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Original Article

Changes in spatial and temporal variability of prey affect functional connectivity of larval and juvenile cod

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Changes in structural connectivity as it can affect functional connectivity, the biological and behavioural responses of an organism, has been examined here over 2 contrasting years when the spatial distribution of larval and juvenile cod and their prey shifted from the flank to the crest on Georges Bank. New data on the gut contents of pelagic juvenile cod are compared with known prey distributions, potential growth and how climate warming can change connectivity in this region. Centropages spp. was the most important prey for pelagic juveniles, especially in June 1987 when they had high abundance on the crest and were dominant in the cod stomachs. In June 1986, copepod abundance was low where the juveniles were distributed along the flank. The potential growth of juvenile cod was greater in June 1987, consistent with the higher abundance of Centropages spp., and with higher recruitment survival, compared with June 1986. Annual changes in the spatial distribution of cod early life stages within the environment of cold or warm years can have different impacts on their growth and survival. Whereas the small copepods, Pseudocalanus spp., are primary prey for cod larvae and very abundant in cold years, larger copepods, Calanus finmarchicus and Centropages spp., are important prey for the pelagic juveniles and the latter species can have a high impact in warm years on the crest. The different spatial structure during cold or warm years provides an explanation why different year classes respond differently to environmental change. Depending on the presence or absence of specific prey, the functional connectivity response changes pathways that determine the growth and survival of early life stages and ultimately a role in recruitment.

Keywords: copepods, Georges Bank, juvenile cod, prey selection.

Introduction

Connectivity in fisheries is generally thought of in terms of exchange of individuals between stocks by advection of eggs and larvae from spawning sites or migration of juvenile and adults (Zemeckis et al., 2014). The biological and behavioural responses of an organism to an environment can be considered functional connectivity, while changes in the physical environment that affects connectivity and movement can be considered the structural connectivity (Gerber et al., 2014). Evidence suggests that climate warming may reduce the larval fish dispersal distance through faster developmental times and therefore the functional connectivity. The structural connectivity is also affected by climate change and year-to-year variability through considerable changes in the spatial distribution of prey resources and ocean temperatures, which leads to changes in the spatial survival pattern of larval fish and possibly changes in population persistence (Vikebø et al., 2005; Beaugrand and Kirby, 2010; Hinrichsen et al., 2012; Kristiansen et al., 2014; Petrik et al., 2014; Pitois and Armstrong, 2014; Daewel et al., 2015; Akimova et al., 2016; and others). Structural changes can also be alterations in the physical dynamics of a region such as increased stratification due to melting sea ice or increased river-run off, changes in ocean currents caused by changes in atmospheric forcing, changes in the ocean light conditions affecting marine habitats (Varpe et al., 2015), or simply seasonal changes in weather patterns such as monsoons (Turner and Annamalai, 2012) affecting structural dynamics of the ocean. These changes in the structural dynamics can be related to both climate variability, and climate change, but

fundamental changes to connectivity for fish populations is most likely caused by physical changes as a result of global warming.

In this study, the main objective is on the indirect effects of changes in the physical environment and thereby how the structural connectivity affects the spatial distribution and temporal variability of certain prey important for the early life stages to recently settled cod on Georges Bank. The large variation between years in distribution of prey leads to great variability in survival of larval and juvenile fish, suggesting that their connectivity is strongly affected by the structural changes in the physical environment affecting their biological boundaries. It is obvious that having a high abundance of appropriated size prey at the right time and place can provide the most efficient transfer of energy for optimizing growth and survival, important components leading to recruitment.

Connectivity, development, and survival to recruitment of early life stages of marine fish is strongly linked to the dynamics of zooplankton communities that influence the abundance of suitable prey types (Beaugrand *et al.*, 2003; Buckley and Durbin, 2006; Heath and Lough, 2007; Pitois and Fox, 2008; Petrik *et al.*, 2009, 2014; Mountain and Kane, 2010; Kristiansen *et al.*, 2011, 2014; Voss *et al.*, 2012; Friedland *et al.*, 2013; Nicolas *et al.*, 2014). In fact, prey availability combined with temperature are two important factors that strongly influence the survival and development of larvae and pelagic juvenile cod (Nicolas *et al.*, 2014). However, these factors also can act as boundaries for larvae and pelagic juvenile cod habitat envelope, the structural requirement for connectivity. Atlantic cod stocks (*Gadus morhua*) located on their most southerly range, such as on Georges Bank and in the North Sea, who depend on cold water copepods *Calanus finmarchicus* and *Pseudocalanus* spp., are especially affected by warming temperatures associated with climate change. During warm years there is an early onset and extended duration of the spring bloom so the overlap between larvae and prey is prolonged resulting in enhanced cumulative growth and survival (Kristiansen *et al.*, 2011). Since higher temperatures require higher prey abundance to meet metabolic requirements, there is an optimum window for larval growth and survival (Buckley *et al.*, 2010). On Georges Bank, observed growth rate of larval cod increased during spring (February–May) due to the increasing temperature and photoperiod, the latter more important since more time was available for feeding (Buckley *et al.*, 2010). Growth and cohort biomass can increase when mortality falls below growth. In some years this window of survival can occur in February–March when temperatures are at annual minimum and prey are scarce but predators are low. Rapidly growing cohorts later in the season can be lost to the increasing abundance of predators (Garrison *et al.*, 2000).

The physical structure of habitats can have important consequences for food-web and zooplankton community dynamics. This consequently shapes fish population dynamics including their successful dispersal from spawning to nursery grounds (Guichard *et al.*, 2004) and connections with other populations (Edwards *et al.*, 2007). Modelling studies from the Gulf of Maine suggest that dispersal distance from spawning grounds can be dependent on their seasonality in physical conditions (Edwards *et al.*, 2007). Georges Bank cod spawn in the winter–spring along the northern part of the bank and their eggs and larvae generally drift south and west in the residual circulation until settlement as demersal juveniles in summer (Lough, 2010). Although most of the pelagic stages appear to be transported southwest with the

mean current, some of them are retained on the shoals through the developing tidal front near the 60-m isobaths (Lough and Manning, 2001; Aretxabaleta *et al.*, 2005). Those larvae and pelagic juveniles that arrive on the northwest part of Georges Bank diverge and some may cross the Great South Channel to Nantucket Shoals and others may continue eastward along the northern part of the Bank and reside on the northeast part. However, those pelagic juveniles that settle on the western part of the Bank do not appear in any numbers as demersal 0-group (see Supplementary Figure S1). It was suggested by Lough (2010) that the western part does not have the most suitable habitat since it does not have the extensive bottom relief that would limit predation as well as provide suitable prey.

During the pelagic plankton stage when larvae and juveniles are drifting with the prevailing currents, the larvae feed primarily on the copepod *Pseudocalanus* spp. in the Gulf of Maine/Georges Bank region (Broughton and Lough, 2010), the pelagic juveniles are capable of capturing larger prey such as the adult stages of species like *C. finmarchicus*, *Centropages typicus*, *Centropages hamatus*, and juvenile euphausiids (Heath and Lough, 2007). *C. finmarchicus* emerge from diapause in the Gulf of Maine and are transported onto Georges Bank in the winter and reach maximum abundance in the spring around the perimeter (Durbin and Casas, 2006). The two genera of *Pseudocalanus* (*P. moultoni* and *P. newmani*) are cold water species and originate from different sources and intermix on Georges Bank, reaching maximum abundance by May–June (Bucklin *et al.*, 2001; Kane, 2014). The two warm water species *C. typicus* and *C. hamatus* have a more southerly distribution on the shelf (Durbin and Kane, 2007). *C. hamatus* adults have peak abundance in the summer on the crest of Georges Bank, whereas *C. typicus* reach maximum abundance in the late summer-early fall and have a widespread coastal distribution. Copepod size and energy content can have a potential effect on fish growth (Coyle *et al.*, 2011; van Deurs *et al.*, 2015). Cod larvae and juveniles reach a size where preying on smaller prey cannot meet their metabolic demands given constraints on foraging behaviour. The higher growth and survival of the pelagic juveniles in June 1987, compared with June 1986, appeared to be related to the increased abundance and overlap of the *Centropages* spp. (Lough, 2010).

