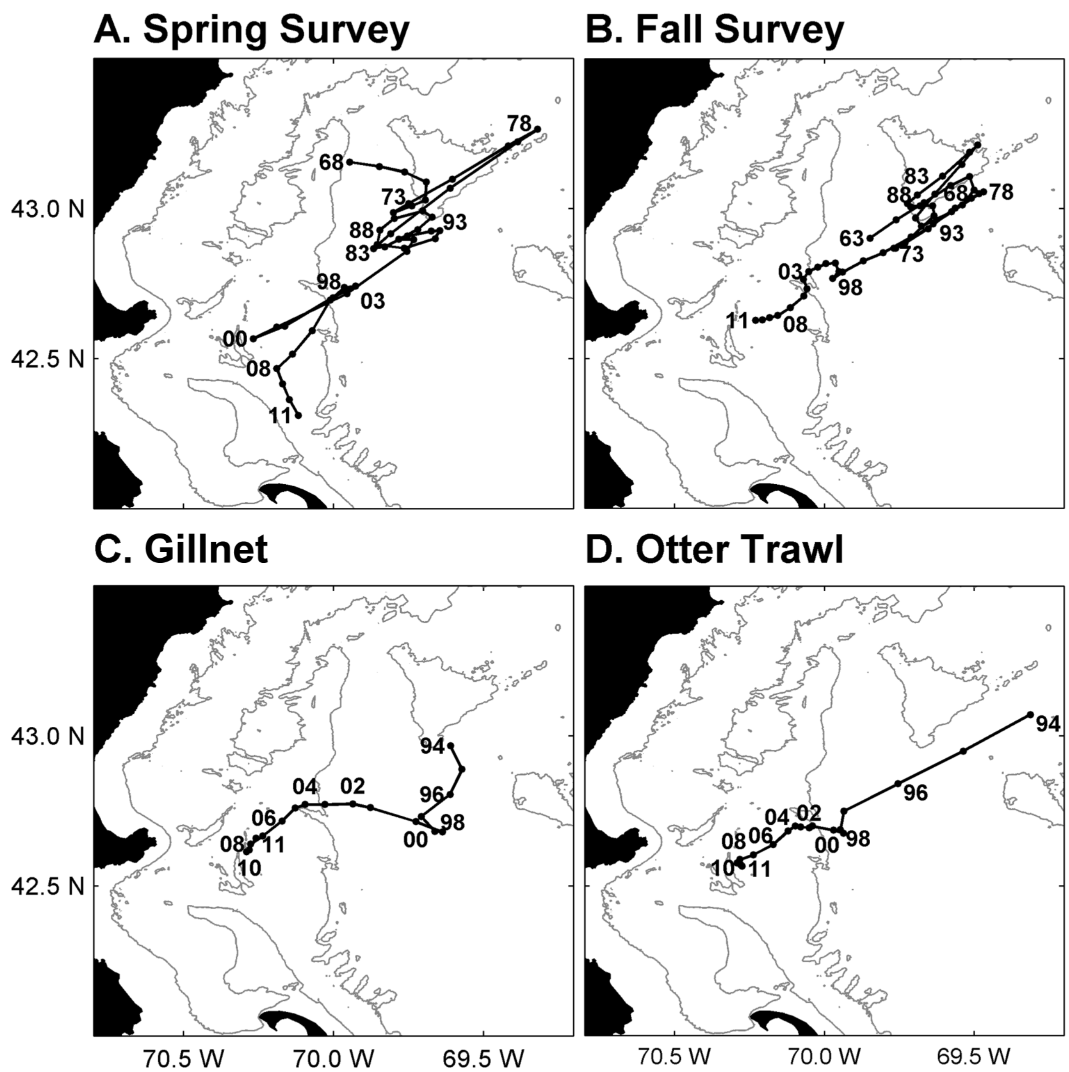
A total of 91 out of 1573 stations (5.7%) at which cod stomach contents were sampled were identified as simultaneously being in the top 20% of cod abundance and the top 20% of relative stomach mass of cod. Atlantic herring was the primary stomach content defined by mass at 37 of these stations, and sand lance was the primary stomach content at 13 of these stations. Recorded diets at the remainder of hotspot stations were comprised primarily of unidentified fish remains (n = 12), silver hake (*Merluccius bilinearis*; n = 3), brittle stars (n = 3), and a mixture of various invertebrate and fish taxa, each dominant at one to two stations. The hotspot stations of Atlantic cod feeding on Atlantic herring and other prey items occurred throughout the western Gulf of Maine and in a few locations within the eastern Gulf of Maine. The hotspot stations of cod feeding on sand lance were all clustered on and around Stellwagen Bank (Fig. 1F).

Atlantic cod in the Gulf of Maine became more aggregated from 1980 to 2010 during both the spring and fall as indicated by increase in the Gini indices (Fig. 3A). The Gini indices were stable or slightly declining from the 1960s to 1980. A southwestward shift of the center of abundance of Gulf of Maine Atlantic cod was also evident over the time series in both the spring and the fall (Figs. 4A, 4B).

