



NOAA Technical Memorandum NMFS-NE-217

**General Trends and Interannual
Variability in Prey Selection by
Larval Cod and Haddock from the
Southern Flank of Georges Bank,
May 1993-1999**

**US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole, Massachusetts
May 2010**

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General Trends and Interannual Variability in Prey Selection by Larval Cod and Haddock from the Southern Flank of Georges Bank, May 1993-1999

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ABSTRACT

Stomach samples were examined from 1080 larval cod (*Gadus morhua*) and 2586 larval haddock (*Melanogrammus aeglefinus*) collected in May of 1993, 1994, 1995, 1997, and 1999 from mixed and stratified waters on the southern flank of Georges Bank. Larvae were grouped into 3 size classes: 3-5 mm, 6-8 mm, and 9-13 mm. Prey were grouped into 28 species and life stage based categories. Copepods comprised 98% of prey consumed. Individual years could be categorized into three groups: 1993-94, 1995 and 1999, and 1997. In 1993-1994, smaller larvae ingested *Pseudocalanus* spp. nauplii, adding gravid female *Pseudocalanus* spp. in larvae larger than 5 mm standard length (SL). In 1995 and 1999, larvae ingested similar prey numbers and had the same range of total stomach biomass as in 1993-94 but selected a wider range sizes and copepod species. In 1997, larvae consumed comparable numbers of *Pseudocalanus* spp. but mean prey size and total stomach biomass were lower than in other years. Chesson's α values for each larval size class showed positive selection for all life stages of *Pseudocalanus* spp. and varying life stages of *Oithona* spp. *Calanus finmarchicus* was rarely selected by any larvae. As larval length increased, stomach biomass increased and larger prey were selected. An analysis of niche overlap showed cod and haddock diets had high degrees of overlap. Individual years showed a high degree of overlap of the species of larval prey between the mixed and stratified sites. Combining larvae from all years showed significant differences in mean prey count, prey length, and stomach biomass between larvae taken from the mixed and stratified sites. Feeding at the mixed site did not vary with depth, but larval feeding was affected by depth at the stratified site. All larvae showed a diel feeding pattern with feeding increasing soon after dawn and decreasing after dusk.

INTRODUCTION

Larval fish feeding patterns are an important component of early life history studies, recruitment studies, and more recently, coupled physical-biological growth models and ecosystem based fishery management plans. Understanding factors that influence interannual variations in prey selection and general feeding patterns has the potential to contribute to defining essential fish habitat as well as increasing model and recruitment prediction accuracy. There is a general hypothesis that favorable prey conditions lead to rapid growth which reduces the larval period resulting in greater survival and recruitment (Lough et al. 2005). Prior larval gadid feeding studies agree that early larvae prey predominately on calanoid copepod nauplii progressing to copepodites and smaller copepod adults as they get larger (Heath and Lough 2007). However, prior studies have also shown significant variation in the copepod species selected and additional noncopepod items included in the diet. Mayer and Wahl (1977) noted larval feeding was affected by a complex mix of size and taxa preferences creating an apparent lack of consistent patterns in larval prey selectivity. On Georges Bank, larval gadid feeding patterns have been inferred from single year studies (Marak 1960; Sherman et al. 1981; Kane 1984; Lough et al. 1996) or a data set which combined years but did not differentiate between them (Auditore et al. 1994; Lough and Mountain 1996). While single year studies provide insight about factors influencing larval diet for that year, they provide incomplete information on factors that may consistently impact larval feeding patterns. The Northwest Atlantic Global Ocean Ecosystem Dynamics (GLOBEC) process studies offered a unique opportunity to collect a multiyear, geographically similar, depth stratified, larval gadid feeding and prey field database. Information was collected on the size, species, and life stage for all larval gadid prey. This database currently provides several individual based modeling studies with prey fields, feeding intensity curves, and field data used to compare modeled results with in situ feeding (Petric et al. 2009; Kristiansen et al. 2009; Lough et al. 2005,2006). This technical memorandum presents an overview of five years of prey field composition, oceanographic conditions, and larval gadid species based feeding.