Understanding the structural connectivity on Georges Bank is still an area of research, and currently there are no studies specifically relating a high abundance of *Centropages* spp. to the abundance of 0-group demersal juveniles or age-1 recruits. This is not surprising since no single stage or process has been found to be responsible for many fish stocks but the integrated, cumulative effects on all stages (Houde, 2009; Lough and O'Brien, 2012; Stige *et al.*, 2013). In some years recruitment can be controlled more during the egg and larval stages and in other years during the juvenile stages. Multiple hypotheses are needed to explore recruitment and connectivity processes. A hypothesis developed in this article is that the increased abundance of *C. hamatus* in the summer on the crest of Georges Bank can provide a higher energy prey source for the pelagic juvenile cod at a time when they are transitioning from the smaller copepod prey, *Pseudocalanus* spp., to the larger *C. finmarchicus*. Consequently, dispersal and connectivity between populations of cod on Georges Bank and Gulf of Maine can vary between years due to the variability in the structural landscape caused by variations in prey distribution. Particularly, as shown in this study, *Centropages* spp. may provide an important link as a cause for this variability.
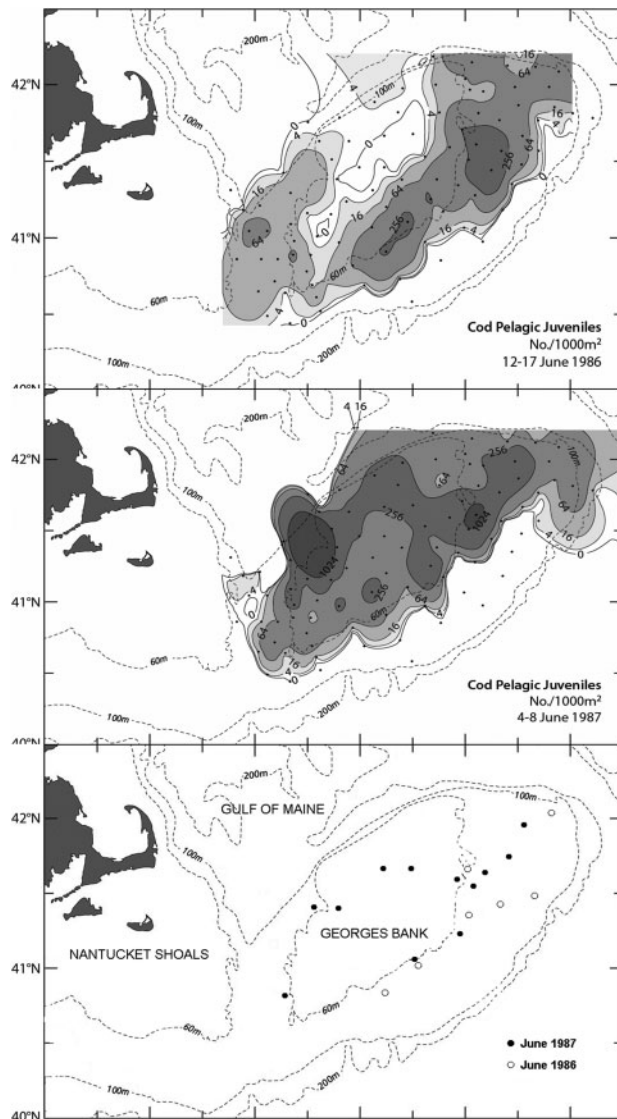
Figure 1. Pelagic Juvenile cod (2–5 cm) distribution and abundance (no./1000 m^2) on Georges Bank collected during 12–17 June 1986 (top) and 4–8 June 1987 (middle) (redrawn from Lough, 2010). Factor 4 contouring was used. Bottom figure (bottom) shows 10 m^2-MOCNESS stations sampled where cod guts were examined. June 1986 stations are represented by open circles and June 1987 solid circles.

Methods

Pelagic juvenile cod were sampled by a Multiple Opening and Closing Net Environmental Sensing System (MOCNESS) having a fixed mouth opening (10 m^2) and nets of 3-mm mesh size (Wiebe et al., 1985; Potter et al., 1990). Maximum depth of the MOCNESS tows was <2 m off the bottom. At each station, 18–22 km apart, a single net was towed from the sea surface to the sea bed and back to the surface (resulting in a double-oblique profile of the water column) for a total of 30 min at two knots (3.7 km h^{-1}). The volume of water filtered was monitored electronically and averaged 19 000 m^3 during a 30-min tow (Potter et al., 1990). Samples were preserved in 5% formalin and seawater. Pelagic juveniles were sorted from the 10-m^2 MOCNESS samples in the lab, identified to species, measured to the nearest

0.01 mm and transferred to 85% EtOH. The MOCNESS station catches were standardized to number per 1000 m^2 of sea surface and all the Georges Bank station abundance data from the June 1986 and 1987 surveys were plotted and contoured by factor of 4.

Pelagic juveniles were selected for gut content analysis from seven stations located across the main cod distributions from the 1986 survey and 12 stations were from the 1987 survey (Figure 1). From each of the MOCNESS stations up to 20 cod were selected from three size categories (Figure 2). All the cod in the smallest size category and then the next 10 smallest in the vial were processed creating three size categories: 15–19, 20–25, and 26–40 mm. With the aid of a dissecting microscope, the entire digestive track was removed from each fish and opened using mounted surgical needles and forceps. There were no fish examined that did not have some prey remains. Gadoid juveniles have a differentiated stomach after ∼15 mm standard length (SL) (Economou et al., 1991); however, prey items were removed and analyzed from the entire digestive system to be consistent with the larval data. Each prey item was identified to the lowest taxonomic and life stage possible. Prey length and width measurements were made to the nearest 0.02 mm with an ocular micrometer. Copepod measurements included only the cephalothorax. It was assumed there was no shrinkage of prey items due to digestion or preservation. The mean measurements for each prey type, from all fish of the same year, species and size category, were used to approximate prey measurements which could not be taken due to an advanced digestive state or fragmentation. Prey biomass for species <1.5 mm in length was estimated using the length to dry weight conversion equations from Cohen and Lough (1981). Biomass for larger prey was estimated using values from literature. Prey was originally grouped into 17 categories based on species and life stage. The *Centropages* (cent) are almost all *hamatus*. The phytoplankton (phyto) category is all centric diatoms. The "cop" category is unidentified copepods, mostly *C. hamatus* and *Pseudocalanus* spp. copepodites with a few *Temora* spp. The "other" category is juvenile gammarids of several species, unknown invertebrate egg (∼0.60 mm), euphausiid furcillia and juvenile *Neomysis americana*. Since the "other" category was large in 1986, Amphipod and Shrimplike were split out into new categories. Later categories were combined into larger groupings to better match the zooplankton prey distributions and modelled data prey categories.

Index of relative importance (IRI) (Pinkas et al., 1971) was calculated for all fish in the three size classes. IRI was selected as it accounts for prey counts and biomass as well as the occurrence of the prey item in the population.

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

%O, percent occurrence of the prey item in the population of larvae in the same sampling category;