Atlantic cod were more concentrated when feeding on sand lance. The abundance of Atlantic cod collected per tow was significantly different based on the primary prey item (*Ammodytes* spp., Clupeidae, other) they were feeding on at that station (Kruskal–Wallis, $P < 0.001$; multiple comparisons $p < 0.05$). The median abundance of cod per tow was 19.9 (interquartile range (IQR): 10.5–59.0), 6.3 (IQR: 3.7–37), and 2.5 (IQR: 1–7.3) for stations in which cod were feeding on sand lance, clupeids, and other prey items, respectively. The bootstrapping procedure indicated that these results were not confounded by the temporal trends of cod, sand lance, and herring; only 5.4% of the bootstrap samples were significant at $p < 0.05$. Calibrated catches of over 100 cod per tow occurred at 23% of the stations (8/34) in which cod were feeding on sand lance, 1.7% of the stations (2/117) in which cod were feeding on Atlantic herring, and 0.3% of the stations (4/1424) in which cod were feeding on other prey items.

Both sand lance and Atlantic herring have been a large component of the diet of Gulf of Maine Atlantic cod during various multiyear periods of time (Fig. 5A). These diet patterns generally match the out-of-phase population cycles of Atlantic herring and sandlance as reflected by the composite indices of abundance (Fig. 5B). These indices indicate that Atlantic herring was at above average abundance until the mid-1970s and from 1991 to 2005, and sand lance was at above average abundance during 1976–1991 and 2006–2010. In 1976, 1981, and 1988, sand lance was >20% of the estimated diet of cod. In some of the early years, insufficient stomach samples were collected in the Gulf of Maine to estimate diet composition, or no stomach samples were collected on Stellwagen Bank, and thus the broad-scale information may have underestimated sand lance in the cod diet. From 2006 to 2010, sand lance was estimated to comprise 20%–60% of the cod diet in the Gulf of

Fig. 4. The mean center of abundance of (A, B) cod on the fisheries-independent trawl surveys and (C, D) commercial landings in the gillnet and otter trawl fisheries. The center of abundance for each year corresponds to the abundance-weighted mean of the latitude and longitude of cod caught in either the fishery or on the trawl survey, but does not necessarily correspond to the location of highest catch. A smoother was applied to both time series before plotting.



Maine. The family Clupeidae, which includes Atlantic herring, was consistently 10%–30% of the estimated Gulf of Maine cod diet from 1988 to 2008 before dropping to <3% in 2009 and 2010. Other clupeids, primarily the anadromous river herring and shad (*Alosa* spp.), are included in this family-level grouping, but are much less common in the diet analyses compared with Atlantic herring given their lower relative abundances and the predominantly offshore survey sampling range.

During periods of high sand lance abundance, the number of cod sampled per tow was higher on Stellwagen Bank versus within the remainder of stratum-26 (Fig. 6). Significant differences between areas were found during both periods of high sand lance abundance (1976–1991, 2006–2010) but not during periods of high Atlantic herring abundance. For the 2006–2010 period, cod abundance on Stellwagen Bank was >10-fold higher than the surrounding areas of stratum-26, though only 10 stations were sampled on Stellwagen Bank during this time period.

Fishery distribution and catch rates

The source location of Gulf of Maine cod landings contracted from 1994 to 2011 in both the gillnet fishery and the trawl fishery (Fig. 3B). This aggregation of the catch, as measured by an increase in the Gini index, was accompanied by a southwestward progression of the catch-weighted center of the fishery (Figs. 4C, 4D).

The top five 10-minute squares with respect to annual contribution to Gulf of Maine cod landings are all located in the western Gulf of Maine to the west of the Western Gulf of Maine Closed Area (Fig. 7A). These five 10-minute squares cumulatively accounted for 10% to 65% of the total Gulf of Maine cod commercial landings in any year between 1994 and 2011, with the contribution generally increasing over time (Fig. 7B). This increased contribution by a relatively small area of the Gulf of Maine is consistent with the concentration indicated by the Gini indices (each 10-minute square represents <0.5% of the total Gulf of Maine surface area). Examination of the annual trends of each of the 10-minute squares shows that one 10-minute square, 427044, is the predominant 10-minute square, accounting for >45% of the total commercial landings in 2010. In terms of total landings contribution, the 427044 square is unlike any other region in the Gulf of Maine. The second most important 10-minute square only contributed 10% to the total landings in a given year (427034) and is located directly to the west of 427044.

Fig. 5. (A) Time series of the proportion of different prey items in the diet of Gulf of Maine Atlantic cod on the spring and fall trawl surveys. Black squares at the top of panel A indicate the years during which stomachs were sampled from cod caught on Stellwagen Bank. (B) Composite time series of sand lance (*Ammodytes* spp.) and Atlantic herring (*Clupea harengus*) abundance. The surveys used to develop these indices are listed in Table 2.