MATERIALS AND METHODS

Plankton samples were collected in May from 1993-1999 along the southern flank of Georges Bank as part of the process studies of the Northwest Atlantic GLOBEC program (Wiebe et al. 2003). Each cruise first conducted an east to west grid of transects spaced 5nm apart along the southern flank. Standard Marine Resources Monitoring, Assessment, and Prediction (MARMAP) sampling (Jossi and Marak 1983) was conducted with a 61cm bongo equipped with 333 μ m and 505 μ m mesh nets. Ichthyoplankton from the 505 μ m net were sorted and identified at sea to establish areas within the grid containing high concentrations of gadid larvae. Two sampling sites were chosen each year that represented well-mixed and stratified water column conditions (Fig. 1). Ichthyoplankton were collected with a 1-m² Multiple Opening Closing Net Environmental Sensing System (MOCNESS) equipped with nine 333 μ m mesh nets opened at 10 m depth intervals. The prey field was concurrently sampled with a 1/4-m² MOCNESS equipped with nine 64 μ m mesh nets opened at 10m depth intervals. Both net systems had environmental sensing packages which recorded depth, temperature, and conductivity at 4 second intervals. The 1-m² MOCNESS additionally recorded fluorescence and down-welling light intensity in 1995 - 1999. Larval fish shrinkage is known to vary widely with water temperature and the time

between death and preservation (Theilacker 1980; Hay 1981; Lindner 1996). To minimize shrinkage, plankton samples were processed as quickly as possible and preserved in a 5% formaldehyde and seawater solution.

Ichthyoplankton were sorted from the 1-m² MOCNESS samples, identified to species, measured to the nearest 0.01mm, and transferred to 85% Ethanol. A gadid subsample was taken from each net to be used for gut content analysis (Table 1). Each subsample consisted of up to ten randomly selected cod and haddock larvae in each of 4 size categories: 3-5mm, 6-8mm, 9-13mm and 14+ mm. Each larva was weighed to the nearest 0.001g by using a Mettler AC 100 electronic balance. Morphometric measurements to the nearest 0.01mm were taken using a dissecting microscope with video camera and Optimas image analysis software. Wet weight, standard length (SL), body height, maxillary length, and skull width were recorded. All larval measurements were corrected for shrinkage by using Theilacker's (1980) algorithm. With the aid of a dissecting microscope, the entire digestive track was removed from each larva and opened with mounted surgical needles and forceps. Gadid larvae do not have a differentiated stomach until ~15mm SL, (Economou et al. 1991) so prey items were removed and analyzed from the entire digestive track. Each prey item was identified to the lowest taxonomic and life stage possible. Prey item length and width measurements were made to the nearest 0.02mm with an ocular micrometer. Adult copepod and copepodite measurements included only the cephalothorax. It was assumed there was no shrinkage of prey items from digestion or preservation. Average measurements for each prey type from all larvae of the same year, species, and size category were used to approximate prey measurements which could not be determined because of advanced digestion or fragmentation. Prey biomass was estimated by using the length to dry weight conversion equations from Cohen and Lough (1981) for prey under 1.5mm in length and literature values (Davis 1984) for larger prey.

A Folsom plankton splitter was used to take a zooplankton subsample of 500-1000 individuals from the ¼-m² MOCNESS samples. All individuals in the subsample were identified to species and life stage. Plankton counts were averaged from all depths at each site and were standardized to number per cubic meter. Lengths were assigned from literature values (Murphy and Cohen 1978; Davis 1984), and biomass was estimated with the same methods used on the prey items. Larval fish predators and zooplankton over 2.5mm in length were considered too large to be selected as prey items and were not included in the potential prey field.

Prey was grouped into 28 categories based on species and life stage. *Pseudocalanus* spp. and *Oithona* spp. eggs, which are carried in sacs by the female, were included in biomass calculations for the adult stage but were counted as a single prey item with the adult female. Because of their low occurrence as prey items in all years, *Centropage* spp., *Temora longicornis*, and *Metridia lucens* were combined into the Copepoda category. Individually, these species were too rare to be statistically relevant. Combining them into the Copepoda category allowed these data to be included in the Chesson's calculations and statistical analysis.

The Index of Relative Importance (IRI, Pinkas et al. 1971) was calculated for all fish containing prey. IRI was selected as it accounts for prey count and biomass as well as the occurrence of the prey item in the population.

$$IRI = \%O(\%N + \%W)$$

%O = percent occurrence of the prey item in all larvae of the same sampling category

%N = the proportion of the prey item in ingested prey count

%W = the proportion of the prey item in ingested prey biomass.