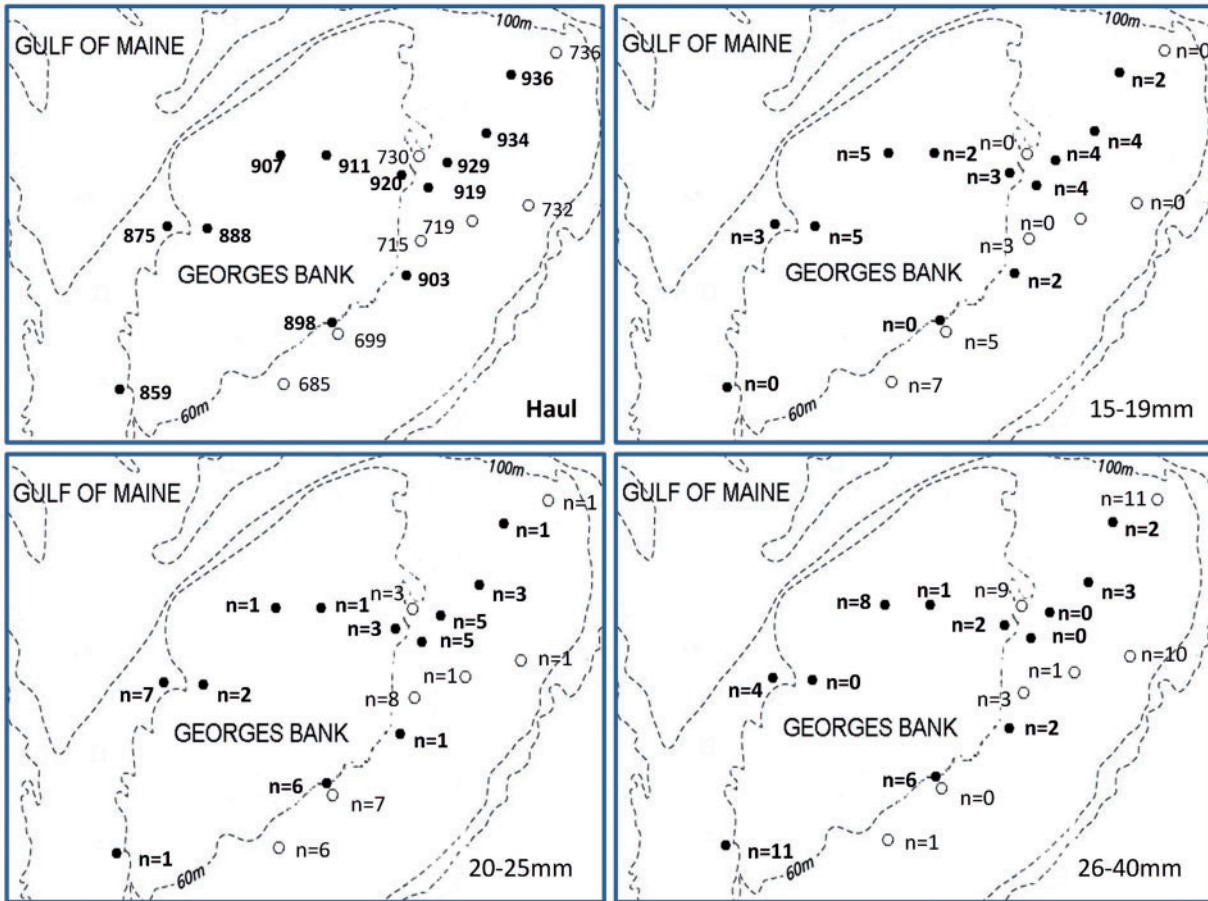%N, the proportion of the prey item in total prey count;

%W, the proportion of the prey item in total prey biomass.

IRI values are presented as %IRI to facilitate comparisons (Cortés, 1997).

$$\%\mathrm{IRI} \; = \; \frac{\mathrm{IRI}_i}{\sum_{i=1}^{n} \mathrm{IRI}_i}$$

where n is the number of prey categories; %IRI also was plotted by survey stations for June 1986 and 1987 cod juveniles containing prey in the three size classes.

Figure 2. Station haul plots showing number of cod juveniles by three size classes examined for prey. June 1986 represented by open circles and June 1987 solid circles.

With new prey information now available on the gut contents of the cod pelagic juveniles from the June 1986 and June 1987 surveys, this study will (i) characterize the prey captured by three cod size categories: 15–19, 20–25, and 26–40 mm; (ii) compare the juvenile gut data with prey distribution and abundance from the MARMAP plankton survey data in the same years; (iii) use the gut data to explain the difference in potential growth for the 15-mm cod estimated in previous growth simulations (Lough and Kristiansen, 2015); and (iv) infer changes in the prey field for Georges Bank cod early life stages due to climate warming.

Prey distribution and abundance May–June

Fine-mesh zooplankton samples were not collected on the same June 1986 and 1987 MOCNESS 10-m surveys so the MARMAP May–June zooplankton data were used as the best available prey field (Kane, 2007). However, if you examined figures from the GLOBEC Georges Bank 1995–1999 surveys for the same common copepods from the 5-year monthly station means, January through June (Durbin and Casas, 2006), you can see that the general patterns are very similar for May and June. The MARMAP zooplankton was sorted, counted and identified to the lowest level possible. These same plankton data were used as prey field data in the modelling study by Lough and Kristiansen (2015) where the authors modelled potential growth of the pelagic juveniles. The study used an individual-based model (IBM) for juvenile cod to

calculate growth and development rates through the seasons and years (1978–2006) based on the MARMAP prey data and observed ocean temperature as a source for variability in environmental conditions consequently affecting recruitment (for more details on the IBM please see Lough and Kristiansen, 2015). However, that study did not have the benefit of having the actual gut content data for comparing with the modelled results and we therefore incorporate some of the modelling results in this study. Feeding data was modified to include only the copepod species and life stages included in the Lough and Kristiansen (2015) study. %IRI was recalculated using the reduced prey categories. Prey selection in their study was based on fish mouth gape. Plots (no./m^3) from the May–June MARMAP data were made for *C. finmarchicus* A, C4-5, *Pseudocalanus* spp. A, C4-5, and *C. hamatus* all stages.

Results
June 1986 prey selection

Pelagic cod in June 1986 selected copepods that were more common on the southern flank (Supplementary Table S1). *Pseudocalanus* spp. was the most selected prey by numbers and biomass followed by *C. finmarchicus* for the 15–19 mm fish. There were few *C. hamatus* (cent A) selected by 15–19 mm fish (4.5%), but more were selected by the 20–25 mm fish (24%). The 20–25 mm fish transitioned to selecting more *C. finmarchicus* that
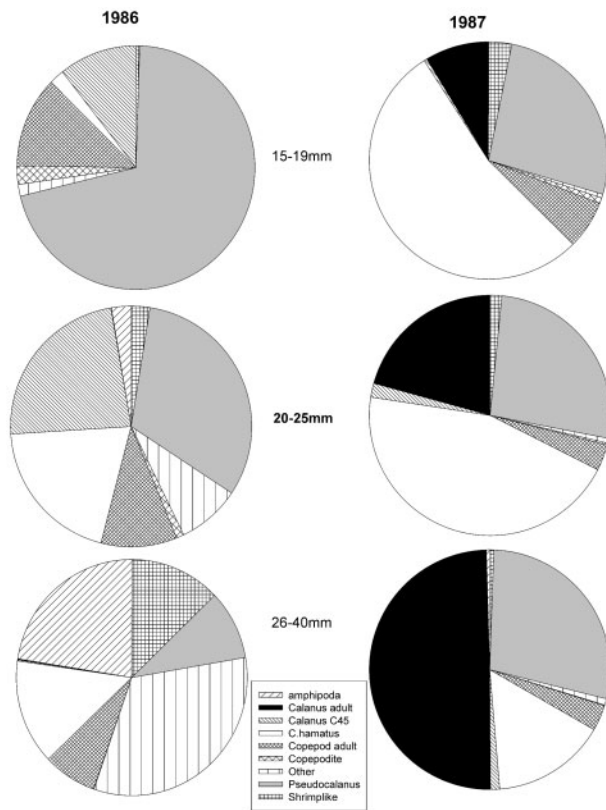
Figure 3. IRI plotted for all June 1986 and 1987 cod juveniles containing prey in the three size classes: 15–19, 20–25, and 26–40 mm.

increased its biomass contribution (79.5%) over that of *Pseudocalanus* spp. (13.8%). *C. hamatus* (cent A) made the greatest contribution in prey numbers and biomass for the 26–40 mm fish (22.0 and 6.6%, respectively) followed by *Pseudocalanus* spp. (17.8 and 5.6%, respectively). Fewer *C. finmarchicus* were selected by the 26–40 mm fish; instead they increasingly ate shrimp and gammarids (other, 8.5 and 80.9%, respectively).

June 1987 prey selection
The more shoal, northerly distribution of fish in June 1987 selected prey different from those on the southern flank (Supplementary Table S2). For the 15–19 mm fish, *C. hamatus* (cent A) was the highest prey selected by count (45%) followed by *Pseudocalanus* spp. (29.4%) The two smaller size classes had similar prey counts and biomass contributions for *C. hamatus* (cent A) and *Pseudocalanus* spp. Although they had higher prey counts than *C. finmarchicus*, *C. finmarchicus* contributed the greater biomass (30.7 and 43.6%, respectively). Note that the 26–40 mm fish switched to higher prey counts of *C. finmarchicus* (15.5%) and *Pseudocalanus* spp. (42.5%), but fewer *C. hamatus* (cent A) (26.7%). *C. finmarchicus* contributed the highest biomass as prey for the larger fish; however, there was almost no shrimp or gammarids (other) in contrast to the June 1986 largest size class of cod.