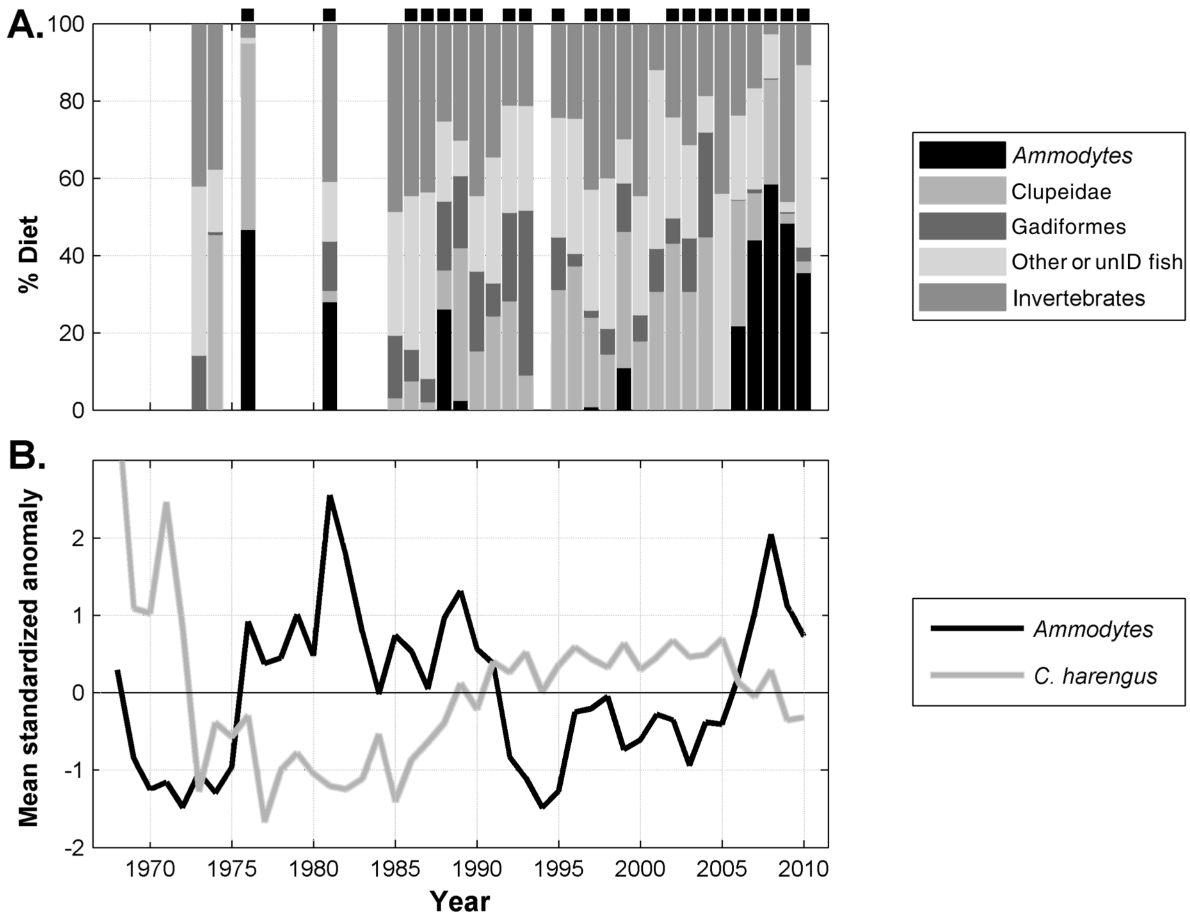
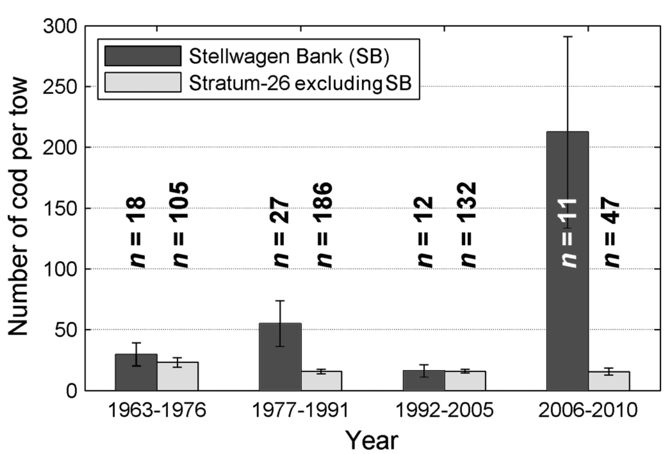


Fig. 6. Abundance of Atlantic cod collected during the NEFSC trawl survey on Stellwagen Bank and the surrounding areas within stratum-26. Time periods are designated based on the abundance of prey items. For the periods 1963–1975 and 1992–2005, sand lance was at low population levels and Atlantic herring abundance was generally high based on the composite time series. For the periods 1977–1991 and 2006–2010, sand lance abundance was high. The number of tows sampled (*n*) on the spring and fall surveys within each time period and in each area are indicated.