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

$$\%IRI = \frac{IRI_i}{\sum_{i=1}^n IRI_i}$$

n=the number of prey categories

Larval prey selectivity was estimated by using Chesson's selectivity index, α (Chesson 1983).

$$\alpha = \frac{(r_i / n_i)}{\sum_{i=1}^m (r_i / n_i)}$$

r_i = percent count of prey type i in larval diet

n_i = percent count (mean number m^3) of prey type i in prey field

m = total number of prey categories, $1/m$ is neutral selection

Chesson's α value is a commonly used selectivity index allowing easy comparisons with other larval feeding studies. Phytoplankton, Other, *Calanus finmarchicus* egg, and Sand prey categories were not utilized to classify selectivity because they were not quantified in the prey fields. Chesson (1983) states that when a food type is rare, it provides a poor opportunity for estimating preference, and thus, there can not be much confidence in the α value. For this reason, α values were not calculated when a prey category represented less than 0.5% of the total prey field.

A modification of Colwell and Futuyama's (1971) estimation of niche overlap (PS) was used to show predator and annual similarities in prey selection.

$$PS = 1 - 0.5 \sum_{i=1}^m (\%IRI_1 - \%IRI_2)$$

m = total number of prey categories

$\%IRI_1$ = value of the first species or site being compared

$\%IRI_2$ = value of the second species or site being compared

PS varies from 0 (indicating diets are entirely different) to 1 (indicating diets are identical). Interannual comparisons by site were virtual estimations of niche overlap. The larvae being compared were not competing in the same space or time for the food resource. Annual niche overlap values between cod and haddock larvae were actual comparisons with the larvae competing in the same space and time for the resource.

Prey count, mean prey length, and total stomach biomass of individual larvae were fitted with a first order regression to show relationships with larval SL. Breaking the annual data down by larval size, site, and depth or time of capture created data groupings too small to be statistically significant, so larvae from all years were combined to analyze the effects of depth and time of capture. Annual depth-stratified prey fields and larval stomach content data for the mixed and stratified sites are presented in tabular form in the appendix.

RESULTS

Water column thermocline depth and strength, water temperatures, and salinity values (Fig. 2) varied annually between sites. Bottom temperatures during the study period ranged from 5.5 to 9.0°C, surface temperatures varied from 6.5 to 11.0°C, and salinities ranged from 32.0 to

33.5psu. The stratified sites in 1994 and 1995 exhibited the widest temperature and salinity ranges. The stratified site had a gradual thermocline from the surface to 30m in 1993, 1994, and 1997. A stronger thermocline from the surface to 15m was present in 1995 and 1999. The mixed site had generally uniform water column temperatures, except in 1997 when a thermocline was present from the surface to 30m. The highest salinities were found in 1994 and in the bottom half of the water column in 1995. The surface waters of the mixed site in 1997 and the stratified sites in 1997 and 1999 had the lowest salinities.

The zooplankton prey field in all years (Fig. 3) was dominated by 3 species of copepods: *Calanus finmarchicus*, *Pseudocalanus* spp., and *Oithona* spp. The Copepoda category combined all other copepod species collected and included *Centropages typicus*, *Centropages hamatus*, *Paracalanus* spp., *Metridia lucens*, *Microsetella* spp., and *Temora Longicornis*. In 1993-1994 the main species in the Copepoda category were *Centropages* spp. and *Temora longicornis*. In 1995 the Copepoda category had about equal numbers of *Centropages* spp., *Temora longicornis*, and *Metridia lucens*. The 1997 and 1999 Copepoda category dominant species were *Temora longicornis* and *Metridia lucens*. Combining all available zooplankton prey species gave mean prey density of 6366 m⁻³ during the study period with a mean prey length of 0.50mm. Total available prey densities varied from 3413 m⁻³ at the 1994 mixed site to 9706 m⁻³ at the 1995 stratified site. The stratified site had slightly higher prey densities than the mixed site for all years. Prey density also varied positively with increasing water temperature. The mean length of the zooplankton increased with increasing site temperature. Mean lengths ranged from 0.36mm at the 1993 mixed site to 0.70mm at the 1999 stratified site. *Pseudocalanus* spp. was numerically dominant in 1993 and 1994. The higher mean prey densities from 1995-1999 were caused by an increase in *C. finmarchicus* and *Oithona* spp. while *Pseudocalanus* spp. numbers declined only slightly.

Larvae in the 3-5mm size class of both species fed predominantly on *Pseudocalanus* spp. nauplii (Fig. 4). In 1993 mixed site larvae of both species were also consuming adult *Pseudocalanus* spp. In 1994 only 3-5mm cod larvae were consuming adults. *Pseudocalanus* spp. adults in 1994 were larger, averaging 1.1mm in length compared to 0.8mm in length in 1993. The larval diets in 1995, 1997, and 1999 did not include many adult *Pseudocalanus* spp. but were more diversified. They included smaller *Oithona* spp. nauplii and *Calanus finmarchicus* eggs in addition to *Pseudocalanus* spp. nauplii. In 1999 3-5mm haddock also consumed phytoplankton of the genus *Peridinium* and *Ceratium*. No cod larvae in the 3-5mm size class were caught at the mixed site in 1999.