Index of relative importance
June 1986% IRI (Supplementary Table S3 and Figure 3) indicated that *Pseudocalanus* spp. adults were the most important prey for

the 15–19 mm juveniles (65.90%) decreasing for the 20–25 mm (31.66%) and 26–40 mm fish (9.28%). They were most abundant on the southern flank stations. *Centropages* spp. adults increased in importance with size (1.43, 20.82, and 14.16%) as well as *C. finmarchicus* stages 3–4 copepodites (11.05 and 19.49%) except for the largest size class (0.23%). Both species were found mostly on eastern Georges Bank stations. Also, gammarids and shrimp were especially important for the 26–40 mm fish (22.94 and 13.01%, respectively) and primarily found on the northeastern Georges Bank stations. Phytoplankton increased significantly with fish size (1.30, 7.57, and 31.94%) and also found most abundant on northeast Georges Bank station, which is unusual for the larger fish. Nutritional value of phytoplankton is unknown.

June 1987%IRI (Supplementary Table S4 and Figure 3) indicated that *Centropages* spp. adults were most important for the 15–19 and 20–25 mm fish (43.08 and 32.55%, respectively), whereas *C. finmarchicus* adults were more important for the larger size classes 20–25 and 26–40 mm (22.53 and 51.70%, respectively). *Pseudocalanus* spp. adults had similar importance across all size classes (27.29, 27.40, and 25.98%). Other prey categories were unimportant. *Centropages* spp. were more abundant on the shoal crest region, whereas *C. finmarchicus* were more abundant on the flank. *C. finmarchicus* could be more important for the larger size class 26–40 mm depending on the overlap of the pelagic juveniles.

Prey selection in relation to prey distribution and potential growth
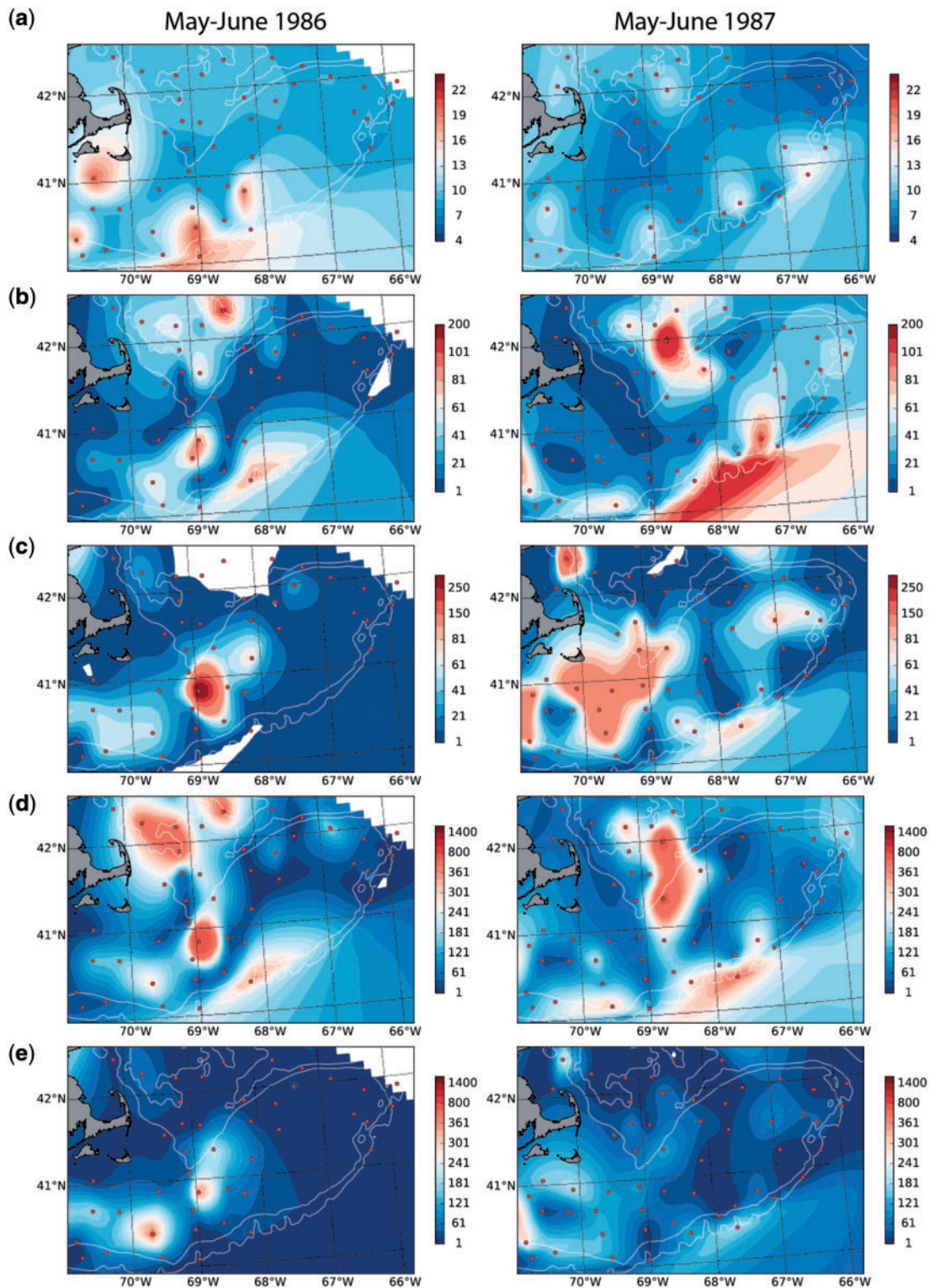The MARMAP May–June 1986 and 1987 distribution of *C. finmarchius* adults show low numbers across the Bank in 1987, but somewhat higher numbers in 1986, especially in the southern part of the Great South Channel and Nantucket Shoals (Figure 4a). The C5-4s had order of magnitude higher numbers near the western part of the Bank coinciding with the adult distribution in 1986. In 1987, the higher numbers of C5-4s were located mostly off the southern flank in the Slope Water and a smaller area in the Gulf of Maine impinging on the northeast part of the Bank (Figure 4b).

Centropages spp. C5-6 distributions, in 1986 were found across the Bank with a high concentration at the western end in the Great South Channel (Figure 4c). In 1987, the highest numbers were found extensively in the Great South Channel and Nantucket Shoals.

Pseudocalanus spp. C6 adults were abundant across the Bank with high concentrations on the western side. In 1986 the high concentration was in the Great South Channel and in 1987 a high concentration was on the northwest part (Figure 4d). The C4-5s were generally lower in abundance that the adults, and less abundant in 1987 than 1986 (Figure 4e).

Comparing the station %IRI cod size classes by the three copepod prey provides some additional spatial patterns despite the limited number of stations and few fish within a size class. *Centropages* spp. (Figure 5a–c) had consistently the highest %IRI values on the northern half of the bank from crest to flank for all three cod sized classes, especially for June 1987. The June 1986%IRI values were very low on all stations, <20%. *C. finmarchicus* adults (Figure 5d–f) tended to have higher %IRI values around the deeper flank, especially for the larger cod and in June 1987. Again, the June 1986%IRI station values were very low, <26%. *C. finmarchicus* C4-5 (Figure 5g–i) were an un-important

Figure 4. Distribution and abundance of *C. finmarchicus* Adult (a), Copepodids C4-5 (b), *C. hamatus* Copepodids C5-6 (c), and *Pseudocalanus* spp. Adult (d), Copepodids C4-5 (e) on Georges Bank in May–June 1986 and 1987, contoured from MARMAP survey data.

part of the cod prey and only a few stations had a %IRI of 30–60%. *Pseudocalanus* spp. adults (Figure 5j–l) had the highest station %IRI values in 1987 and generally around the flank. The 20–25 mm cod had the most stations with high %IRI values compared with the smaller and larger size classes.