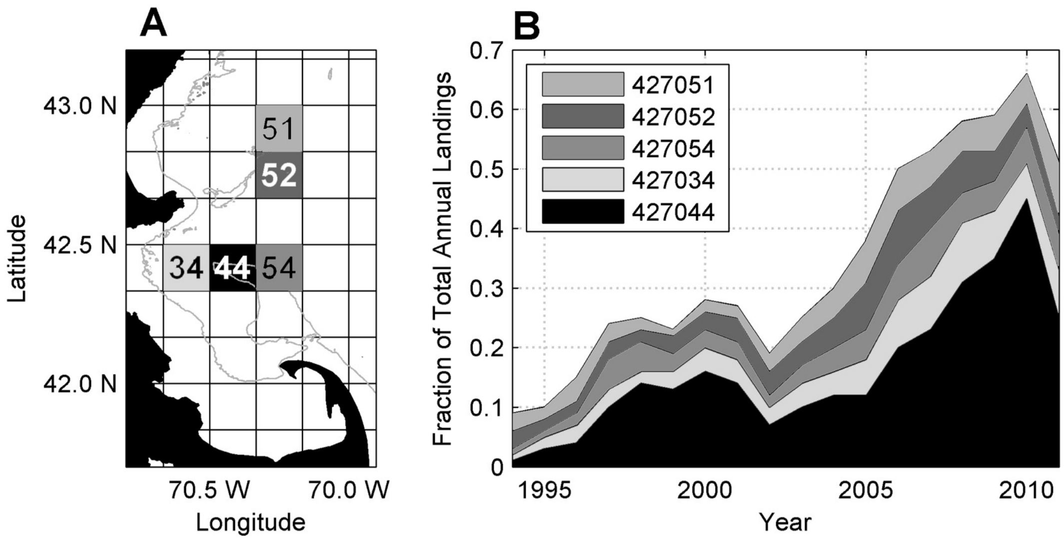


Utilization trends for 10-minute square 427044 estimated from VMS and observer data are similar to those from the VTR data for both the trawl and gillnet fleet (Fig. 8). The observer data indicates slightly more utilization of the area during the 2000 period relative to the VTR data. Caution should be taken in over-interpreting the earlier trends in the observer data because of the low number of observer trips in the early part of the time series. Overall, three sources provide evidence of strong increase in the utilization of 10-minute square 427044 beginning around 2006 and persisting through 2010. Evaluation of the observer data shows that the utilization trends apparent in the landings are also evident in discards and, likewise, total catch for both fleets. This would imply that LPUE is positively correlated to CPUE, at least with respect to utilization trends.

Nominal LPUE indices for both the gillnet and trawl fleet inside 427044 exceed those outside the area beginning around 2007, which coincides with the period of heaviest exploitation within the area (Fig. 9). For both gear types there is very little difference in the LPUE inside or outside 427044 early in the time series, though the two trawl LPUE series show greater agreement. Consistent with a decline in the utilization of 427044 in 2011, there is a notable decline in the LPUE for both fleets, which indicates reductions in the fleet's ability to locate cod inside the area.

The utilization by the fishery of the 10-minute square 420744, encompassing the tip of Stellwagen Bank, was not significantly related to either the biomass of cod estimated in the assessment ($R^2 = 0.20$, $p = 0.057$) or the total landings in the fishery ($R^2 = 0.01$, $p = 0.70$) but was strongly related to the sand lance index from

Fig. 7. Location and landings trends of Gulf of Maine cod fisheries hotspots. (A) The top five 10-minute squares in terms of annual contribution to Gulf of Maine cod landings. Square 427044 on the northwest tip of Stellwagen Bank stands out as the most heavily utilized location by the fishery. The 50 m isobath (gray contours) are noted on the map. (B) Fraction of total annual Gulf of Maine cod landings from the top five ranked 10-minute squares between 1994 and 2011.



1994 to 2010 (R^2 = 0.67, p < 0.0001; Figs. 10A, 10B, 10C). The LPUE time series from inside square 427044 from 1994 to 2011 was minimally related to estimates of spawning stock biomass (R^2 = 0.25, p = 0.036) and was not related to total landings (R^2 = 0.01, p = 0.70; Fig. 10D, 10E). However, it was significantly related to the sand lance index (R^2 = 0.72, p < 0.001; Fig. 10F). The strongest relationship was between LPUE and the utilization of square 420744 by the fishery (R^2 = 0.85, p < 0.0001; Fig. 10G). During the 2012 stock assessment for cod, an alternate assessment model was advanced that included an increase in natural mortality from 1989 to 2002. The SSB estimates derived from this alternate model were also minimally related to LPUE and the utilization of 427044 (R^2 = 0.070 and 0.074, respectively; not shown). The coefficient of determination utilizing 1000 bootstrapped SSB outputs for the assessment model with a fixed natural mortality rate had high variability for the regressions of SSB on LPUE (median R^2 = 0.25; 95% CI = 0.04–0.50) and SSB on the utilization of square 420744 (median R^2 = 0.20; 95% CI = 0.03–0.44).