Larvae in the 6-8mm size class preyed on more diverse prey ranging from naupliar to adult copepod life stages (Fig. 5). At the mixed site in 1993 and 1994 larvae of both species fed almost exclusively on gravid female *Pseudocalanus* spp. Larvae at the stratified site also consumed gravid *Pseudocalanus* spp. but continued to prey on *Pseudocalanus* spp naupliar stages. Larvae in 1995 and 1999 showed no strong prey preference at either sampling site. They preyed on all life stages of *Oithona* spp., *Pseudocalanus* spp., and *C. finmarchicus* eggs. In 1997 larvae at both sites consumed only the naupliar and early copepodite stages of *Pseudocalanus* spp. The adult *Pseudocalanus* spp. and late stage copepodites present in the 6-8mm larval diet in other years of the study were available but not selected in 1997.

The diet of 9-13mm larvae consisted of larger copepodite and adult life stages (Fig. 6). In 1993 and 1994 larvae continued to consume gravid female *Pseudocalanus* spp. At the stratified site in 1994, larvae also preyed upon *Oithona* spp. adults. Larvae from 1995 and 1999 had a more varied diet consisting of all the copepodite stages of *Oithona* spp. and *Pseudocalanus* spp.

In 1995 at the mixed site, larger cod larvae also preyed on the early copepodite stages of *C. finmarchicus*. No larvae from the 9-13mm size category were caught in 1997.

Chesson's α values showed positive selection shifted from nauplii to copepodites and adult copepods with increasing larval size (Table 2). Recently-hatched 3-5 mm larvae preferentially preyed on the naupliar stages of *Pseudocalanus* spp. and *Oithona* spp. in all years. In 1995-1999 3-5mm larvae had α values indicating negative selection of the adult and copepodite stages of these two species. Positive selection of *Pseudocalanus* spp. for 6-8 mm larvae varied between years and sites. In 1993, 1994, and 1999 there was strong positive selection for adults with weaker positive selection for naupliar stages. In 1995 and 1997 *Pseudocalanus* spp. nauplii were still strongly preferred, with lower but still positive values for copepodites and adults. 6-8mm larvae from all years had positive selection for *Oithona* spp. adults. Chesson's α values for larvae from the 9-13mm size class indicated a shift to positive selection for larger prey. Larvae had positive selection for adults and late stage copepodites but mostly negative selection of earlier life stages of both *Pseudocalanus* spp. and *Oithona* spp. Because of low occurrences as prey, Chesson's α values could not be consistently calculated for *C. finmarchicus* and the Copepoda categories. The α values available for *Calanus finmarchicus* indicated negative selection by larvae of all size classes in all years except 1995. 1995 cod in the 9-13mm size class had positive α values for *C. finmarchicus* stage I - IV copepodites. Chesson's α values in the Copepoda category represent predation predominantly on *Centropages* spp. in 1993-1994, shifting to mostly *Temora longicornis* in 1995-1999.

Trends in individual feeding were similar for cod and haddock (Figs. 7-8). There was a positive correlation between increasing larval SL and higher prey count, stomach biomass, and mean prey length. These correlations were stronger for haddock in all years of the study. Total prey counts varied widely and had the weakest correlations (cod $\bar{x} r = 0.37$, haddock $\bar{x} r = 0.45$) and the shallowest slopes relative to larval size. Mean prey length consumed by individual larvae showed stronger positive correlations with increasing SL (cod $\bar{x} r = 0.49$, haddock $\bar{x} r = 0.57$). In 1993 and 1994, mean prey length had a bimodal distribution caused by larvae of the same size consuming both copepod nauplii and female *Pseudocalanus* spp., but not the intermediate sized copepodites. Mean prey size in 1995 and 1999 increased with larval length more gradually than in 1993-1994, and the relationship in 1997 had the lowest slope, indicating very little increase in prey size with increasing larval SL. All years showed a strong positive correlation between total biomass consumed and increasing larval SL (cod $\bar{x} r = 0.59$, haddock $\bar{x} r = 0.62$). Lower stomach biomasses in 1997 were caused by larvae consuming equivalent prey numbers but selecting smaller sized prey compared to other years of the study.