The %IRI was calculated for the simulated fish of 15 and 18 mm and combined to compare with the 15–19 mm fish %IRI from the field caught fish. Juveniles caught with the 10-m MOCNESS were from integrated water-column tows similar to the MARMAP tow profiles for the zooplankton. However, even
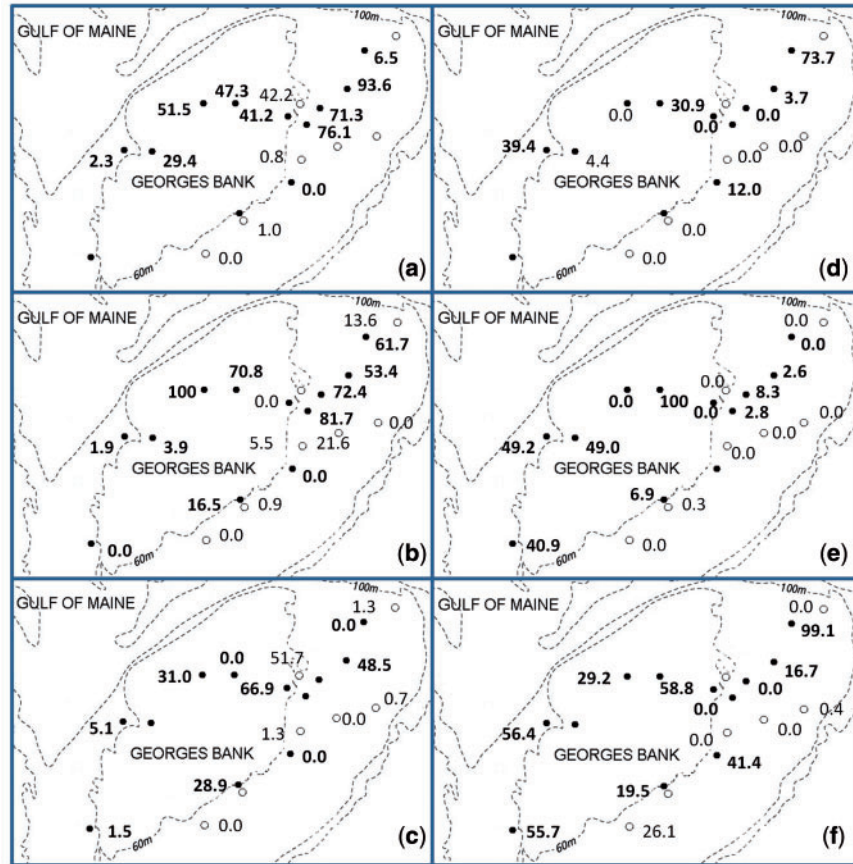
Figure 5. The Index of Relative Importance (%IRI) is plotted on each station for the four copepod categories for each of the cod size classes: (a) cod 15–19 mm %IRI *Centropages* spp., (b) cod 20–25 mm %IRI *Centropages* spp., (c) cod 26–40 mm %IRI *Centropages* spp., (d) cod 15–19 mm %IRI *Calanus* Adult, (e) cod 20–25 mm %IRI *Calanus* Adult, (f) cod 26–40 mm %IRI *Calanus* Adult. Station %IRI values are in bold for June 1987.

after modifying the prey fields and size categories to match the modelled prey field data, the %IRI prey selection comparison between the field gut contents and modelled potential prey did not correlate closely due to the wide differences in station locations and dates. Simulated prey gut contents were only from fish fixed at 20 m so the modelled prey captured were not expected to quantitatively match the observed prey captured since the pelagic juveniles can migrate through the water column. In addition, the prey field available in the simulations was constant with depth since only depth integrated values of prey distribution were available from MARMAP. This difference probably is the reason for field fish having more epibenthic prey than the model fish. Only the major prey contributions to the diet were considered since these species were the dominant ones which we have data for use in the model. For each MARMAP station the IBM was run for several days using many individuals, so each station represents the average feeding composition.

Potential May–June Specific Growth Rate (SGR) was generally 1–2% d^{-1} higher for a 15 mm than an 18 mm fish (Lough and Kristiansen, 2015; see Supplementary Table S5). On Western Georges Bank, SGR for a 15 mm fish was about 8% d^{-1} and for an 18 mm fish about 7% d^{-1} in both years. On Eastern Georges Bank, there was a higher SGR for a 15 mm fish in 1987 than 1986 (6.16 vs. 4.50% d^{-1}), but lower for an 18 mm fish (4.98 vs. 6.94% d^{-1}) (also see Supplementary Figure S2). Note that the modelled

prey selection only included copepods, whereas the gut content %IRI indicated that shrimp and amphipods were increasingly important for the fish larger than 20 mm in 1986.

Discussion
Past and future changes in structural connectivity

A recent vulnerability assessment on the effect of climate change on the Northeast US Shelf (Hare *et al.*, 2016) linked increases in temperature to climate-related changes in prey and decreases in recruitment on Georges Bank and Gulf of Maine (Friedland *et al.*, 2013; Lough and Kristiansen, 2015; Pershing *et al.*, 2015). It is expected that species at the southern end of their range, such as cod, will lose suitable habitat with continued warming, with implications for connectivity between local populations. Although the Gulf of Maine stock is managed separately from the Georges Bank stock, there is potential for transport and migration from western Gulf of Maine to Nantucket Shoals and Georges Bank (Huret *et al.*, 2007). Friedland *et al.* (2013) indicated that these stocks have responded differently to environmental conditions in recent years. During the 1997–2001 warming trend, cod was in reduced abundance on Georges Bank, Nantucket Shoals and Gulf of Maine, whereas in the 2007–2011 cooling period the pattern shifted to higher abundances in western Gulf of Maine and Nantucket Shoals and to
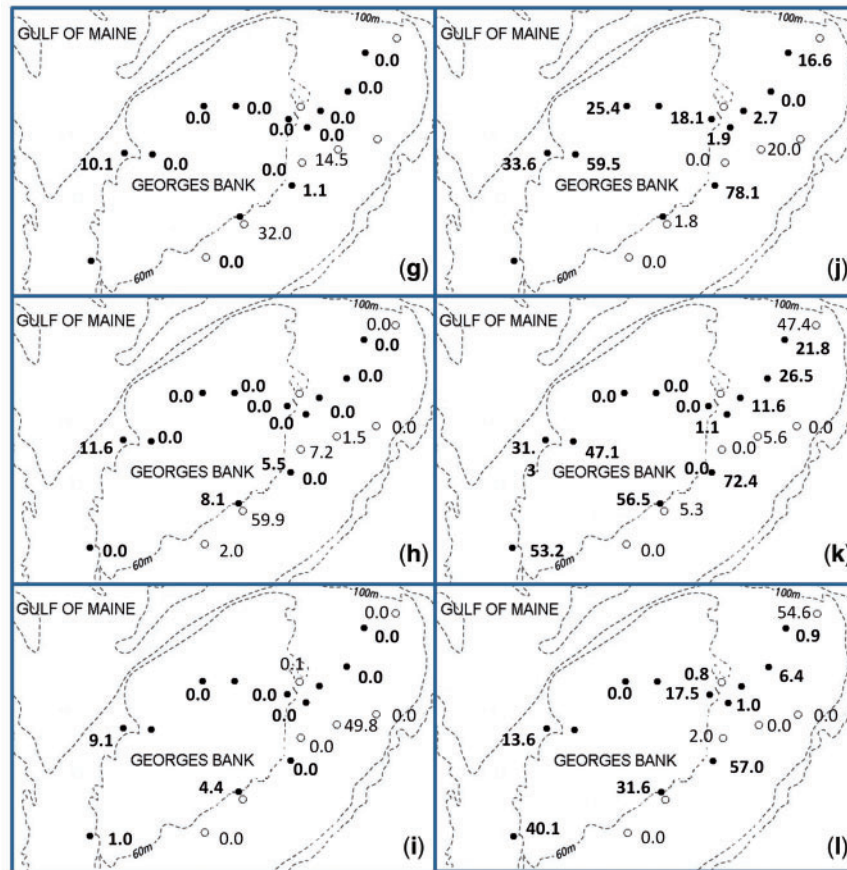
Figure 5. Continued. The Index of Relative Importance (%IRI) is plotted on each station for the four copepod categories for each of the cod size classes: (g) cod 15–19 mm %IRI *Calanus* C4–5, (h) cod 20–25 mm %IRI *Calanus* C4–5, (i) cod 26–40 mm %IRI *Calanus* C4–5, (j) cod 15–19 mm %IRI *Pseudocalanus* spp., (k) cod 20–25 mm %IRI *Pseudocalanus* spp., (l) cod 26–40 mm %IRI *Pseudocalanus* spp. Station %IRI values are in bold for June 1987.

lower abundances on Georges Bank and eastern Gulf of Maine. Generally, *Pseudocalanus* spp. spring abundance declined in those habitats where warming occurred and cod increased in abundance where *Pseudocalanus* spp. had not declined. Possible explanations for the decline of *Pseudocalanus* spp. are discussed by the authors that include advective displacement, primary production patterns and zooplankton interactions.