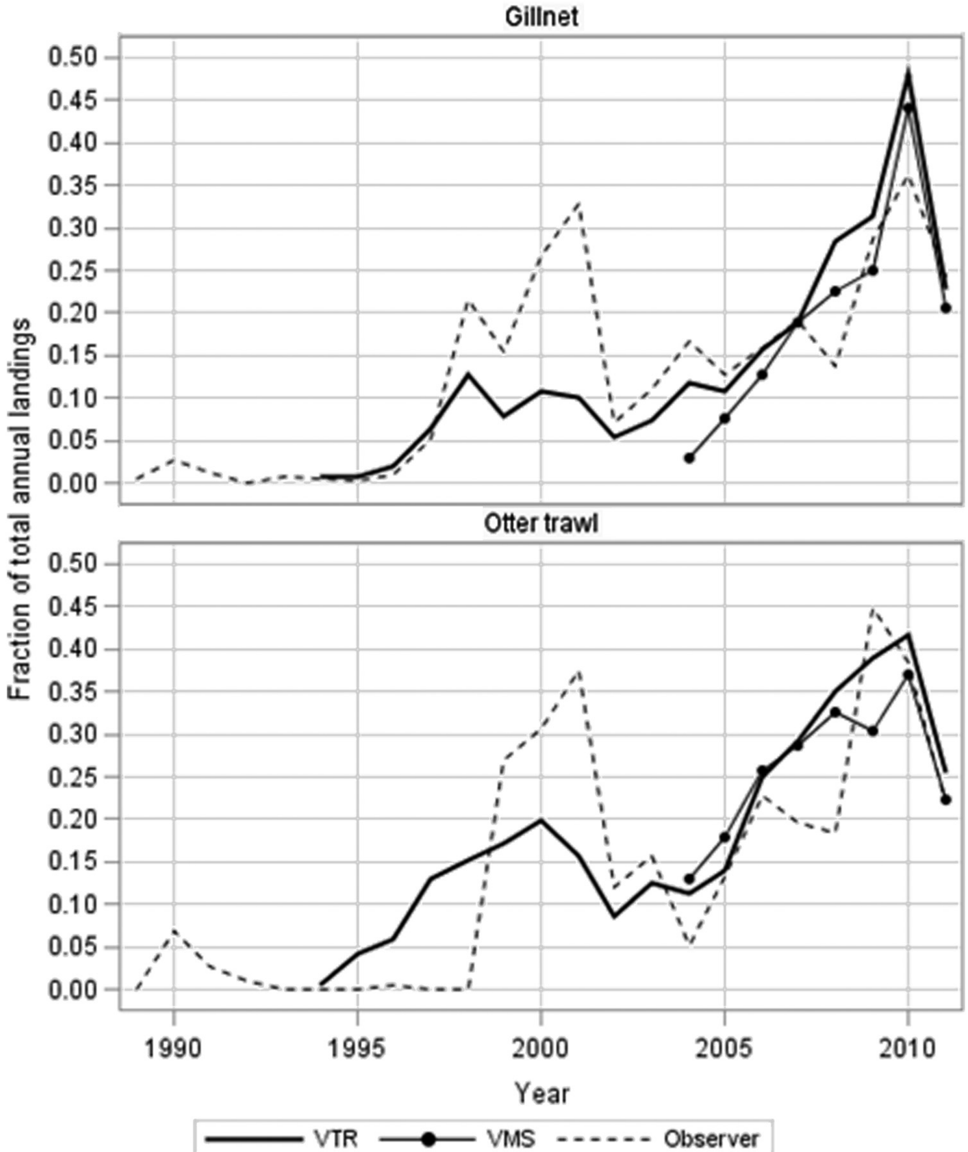
Discussion

The primary focus of this study was to address why there was a disconnect between the status of Gulf of Maine cod stock estimated in the 2011 assessment model versus the perceived status of the stock reported by fishermen leading up to the assessment. Our analysis provides support for a three-part mechanism in which an increase in sand lance abundance resulted in increased catch rates of cod in the Gulf of Maine independent of changes in cod abundance. First, the spatial distributions of forage fish and forage fish in cod stomach contents showed that sand lance have a more aggregated and predictable spatial distribution than Atlantic herring. This pattern is consistent with the obligate association of sand lance with sand bottom habitat and the restricted amount of sand habitat in the Gulf of Maine. Second, when sand lance populations were high regionally, cod shifted their distribution to match that of sand lance, resulting in higher cod abundances on Stellwagen Bank and a higher proportion of sand lance in the stomach contents of cod sampled in the Gulf of Maine region as a whole. Finally, when the sand lance population was high, the fishery both shifted effort towards Stellwagen Bank and achieved higher catch rates when fishing on Stellwagen Bank. The general implications of these results are that the cod population trends in the areas fishermen are targeting may not match the region-wide trends important to the assessment. This lack of coherence between small-scale and stock-wide abundance trends likely explains some of the disconnect among views on the status of the Gulf of Maine cod population. Additionally, these results provide a good example of the difficulties faced when attempting to include fisheries-dependent LPUE time series as indices of abundance in an assessment model.