Interannual niche overlap values show that 1993 and 1994 had the most consistent high overlap values for both gadid species (Table 3). No other interannual patterns were readily apparent. Niche overlap values between cod and haddock larvae of the same year and size class were consistently high (Table 4), with a mean PS value of 0.72 and 89% of PS values over 0.5. There was no significant difference between the annual PS values for cod and haddock within each size class (Mann-Whitney Rank Sum Test). The lowest overlap was in the 3-5 mm categories for 1993 and 1994. These lower values reflect cod larvae feeding on *Pseudocalanus* spp. adults at a smaller size than haddock. PS values comparing the mixed and stratified site larvae showed considerable high overlap in all years (Table 5). Location in a well mixed or stratified environment did not seem to strongly affect the species and life stage of prey consumed by early gadid larvae.

A Mann Whitney Rank Sum Test run on all the larvae from this study showed prey count, total stomach biomass, and mean prey length consumed by individual larvae, varied significantly between larvae taken from the mixed and stratified sites (Table 6A). A series of Kruskal- Wallis ANOVA on Ranks tests was run to see if the differences seen between the sampling sites were influenced by depth. Larvae from the mixed site, which had consistent oceanographic conditions with depth, had little significant diet variance with depth (Table 6B). At the stratified site, which had varying water column oceanographic conditions, all but the 3-5mm larvae showed significant dietary variance with depth (Table 6C).

Since mixed site larvae did not show significant differences in diet with depth, only the stratified site prey data were analyzed by 10m depth intervals (Fig. 9). Mean prey counts for both cod and haddock larvae show an increase at 20-30m depth, the average depth of the thermocline during the study years. Mean prey length increased with depth for all larvae. Total stomach biomass had two areas with higher stomach biomasses: near the thermocline depth because of increased numbers of prey consumed and near the bottom because of the larger size of prey consumed.

A second series of Kruskal-Wallis ANOVA on Ranks tests that compared feeding of larvae grouped in one hour bins determined by time of capture showed prey counts, mean prey size, and total stomach biomass were all significantly different. Mean prey size, mean prey count, and mean total stomach biomass for all larvae captured within a one hour increment were calculated and fitted with a third order regression. There was no discernable time pattern to mean prey size ingested in hourly increments; however, both cod and haddock larvae showed a strong diel pattern for prey count and mean stomach biomass (Fig. 10). Correlation with the fitted curves was good, with r values ranging from 0.43 to 0.75 and a mean of 0.65. All larvae had the lowest prey counts and stomach biomass between 0400 and 0800 and highest counts and prey biomass around 2000 in the evening. Cod larvae showed less variation in prey counts and stomach biomass with time than did haddock.

DISCUSSION

The broad trends in larval feeding from this GLOBEC study matched earlier field studies. Feeding incidence was over 95% for all size classes but was lowest for the 3-5 mm size class. Early larvae with no food in their gut often had yolk sac remnants, indicating they may not yet have begun feeding. It is possible these early larvae were eating protozoa (de Figueiredo et al. 2005), which digest too quickly to be detected by this study's sampling methods. Protozoa were identified in pump sampling done concurrently with the MOCNESS sampling and so were available to the larvae as possible prey. Field studies covered in Heath and Lough's (2007) synthesis of literature describing larval cod diets showed that *Pseudocalanus* spp. and *Paracalanus* sp. were the dominant species of prey for early cod larvae found south of 55° 00'N while *Calanus* spp. dominated in the northern part of the range. Chesson's α values showed both cod and haddock larvae from the southern flank of Georges Bank had strong positive selection for all life stages of *Pseudocalanus* spp. Studies from the Scotian Shelf indicated larval gadids preyed on *Pseudocalanus* spp. but also preyed preferentially on *Paracalanus* sp. (McLaren and Avendaño 1995; McLaren et al. 1997). *Pseudocalanus* spp. and *Oithona* spp. were the most numerous zooplankton species on the southern flank of Georges Bank in May 1993-1999. *Paracalanus* sp. had low mean abundances in May of 1993-1999, ranging from 320 m⁻³ to less than 10 m⁻³, so were not readily available as prey to larvae on Georges Bank. Larvae on Georges

Bank showed positive selection for most stages of *Oithona* spp. rather than selecting *Paracalanus* sp. like Scotian Shelf larvae. The Georges Bank larvae in this study appear to have substituted the available prey item, *Oithona* spp., which is the same size range as *Paracalanus* spp. This changeover suggests that prey size and availability may be more important than prey species in determining positive selection.