Variability in structural connectivity can be quantified through variability in historical observations of prey distributions across cold and warm years. For example, Friedland *et al.* (2015) examined variability of the production cycle on the Northeast US Shelf using SeaWiFS derived chlorophyll-a concentration and SST satellite data. The authors found that increasing winter temperature leads to early and increased stratification affecting distribution of nutrients; however, early blooms are constrained by seasonal availability of light. Species composition also shifts from large siliceous phytoplankton and a change in the micro-zooplankton diversity. Spring bloom on Georges Bank started mid-March and early blooms tended to be larger and last longer. On Georges Bank, spring chlorophyll concentration was positively correlated with zooplankton biovolume. The direct bottom-up influence on zooplankton is most likely due to the predominance of small copepod species on Georges Bank that have faster growth rates and can rapidly increase their population abundance. Early blooms may therefore be favourable for larval

cod since the copepod *Pseudocalanus* spp. is a primary prey for southern cod.

Nevertheless, *Pseudocalanus* spp. has shown a downward trend since 2000 for Georges Bank and Eastern Gulf of Maine (Friedland *et al.*, 2013; Lough and Kristiansen, 2015). Winter spawning cod (February–March) on these areas were structurally associated with the decline of *Pseudocalanus* spp. (February–April). Friedland *et al.* (2013) reported SST warming trends over the northeast shelf during spring 1997–2011 except for eastern Gulf of Maine and Georges Bank. However, Lough and Kristiansen (2015) did not show a significant change over the time series for January–February and March–April based on mean temperature from the upper 20 m of the water column. Instead, a warming trend was shown for May–June 1990–1999 across all northeast shelf areas. Their 1978–1989 and 2000–2006 periods had similar lower temperatures. The potential growth rate of cod 12–18 mm also peaked in May–June when temperatures warmed, prey increased in abundance and there were longer hours for feeding (Lough and Kristiansen, 2015). Cod juvenile growth decreased sharply during 2000–2006, the cool period, co-incident with the decline of average prey size and abundance of *Pseudocalanus* pp. and *Centropages* spp.

Cod pelagic juveniles become more demersal oriented residing near bottom by day and feeding on planktonic and epi-benthic prey (Lough, 2010). By mid to late summer, when they are larger

than about 7 cm, their diet reflects more of the benthic prey as they transition to recently settled juveniles. Although the copepodids of *C. finmarchicus* are significantly larger than those of the other common copepods on Georges Bank, *Pseudocalanus* spp. copepodids are intermediate in size between the smaller *Paracalanus parvus* and *Oithona similis* and the larger *Centropages* spp. (Cohen and Lough, 1981). Developing stages of the smaller copepods are the preferred prey of cod larvae, while the pelagic juveniles prefer the larger copepods if available. On the crest of the Bank, copepods are distributed through the water column by the well-mixed water (Durbin and Kane, 2007). On the deeper stratified flanks, the copepods are generally found above the thermocline in the surface 10-m. *Centropages* spp. is considered a non-migrator but may undergo vertical migration depending on a number of factors. *Centropages* spp. can be the intermediate link between the smaller copepods and the larger *Calanus* and other crustacean prey such as euphausiids. The larger *C. finmarchicus* copepodids are still too large for the smaller pelagic juvenile size class, 15–19 mm, until the 20-mm size class. The pelagic juveniles will continue to prey on the smaller *Pseudocalanus* spp. if larger copepods are scarce. Since the pelagic juvenile cod are diel vertical migrators, there may be more contact with the *C. hamatus* copepodids beginning in May–June on the crest where they are mixed through the water column. However, on the deeper flank the copepods are located more near the surface whereas the pelagic juveniles become increasingly bottom oriented so there is less overlap for feeding.

Changes in the structural connectivity between cod and its prey can affect the different contact and capture probabilities of prey. Petrik *et al.* (2009) demonstrated in a modelling study for cod larvae, the positive selection for *Pseudocalanus* spp. and negative selection for *C. finmarchicus* and the low selection for *C. typicus* can be explained by differences in the encounter and capture probabilities of the prey. *Pseudocalanus* spp. usually high in abundance are relatively easy to catch due to their high deformation rate threshold, slow swimming speed and slow escape jump speed. The low incidence of *C. typicus* and especially *C. finmarchicus* in larval guts are due to their low deformation rate threshold, fast swimming speed, escape jump speed and many developmental stages wider than their mouth gape. In contrast to the larvae, the pelagic juveniles have the capability to select the larger stages of *Centropages* spp. and *C. finmarchicus* that provide a greater energetic benefit. Spatially explicit IBM models need to incorporate both dispersion and functional connectivity effects to more accurately estimate feeding, growth and survival of early life stages. Also, more information is needed on the available local prey and the cod feeding preferences, as well as the ambient temperature.

The early life stage survival of Georges Bank cod was especially intriguing in 1986 as there was a marked decrease in abundance between the 9–11 mm larvae and the 20–50 mm pelagic juveniles, whereas in 1987 the between stage abundances stayed about the same (Lough, 2010). Both larvae and pelagic juveniles were located more on the flank of Eastern Georges Bank in June 1986, whereas in June 1987 they were distributed mostly across the shoal, central part of Western Georges Bank (Figure 1). Lough and Kristiansen (2015) found that the potential growth for 15-mm cod was lower in May–June 1986 than 1987 for both Eastern Georges Bank (4.50 and 6.16% d^{-1} respectively) and Western Georges Bank (7.59 and 8.03% d^{-1}, respectively), consistent with recruitment survival (0.35 and 0.41, respectively). There also was a decrease in copepod density and biomass in 1986 for

May–June Eastern Georges Bank and Western Georges Bank, relative to 1987. The relative contribution of *C. typicus* increased from 5.2% on Eastern Georges Bank in May–June 1986 to 36.4% on Western Georges Bank in May–June 1987. The higher apparent mortality of pelagic juveniles during June 1986, compared with June 1987, appeared to be related to the low numbers of *Centropages* spp. for the 15–19 mm size group. High numbers of *Centropages* spp. were found in guts of the same size group in June 1987 in this study, consistent with their higher abundance on the bank crest and greater potential growth of the juveniles. Although the modelled fish were fixed at 20-m depth, evidence from the gut prey and known behaviour indicated the field fish were vertically migrating. Another reason for the higher mortality of the 1986 pelagic juveniles could be indicated by the increased numbers of epi-benthic prey such as gammarids and mysids in their prey selection. Their presence indicated that cod were venturing closer to the bottom in search of prey leaving them vulnerable to not only pelagic predators but to groundfish predators. In June 1986, the well-mixed water column with cooler temperatures persisted to about the 80-m isobaths that may have changed the cod's vertical migration pattern along the flank of the Bank (Lough and Potter, 1993). Residing lower in the water column also would reduce transport time and perhaps create a smaller distribution area.

The potential impact of prey availability for cod larvae, pelagic and demersal juveniles on the Georges Bank flank vs. crest habitat during cold and warm years is described in Table 1. Impact is defined as having a high, intermediate or low potential influence or control on the cod life stage in terms of feeding, growth, and survival.

Pseudocalanus spp. are primary prey for cod larvae and very abundant in cold years across Georges Bank. They are of intermediate importance for the pelagic juveniles and lower in importance for the demersal juveniles. In warm years they are of intermediate importance for the larvae and of lower importance on the flank for the pelagic juveniles

Centropages (*hamatus*) spp. is of low importance for the larvae both cold and warm years. They are of intermediate importance for the pelagic juveniles on the crest and for the demersal juveniles on the flank in cold years. However, in warm years they can have a high impact for the pelagic juveniles on the crest and intermediate impact on the flank. *Centropages* spp. can bridge the size-nutritional continuum between the smaller *Pseudocalanus* spp. and the larger copepodids of *C. finmarchicus*.