The dynamic of the interaction between cod and sand lance during the 2006–2011 period also illustrates the challenges inherent in developing monitoring programs that can resolve critical ecosystem processes. A majority of the data we utilized came from the NEFSC trawl survey, which was designed in the early 1960s to produce abundance indices for dozens of species across the ≈250 000 km² area of the northeast US continental shelf, with additional processing of the catch added over time to resolve ecological processes and life-history traits (Link et al. 2008). Stellwagen Bank, within the 50 m isobath, encompasses just 405 km² of the NEFSC trawl survey area and is embedded within a 3369 km² stratum. Stellwagen Bank is thus not sampled on every survey, adding uncertainty to the annual estimates of cod diet and necessitating broader temporal windows when evaluating on-Bank and off-Bank abundances of cod. Furthermore, our analysis of sand lance population trends was reliant on data from across the northeast US shelf rather than on Stellwagen Bank specifically. In general, a broad coherence in decadal-scale trends in sand lance is evident across the northeast shelf (Sherman et al. 1981). However, sand lance are short-lived and do not migrate; thus, in any one year it is possible that a particular location, such as Stellwagen Bank, may not track the shelf-wide population trends. These limitations in the available fisheries-independent data add uncertainty to our understanding of how changes in forage fish abundance affect cod. The development of finer-scale and process-oriented monitoring programs at foraging "hotspots," such as Stellwagen Bank, could help resolve important issues including the seasonal cycles in the use of Stellwagen Bank by cod and whether changes in diet affect cod condition and growth.

As with the fisheries-independent survey data there are a number of caveats to consider when analyzing and interpreting the fisheries-dependent data. The coherence among the three fisheries-dependent data sources (self-reported VTRs, VMSs, and observer data) and between the gillnet and trawl fishery provides a high degree of confidence in the timing and extent of aggregation of

Fig. 8. Fraction of the total annual Gulf of Maine cod commercial gillnet and otter trawl landings reported caught from 10-minute square 427044. Fractional landings are calculated using three data sources: vessel trip reports (VTR), vessel monitoring data (VMS), and data collected by at-sea observers (Observers). Not all data sources are available for all years.



the fishing fleet on Stellwagen Bank. Similarly, the increasing trend from 2005 to 2010 in the LPUE time series agrees with reports from the fishing industry and is robust to different approaches used to calculate the LPUE time series. Unfortunately, during the earlier period of high sand lance abundance in the late 1970s and 1980s, high-quality data on cod fishing locations is lacking, and it is not possible to evaluate whether the fleet also aggregated on Stellwagen Bank during this period. Additionally, while we have focused on how changes in forage fish abundance can affect the behavior of the fishery, it is also important to recognize the simultaneous changes in other drivers of fishing behavior during this time period. For example, fuel prices exhibited a general increase from 2001 to 2008, a sharp decline in late 2008, and then a return to high levels through 2012. Increasing fuel prices favors fishing close to port. For fishermen out of Gloucester, where 60% of Gulf of Maine cod was landed in 2010, Stellwagen Bank is a short trip that minimizes fuel costs. Additionally, in 2006 further restrictions were placed on the number of days at sea fishermen were allowed to fish for groundfish within the western Gulf of Maine. A potential effect of this management change was increased targeting of the highest valued and easiest to target groundfish species, which during this period was cod. This driver may be partly responsible for the increases in nominal LPUE indices outside of 427044 (Fig. 10). The high degree of concentration of the fishery by 2010 was thus likely driven by management and economic factors that provided an incentive for short fishing trips close to port and the increased aggregation of cod on Stellwagen Bank, which allowed these trips to be successful.

The example of the Newfoundland cod illustrates a potential downside to a fishery if CPUE is decoupled from abundance. During the late 1980s, the Newfoundland cod assessment overestimated the size of the cod stock, in part because of the inclusion of a CPUE time series in the assessment model that did not reflect the trend in the stock(Baird et al. 1990; Rose and Kulka 1999). This biased assessment contributed to the maintenance of high quotas. If CPUE was proportional to abundance, a negative feedback loop would have been expected, in which declining abundance led to decreased CPUE, eventually leading individual fishermen to drop

Fig. 9. Nominal landings per unit effort (LPUE) of Gulf of Maine cod by the trawl and gillnet fleet both inside and outside 10-minute square 427044 from 1994 to 2011. The LPUE is expressed as the annual mean landings (lbs, hail weight; 1 lb = 0.453 kg) per days absent. Error bars represent ±1 standard error.