The lack of variability in larval gadid prey species selection during this 5 year study is mirrored by prey fields that did not vary extensively. Cluster and nonmetric multidimensional scaling (MDS) analysis of the National Marine Fisheries Service MARMAP and Ecosystem Monitoring plankton survey data showed the community structure of the zooplankton during the five years of the study period was strongly grouped (Kane 2007). The same type of analysis, using the GLOBEC broadscale survey copepod data from May 1995-1999, indicated the southern flank stations in the tidal front region of the study were closely clustered with high abundances of *Pseudocalanus* spp. and *Oithona* spp. (Durbin and Casas 2006). The slight tendency from 1993 to 1999 of increasing prey species diversity in the larger two larval size classes parallels an increasing trend in the mean Shannon diversity index (Kane 2007).

The diets of cod and haddock larvae from individual years were comparable with high niche overlap values. Niche overlap values between cod and haddock for all years of this study were highest for the 3-5mm size class ($\bar{x} = 0.79$) and lowest for the 9-13mm sized larvae ($\bar{x} = 0.66$). Kane (1984) had similar dietary overlap values (0.77-0.88) between 3-7mm cod and haddock larvae compared in 1 mm size categories. Larval cod and haddock have comparable early life histories. Age at length through 45 days post hatch (Bolz and Lough 1988) and gape to larval SL (Rowlands et al. 2006) curves were not significantly different for the two species. This implies that cod and haddock larvae of the same size have similar ability to capture prey. Larval gadids consume their prey whole. This creates a defined prey size range whose lower end is prey too small to be detected and whose upper end is prey too large to pass through the larvae's mouth structure (Gill 2003). The smallest larvae fed almost exclusively on 0.2-0.3mm prey, which could explain *Pseudocalanus* spp. nauplii's consistent positive selection. All but stage VI *Pseudocalanus* spp. nauplii fall within the 0.2-0.3mm size range. *Oithona* spp. naupliar stages I-IV are smaller and thus harder for the larvae to detect, and *Calanus finmarchicus* stage III-VI nauplii are larger than the larvae can easily ingest. Early larvae also consumed copepodites and copepod adults whose length suggests they would be too large to fit in the larvae's mouth structure. The larger copepod's cylindrical shape and 0.2-0.4mm cephalothorax widths require the same mouth gape as 0.2-0.4mm nauplii if they are sighted and ingested from an end rather than the side. Petric et al. (2009) noted differences in copepod escape behavior affected prey selection more than encounter rates. *Oithona* spp. and *Pseudocalanus* spp. have the slowest swimming speed of the available copepod species in the prey field, making them easier for the larvae to capture. *Centropages* spp., which was consistently not selected as prey, is an omnivorous copepod with more aggressive movements and higher swimming speeds (Davis 1984). Prey species selection appears to be a combination of prey size and prey behavior rather than a true preference for a specific copepod species.

There are some developmental differences between cod and haddock larvae which did affect feeding. Haddock larvae developed fin rays faster, had higher fin ray counts, larger fins, and a greater body depth than did cod larvae (Auditore et al. 1994). Kane (1984) noted that first feeding cod were more aggressive predators which fed on larger prey soon after yolk sac absorption, while haddock were more passive foragers relying on less mobile prey. The 3-5mm larvae in this study showed some similar behavior, but this was not consistent throughout the

study. Passive items such as *Calanus finmarchicus* eggs and phytoplankton were found in haddock diets in 1995-1999 but were absent in cod diets. In 1994, cod larvae shifted from feeding on copepod nauplii to adult copepod stages at a smaller size than haddock.

Reiss et al. (2005) showed significant positive relationships between increasing larval SL and the number and biomass of the prey. In this GLOBEC Georges Bank study there was a strong positive relationship ($\bar{x} r = 0.61$) between increasing larval SL and stomach biomass but a much weaker positive correlation ($\bar{x} r = 0.33$) between SL and the number of prey in the stomach. The maximum number of prey consumed by individual larvae within a size class increased very little with larval size. This implies that for 3-13mm gadid larvae there was a maximum number of attack, capture, and consume cycles each larva could conduct in a day, regardless of prey concentrations or prey size. Reiss et al. (2005) examined cod larvae up to 25mm in length. The inclusion of these larger, more developed predators would cause the relationship between larval SL and number of prey consumed to have a steeper slope and stronger positive relationships than those of the 3 -13mm larvae of this study.