C. finmarchius, a cold water species has only an intermediate impact for larvae on the flank if the stages are sufficiently small. In contrast, *C. finmarchicus* can have a high impact on the flank for the pelagic juveniles. In warm years, they would only have an intermediate impact on the flank for the larvae, pelagic, and demersal juveniles.

Mysids (*N. americana*) are very abundant on Georges Bank but are found more on the crest associate with the tidal front at 30–60 m depth (Wigley and Burns, 1971). They are diel vertical migrators as adults residing at bottom by day and ascending to near surface by night (Lough and Aretxabaleta, 2014). Mysids are eurythermal and omnivorous and appear to be abundant in both cold and warm years. Link and Garrison (2002) reported that the small juvenile cod, <10 cm, have a diet primarily of mysids (80%).

It is now consensus that recruitment of marine fish can be determined at any of the early life stages, or some combination of

Table 1. Prey preference impact for Georges Bank (GB) cod larvae, pelagic, and demersal juveniles on flank vs. crest habitat under the influence of cold and warm years.

	Cold years				Warm years			
COD stage	*Pseudocalanus*	*Centropages*	*Calanus*	Mysid	*Pseudocalanus*	*Centropages*	*Calanus*	Mysid
Larvae								
flank GB	H	L	I		I	L	I	
crest GB	H	L	L		I	L	L	
Pelagic juveniles								
flank GB	I	L	H		L	I	I	
crest GB	I	I	L		I	H	L	
Demersal juveniles								
flank GB	L	I	I	I	L	I	I	I
crest GB	L	L	L	H	L	L	L	H

H, high potential impact; I, intermediate; L, low; GB, Georges Bank.

stages, and that drivers come from many environmental and biological sources (Houde, 2008; Lough and O'Brien, 2012; Stige *et al.*, 2013; Ottersen *et al.*, 2014; Hare, 2014; and others). Although regional ocean warming can promote earlier and higher primary productivity, leading to longer overlap in larval cod and their prey and greater cumulative survival, the latitudinal effect on recruitment varies. Increased temperatures were correlated with higher recruitment in low temperature habitats and lower recruitment in high temperature habitats (Planque and Frédou, 1999). Middle range habitats (7–8 °C) were not correlated with recruitment so the author's concluded that other processes may control survival after the larval and juvenile stages. Kristiansen *et al.* (2011) also found high correlations between juvenile cod and recruits for the North Sea and Lofoten, but not for the Iceland and Georges Bank regions. Increasing water temperature increases cod metabolism and development that can be sustained by feeding on increasingly larger prey. Faster growth means larger larvae that are better at avoiding predation and feeding on a wider variety of prey. On the other hand, warming can change the prey species timing and production and not overlap cod development for the best survival (Kristiansen *et al.*, 2011). Long-range projections into the latter half of this century of increased warming may increase larval metabolism beyond the point where prey may be below that required for growth in all northern North Atlantic regions (Kristiansen *et al.*, 2014). However, there is still considerable uncertainty of the impact of these changes on fisheries recruitment and the processes involved (Brander, 2007). Cold water species such as *Pseudocalanus* may be unable to tolerate warmer temperature and not be available in sufficient numbers as prey for cod larvae on the most southern spawning grounds such as Georges Bank. Similarly, *C. finmarchicus* may not be available in sufficient numbers as prey for the pelagic juveniles, although other warm tolerant species may suffice (Beaugrand and Kirby, 2010). Changes to each stock's preferred prey can have different impacts depending on the availability of a suitable substitute. Connectivity among stock may increase as they have to search further for suitable prey. Also, changes in distribution and abundance of invertebrate and vertebrate predators of cod can occur in unpredictable way as well as a host of other ecosystem changes (Kristiansen *et al.*, 2014).

In summary, the June 1986 pelagic cod juveniles were distributed across the southern flank in contrast to June 1987 where they were found more frequently across the shoal crest. The June 1986 gut contents indicated that *Pseudocalanus* spp. adults were

the most important prey for the 15–19 mm juveniles (IRI: 65.9%), whereas in June 1987 *C. hamatus* adults were most important for the 15–19 and 20–25 mm fish (IRI: 43.1 and 32.6%, respectively). The greater potential growth (>6% d^{-1}) and survival of pelagic juveniles (15–25 mm) during June 1987 was consistent with the higher prey selection and abundance of *Centropages* spp. on the Bank crest. *Centropages* spp. can bridge the size-nutritional continuum between the smaller *Pseudocalanus* spp. and the larger copepodids of *C. finmarchicus*. Climate warming can increase the distribution and abundance of both *Centropages* warm water species on the northeast shelf, a development that could be beneficial for the pelagic juveniles during most of the year. The 2 contrasting years illustrate how a changing environment may affect the various cod stocks distributed along the continental shelf in dissimilar ways. Changes in the spatial and temporal variability of specific prey for cod early life stages, or structural connectivity, can affect their growth and survival, or functional connectivity. While only two years of data examined in this study have been used to speculate on the wider structural–functional connectivity of a warming climate, the specific predator–prey information presented is needed for a more complete and integrative understanding the dynamics of fish stocks, and ultimately the ecosystems functioning.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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References

Akimova, A., Hufnagl, M., Kreus, M. and Peck, M. A. 2016. Modeling the effects of temperature on the survival and growth of North Sea cod (*Gadus morhua*) through the first year of life. Fisheries Oceanography, 25: 193–209.

Aretxabaleta, A., Manning, J., Werner, F. E., Smith, K., Blanton, B. O., and Lynch, D. R. 2005. Data assimilative hindcast on the Southern Flank of Georges Bank during May 1999: frontal circulation and implications. Continental Shelf Research, 25: 849–874.

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, 426: 661–664.

Beaugrand, G., and Kirby, R. 2010. Climate, plankton and cod. Global Change Biology, 16: 1268–1280.

Brander, K. M. 2007. Global fish production and climate change. Proceedings of the National Academy of Sciences of the United States of America, 104: 19709–19714.

Broughton, E. A., and Lough, R. G. 2010. General trends and interannual variability in prey selection by larval cod and haddock from the southern flank of Georges Bank, May 1993-1999. NOAA Technical Memorandum, NMFS-NE-217. 32 pp.

Buckley, L. J., and Durbin, E. G. 2006. Annual and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. Deep-Sea Research II, 53: 2758–2770.

Buckley, L. J., Lough, R. G., and Mountain, D. 2010. Seasonal trends in mortality and growth of cod and haddock larvae result in an optimal window for survival. Marine Ecology Progress Series, 405: 57–69.

Bucklin, A., Guarnieri, M., McGillicuddy, D. J., and Hill, R. S. 2001. Spring evolution of *Pseudocalanus* spp. abundance on Georges Bank based on molecular discrimination of *P. moultoni* and *P. newmani*. Deep-Sea Res. II, 48: 589–608.

Cohen, R. E., and Lough, R. G. 1981. Length-weight relationships for several copepods dominant in the Georges Bank-Gulf of Maine area. Journal of the Northwest Atlantic Fishery Science, 2: 47–52.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences, 54: 726-738.

Coyle, K. O., Eisner, L. B., Mueter, F. J., Pinchuk, A. I., Janout, M. A., Cieciel, K. D., Farley, E. V. et al. 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fisheries Oceanography, 20: 139–156.

Daewel, U., Schrum, C., and Gupta, A. K. 2015. The predictive potential of early life stage individual-based models (IBMs): an example for Atlantic cod *Gadus morhua* in the North Sea. Marine Ecology Progress Series, 534: 199–219.

Durbin, E., and Casas, M. C. 2006. Abundance and spatial distribution of copepods on Georges Bank during the winter/spring period. Deep-Sea Research, II, 53: 2537–2569.

Durbin, E., and Kane, J. 2007. Seasonal and spatial dynamics of *Centropages typicus* and *C. hamatus* in the western North Atlantic. Progress in Oceanography, 72: 249–258.