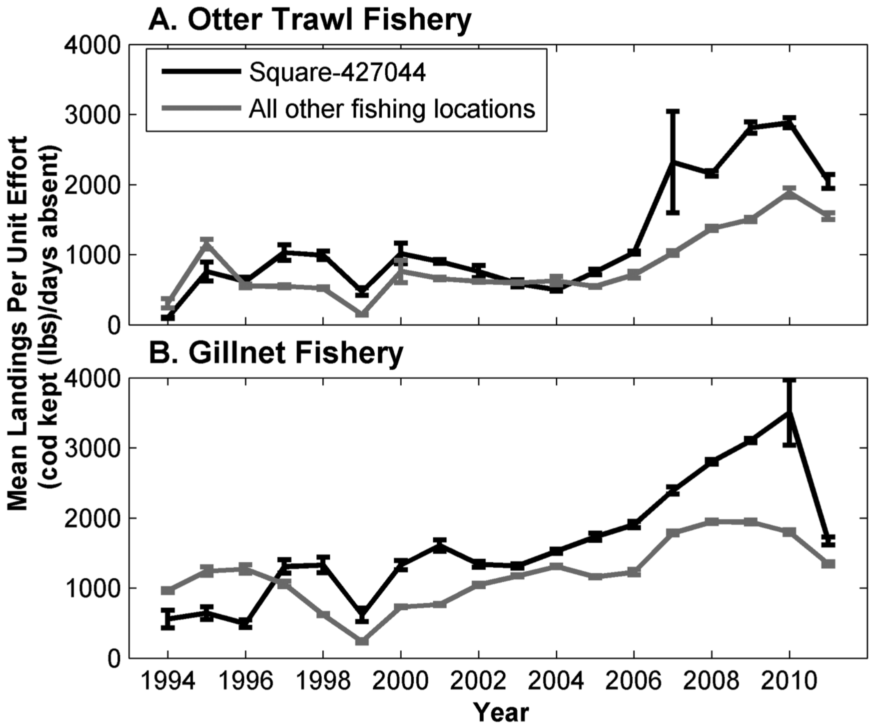
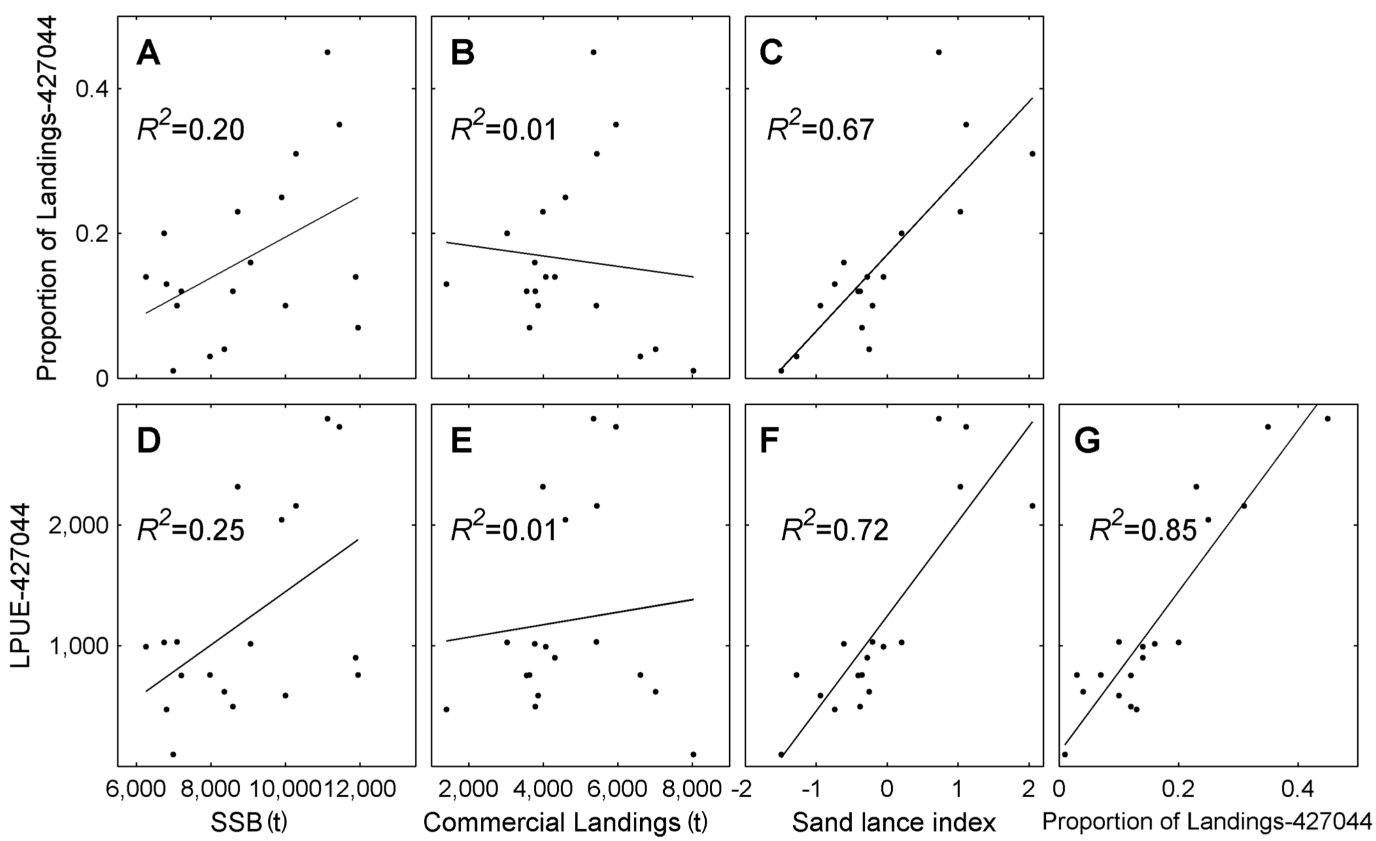