The mixed and stratified sites oceanographic and prey field differences between did not seem to be reflected in the high annual PS values ($\bar{x} = 0.68$) comparing the two sites. From 1993-1999 no major annual differences in species selection were noted between the predation patterns of larvae taken from the mixed or stratified sites on Georges Bank. Larval cod from the well mixed crest water and stratified conditions on the Scotian Shelf also showed no differences in prey selection (Lochmann et al. 1997). Combining larvae from all years of the study allowed a statistical analysis between the two sites of prey count, prey biomass, and stomach biomass with depth. These diet variables did not vary significantly with depth at the mixed site where water column conditions were uniform. At the stratified site, where oceanographic conditions changed with depth, all three values showed significant variability with depth. Larvae from 20 - 30 m depth, which was the average depth of the thermocline on Georges Bank during the study, had higher stomach prey counts. Plankton prey are known to accumulate along fronts (Lough and Manning 2001; Lough et al. 2006) such as the thermocline present at the stratified site in all years of this study. In general, maximum feeding (prey/larva) occurs at intermediate levels of turbulence where prey density is greater than 10-20 prey ℓ^{-1} (Lough and Mountain 1996). Mean water column prey densities for all years of the study were below this threshold, varying from 9.7 prey ℓ^{-1} in 1995 to 3.4 prey ℓ^{-1} in 1994. However, binning the prey field in 10m intervals gives prey densities near the thermocline of 7.1 prey ℓ^{-1} in 1993, 6.9 prey ℓ^{-1} in 1994, 19.9 prey ℓ^{-1} in 1995, 22.8 prey ℓ^{-1} in 1997, and 18.6 prey ℓ^{-1} in 1999. These increased prey densities coincide with the increased ingestion rates of larvae sampled near the thermocline. Mayer and Wahl (1997) predicted larvae may be more selective at higher prey densities. Larvae have the possibility of maximizing feeding gains by selecting larger or more nutritious prey (Gill 2003). This theory was not supported by the field data from this GLOBEC study where the mean biomass of prey items eaten by larvae sampled near the thermocline was not different from the mean biomass of prey items consumed by larvae at other depths. It is possible the higher prey densities caused by frontal aggregation at the study site were not high enough to cause the selective feeding noted by Mayer and Wahl's 1997 mesocosm study where stocked prey densities ranged from a low of 5 prey ℓ^{-1} to a high of 300 prey ℓ^{-1} .

Gadid larvae are visual feeders and are relatively inactive at night (Ellertsen et al. 1984). During this study, dawn was between 0430 and 0530, and dusk was from 1900-2000. Assuming the four hour gut evacuation rate used by Lough and Mountain (1996), the larvae in this study had falling ingestion rates starting just after sunset and increasing ingestion rates beginning about

an hour after dawn. Prey item biomass also varied hourly but with no pattern that could be statistically related to time of day.

The interannual variations seen in larval diets in this study do not seem to be correlated to RNA/DNA growth rates from Georges Bank gadids taken during the same time frame. Buckley and Durbin (2006) found a good correlation between early larval cod and haddock growth and prey biomass estimated for the GLOBEC years 1995-99. Larval growth, based on RNA/DNA ratio analysis, was relatively poor in spring of 1995 when concentrations of their principle prey, *Pseudocalanus* spp., were lowest and greater in 1997 and 1999 when *Pseudocalanus* spp. biomass was higher. Several individual based models (IBM) use the total biomass ingested calculated using this study's database as the feeding variable used to calculate growth (Kristiansen et al. 2009; Lough et al. 2005, 2006). Looking at the slope of the regressions correlating total stomach biomass to larval SL shows 1995 and 1999 have the largest stomach biomass increases with larval size, followed by 1993 and 1994 with 1997 having the smallest biomass increase. This pattern suggests the highest growth rates from this study should be 1995 and 1999 with the lowest in 1997. No larvae from the largest size class were caught in 1997, so it is possible the slope of the regressions could be falsely depressed. Excluding the 9-13 mm size class from the other 4 years of the study decreased the regression slope values, but 1997 still remained the lowest.

Interannual differences were apparent in this study, but general trends were similar to previous field-based feeding studies. This study confirmed that feeding observations from shorter time scale studies were not one-time patterns but were generally consistent over the longer, 7 year time frame of this study. While oceanographic conditions, larval size, larval capture time, depth, and capture site all contributed to observed feeding patterns, prey size, movement, and availability seem to have the strongest influence on prey selection. Continued use of this database to incorporate field-based depth-stratified and time-based data sets for modeling will help further the understanding of how each of these variables interact with oceanographic conditions to create the feeding patterns, growth curves, and mortality rates seen in this and other field studies.