Economou, A. N. 1991. Food and feeding of five gadoid larvae in the northern North Sea. Journal du Conseil Permanent Internationale pour L'Exploration de la Mer, 47: 339–351.

Edwards, K. P., Hare, J. A., Werner, F. E., and Seim, H. 2007. Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. Marine Ecology Progress Series, 352: 77–87.

Friedland, K. D., Kane, J., Hare, J. A., Lough, R. G., Fratantoni, P. S., Fogarty, M. J., and Nye, J. A. 2013. Thermal habitat constraints on zooplankton species associated with Atlantic cod (*Gadus morhua*) on the US Northeast Continental Shelf. Progress in Oceanography, 116: 1–13.

Friedland, K. D., Leaf, R. T., Kane, J., Tommasi, D., Asch, R. G., Rebuck, N., Ji, R. et al. 2015. Spring bloom dynamics and zooplankton biomass response on the US Northeast Continental Shelf. Continental Shelf Research, 102: 47–61.

Garrison, L. P., Michaels, W., Link, J. S., and Fogarty, M. J. 2000. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2455–2469.

Gerber, L. R., Mancha-Cisneros, M. D., O'Connor, M. I., and Selig, E. R. 2014. Climate change impacts on connectivity in the ocean: Implications for conservation. Ecosphere, 5: 33.

Guichard, F., Levin, S. A., Hastings, A., and Siegel, D. 2004. Toward a dynamic metacommunity approach to marine reserve theory. BioScience, 54: 1003–1011.

Hare, J. A. 2014. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. ICES Journal of Marine Science, 71: 2343–2356.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., et al. 2016. A vulnerability assessment of fish and invertebrates to climate change on the Northeast U.S. Continental Shelf. PLoS One, 11: e0146756.

Heath, M. R., and Lough, R. G. 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). Fisheries Oceanography, 16: 169–185.

Hinrichsen, H.-H., Kühn, Peck, M. A., and Voss, R. 2012. The impact of physical and biological factors on the drift and spatial distribution of larval sprat: a comparison of the Baltic and North Seas. Progress in Oceanography, 107: 47–60.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science, 41: 53–70.

Houde, E. D. 2009. Chapter 3. Recruitment variability. *In* Fish Reproductive Variability, pp. 91–171. Ed. by T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness. Wiley-Blackwell, Indianapolis, IN.

Huret, M., Runge, J. A., Chen, C., Cowles, G., Xu, Q., and Pringle, J. M. 2007. Dispersal modeling of fish early life stages: sensitivity with application to Atlantic cod in the western Gulf of Maine. Marine Ecology Progress Series, 347: 261–274.

Kane, J. 2007. Zooplankton abundance trends on Georges Bank, 1977-2004. ICES Journal of Marine Science, 64: 909–919.

Kane, J. 2014. Decadal distribution and abundance trends for the late stage copepodites of *Pseudocalanus* spp. (Copepoda: Calanoida) in the US Northeast Continental Shelf ecosystem. Journal of Northwest Atlantic Fisheries Science, 46: 1–13.

Kristiansen, T., Drinkwater, K. F., Lough, R. G., and Sundby, S. 2011. Recruitment variability in the North Atlantic and match-mismatch dynamics. PLoS One, 6: e17456.

Kristiansen, T., Stock, C., Drinkwater, K., and Curchitser, E. N. 2014. Mechanistic insights into effects of climate change on larval cod. Global Change Biology, 20: 1559–1584.

Link, J. S., and Garrison, L. P. 2002. Trophic ecology of Atlantic cod Gadus morhua on the northeast US Continental Shelf. Marine Ecology Progress Series, 227: 109–123.

Lough, R. G. 2010. Juvenile cod (*Gadus morhua*) and the importance of bottom sediment type to recruitment on Georges Bank. Fisheries Oceanography, 19: 159–181.

Lough, R. G., and Aretxabaleta, A. 2014. Transport and retention of vertically migrating adult mysid and decapod shrimp in the tidal front on Georges Bank. Marine Ecology Progress Series, 514: 119–135.

Lough, R. G., and Kristiansen, T. 2015. Potential growth of pelagic juvenile cod in relation to the 1978-2006 winter-spring zooplankton on the Northeast U.S. Continental Shelf. ICES Journal of Marine Science, 72: 2549–2568.

Lough, R. G., and Manning, J. P. 2001. Tidal-front entrainment and retention of fish larvae on the southern flank of Georges Bank. Deep-Sea Research II, 48: 631–644.

Lough, R. G., and O'Brien, L. 2012. Life-stage recruitment models for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. Fishery Bulletin, 110: 123–140.

Lough, R. G., and Potter, D. C. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin, U.S 91: 281–303.

Mountain, D. G., and Kane, J. 2010. Major changes in the Georges Bank ecosystem, 1980s to the 1990s. Marine Ecology Progress Series, 398: 81–91.

Nicolas, D., Rochette, S., Llope, M., and Licandro, P. 2014. Spatio-temporal variability of the North Sea cod recruitment in relation to temperature and zooplankton. PLoS One, 9: e88447.

Ottersen, G., Bogstad, B., Yaragina, N. A., Stige, L. C., Vikebø, F. B., and Dalpadado, P. 2014. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). ICES Journal of Marine Science, 71: 2064–2087.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A. *et al.* 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, 350: 809–812.

Petrik, C. M., Kristiansen, T., Lough, R. G., and Davis, C. 2009. Prey selection of larval haddock and cod on copepods with species-specific behavior: an individual model-based analysis. Marine Ecology Progress Series, 396: 123–143.

Petrik, C. M., Ji, R., and Davis, C. S. 2014. Interannual differences in larval haddock survival: hypothesis testing with a 3D biophysical model of Georges Bank. Fisheries Oceanography, 23: 521–553.

Pinkas, L. M., Oliphant, S., and Iverson, I. L. K. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. California Fish and Game, 152: 1–105.

Pitois, S. G., and Fox, C. J. 2008. Empirically modelling the potential effects of changes in temperature and prey availability on the growth of cod larvae in UK shelf seas. ICES Journal of Marine Science, 65: 1559–1572.

Pitois, S. G., and Armstrong, M. 2014. The growth of larval cod and haddock in the Irish Sea: a model with temperature, prey size and turbulence forcing. Fisheries Oceanography, 23: 417–435.

Planque, B., and Frédou, T. 1999. Temperature and recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 56: 2069–2077.

Potter, D. C., Lough, R. G., Perry, R. I., and Neilson, J. D. 1990. Comparison of the MOCNESS and IYGPT pelagic samplers for the capture of 0-group cod (*Gadus morhua*) on Georges Bank. Journal du Conseil International pour l' Exploration de la Mer, 46: 121–128.

Stige, L. C., Hunsicker, M. E., Bailey, K. M., Yaragina, N. A., and Hunt, G. L. 2013. Predicting fish recruitment from juvenile abundance and environmental indices. Marine Ecology Progress Series, 480: 245–261.

Turner, A. G., and Annamalai, H. 2012. Climate change and the South Asian summer monsoon. Nature Climate Change, 2: 587–595.

van Deurs, M., Jørgensen, C., and Fiksen, Ø. 2015. Effects of copepod size on fish growth–a model based on data for North Sea sandeel. Marine Ecology Progress Series, 520: 235–243.

Varpe, Ø., Daase, M., and Kristiansen, T. 2015. A fish-eye view on the new Arctic lightscape. ICES Journal of Marine Research, 72: 2532–2538.

Vikebø, F., Sundby, S., Ådlansvik, B., and Fiksen, Ø. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arctic-Norwegian cod. ICES Journal of Marine Science, 62: 1375–1386.

Voss, R., Peck, M. A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M. *et al.* 2012. Recruitment processes in Baltic sprat – a re-evaluation of GLOBEC German hypotheses. Progress in Oceanography, 107: 61–79.

Wiebe, P. H., Morton, A. W., Bradley, A. M., Backus, R. H., Craddock, J. E., Barber, V., Cowles, T. J. *et al.* 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology, 87: 313–323.

Wigley, R. L., and Burns, B. R. 1971. Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the United States in the NMFS Woods Hole collection. Fishery Bulletin, 69: 717–746.

Zemeckis, D. R., Martins, D., Kerr, L. A., and Carin, S. X. 2014. Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. ICES Journal of Marine Research, 71: 1490–1506.

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