Fig. 10. Regression plots of proportion of landings from 10-minute square 427044 on Stellwagen Bank and (A) spawning stock biomass (SSB) (p = 0.14), (B) commercial landings (p = 0.70), and (C) the sand lance index (p < 0.0001). Regression plots of landings per unit effort (LPUE) in square 427044 and (D) SSB (p = 0.04), (E) commercial landings (p = 0.70), (F) the sand lance index (p < 0.001), and (G) the proportion of landings from 10-minute square 427044 (p < 0.0001). See Fig. 7 for the location of 10-minute square 427044.



out of the fishery, reduce effort, or achieve reduced catch for a given effort, all of which would have contributed to a reduction in total catch. However, increasing CPUE allowed the fishery to continue to achieve high catch levels even as the population was rapidly collapsing to ≈1% of historic levels. While the full set of ecological and socio-economic factors that contributed to the Newfoundland cod collapse are still being debated (Hilborn and Litzinger 2009), an unequivocal lesson is that highly aggregated fish populations are very vulnerable to rapid exploitation-driven collapses when catch limits are set too high owing to either biased assessment results or political pressure.

As in many other regions, changes in the distribution of marine fishes have received considerable attention in the Northwest Atlantic over the past decade (Link et al. 2011). Many of these shifts have been attributed to changes in water temperature, larger-scale climatic influences (Nye et al. 2009; Hare et al. 2010; Overholtz et al. 2011), or alternately to density-dependent habitat selection as population sizes have fluctuated (MacCall 1990). All of these factors may be contributing to the shifts in the Gulf of Maine cod population. In particular, the multidecadal-scale to century-scale contraction of cod to the western Gulf of Maine is consistent with density-dependent habitat selection, though from 1993 to 2011 the population was relatively stable but continued to contract, particularly at the end of that time period. Changes in juvenile habitat, extirpation of local spawning aggregations through intense fishing (Ames 2004), and changes in the abundance of the zooplankton prey of larval cod (Friedland et al. 2013) have also been hypothesized to underlie changes in distribution patterns of Gulf of Maine cod. For fish in general, the importance of changes in prey availability to adult fish has received much less attention than other drivers of distribution shifts. The increase in sand lance abundance since 2006 largely appeared to drive a distribution shift in Atlantic cod in the western Gulf of Maine at a relatively fine spatial scale during a period when the stock size was low but relatively stable or increasing. Interestingly, the larger-scale reduction in the proportion of cod in the eastern Gulf of Maine over the past century may also have been related to changes in prey availability. Ames (2004) and Ames and Lichter (2013) proposed that severe declines in population levels of an important prey taxa in the eastern Gulf of Maine, anadromous clupeids (*Alosa* spp.), may have been a factor in the decline of cod in that region. Changes in the composition of the forage fish community in the Gulf of Maine in general may thus be driving distribution shifts in Atlantic cod across multiple spatial and temporal scales.

In conclusion we showed that changes in the abundance of forage fish species in the Gulf of Maine can decouple LPUE in the cod fishery from cod abundance. Importantly, this work does not minimize the usefulness of monitoring LPUE in the fishery. In fact, the trends in LPUE and the spatial dynamics of the fishery provide a very clear and early indicator of broader changes in the ecosystem that may not only affect the spatial distribution of cod, but also other higher trophic-level species that are preying on the same assemblage of forage fish species (e.g., Weinrich et al. 1997). Furthermore, these changes in the ecosystem may be affecting life-history traits of cod such as growth or fecundity that in turn could influence the productivity of the population.

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