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**Table 1. Number of larval stomachs processed in each size category. COD = *Gadus morhua*
HADDOCK = *Melanogrammus aeglefinus***

CRUISE	YEAR	SITE	COD			HADDOCK			ZOOPLANKTON	
			3-5	6-8	9-13	3-5	6-8	9-13	mean ct	mean size
AL9306	1993	Mixed	8	189	57	98	99	31	6672	0.36
		Stratified	32	59	64	148	277	50	4530	0.37
AL9403	1994	Mixed	19	28	9	97	99	31	3414	0.43
		Stratified	30	41	7	148	276	50	4847	0.41
SJ9507	1995	Mixed	8	22	17	16	32	9	7138	0.44
		Stratified	31	72	22	11	111	50	9706	0.40
OC9706	1997	Mixed	13	29	0	65	48	1	4815	0.62
		Stratified	9	16	0	113	38	0	8942	0.64
EL9905	1999	Mixed	2	90	36	57	128	51	6415	0.53
		Stratified	5	86	79	82	213	157	7189	0.70
TOTAL			157	632	291	835	1321	430		

Table 2. Yearly Chesson's α values for each prey category for mixed site cod (cm), stratified site cod (cs), mixed site haddock (hm) and stratified site haddock (hs). 4.8 is neutral selection. Gray shading indicates positive selection. cod = *Gadus morhua* haddock = *Melanogrammus aeglefinus*.

3-5mm	1993				1994				1995				1997				1999			
	cm	cs	hm	hs	cm	cs	hm	hs												
Calanus n1-3												5.1								
Calanus n4-6																				
Calanus c1-2																				1.6
Calanus c3-4																				
Calanus c5																				
Calanus adult																				
Pseudo n1-3	4.4	40.0	7.1	20.2	26.4	14.6	65.2	40.8	36.3	35.2	21.2	33.5	49.8	42.3	51.8	30.8		68.9	6.1	31.2
Pseudo n4-6	1.0		2.5	44.3	13.5	12.8	24.4	25.5	48.8	32.5	62.1	34.7	38.3	29.6	29.7	16.4		14.9	7.8	18.0
Pseudo c1-3			1.9			5.2	1.3	0.3	5.4				11.8						2.2	6.2
Pseudo c4-5	1.1	9.2						0.5				5.1							0.3	0.8
Pseudo adult	14.2	14.1	58.5		38.3	21.7		4.1		5.9		3.7								1.1
Oithona n1-3		30.5		7.9				1.3			3.4	3.2		19.9	4.1	7.8		5.5	0.3	0.5
Oithona n4-6				24.0	21.8			2.4	6.8	7.5	4.8	8.4		8.3	9.5	3.1		10.7	3.5	5.0
Oithona c1-3				3.7				1.0		1.8	1.6	3.3							0.4	1.3
Oithona c4-5								0.3											1.9	0.5
Oithona adult						42.7		1.3	2.6	3.1	1.4	2.3			4.8				2.5	1.5
Copepoda n1-3		6.2	3.9				3.5	6.9		1.2	1.9	0.8							0.3	9.7
Copepoda n4-6						3.0	5.6	15.6			3.5					2.0			0.6	22.7
Copepoda c1-3																				
Copepoda c4-5																				
Copepoda adult																				

Table 2, continued. Yearly Chesson's α values for each prey category for mixed site cod (cm), stratified site cod (cs), mixed site haddock (hm) and stratified site haddock (hs). 4.8 is neutral selection. Gray shading indicates positive selection. cod = *Gadus morhua* haddock = *Melanogrammus aeglefinus*.

6-8mm	1993				1994				1995				1997				1999			
	cm	cs	hm	hs	cm	cs	hm	hs												
Calanus n1-3			1.1									1.1								
Calanus n4-6												3.5								4.3
Calanus c1-2												3.3								0.9
Calanus c3-4	1.7		2.7														0.3			
Calanus c5																				
Calanus adult																				
Pseudo n1-3	0.7	2.1	0.9	22.7	7.6	2.4	6.1	8.6	13.9	24.0	21.4	14.2	35.9	16.0	32.4	19.6	0.5	5.0	1.8	9.0
Pseudo n4-6	0.2	2.6	0.3	7.4	5.9	4.8	1.8	6.1	37.4	36.9	57.5	30.5	33.3	14.5	21.1	18.2	1.3	1.6	2.1	6.8
Pseudo c1-3	0.5	3.7	0.9	7.2		0.5	0.7	0.3	13.8	11.5	0.8	10.4	7.9	2.3	0.2	0.7	4.5	24.2	5.3	13.0
Pseudo c4-5	1.5	10.7	1.6	4.5			1.3	1.8		6.0	0.8	7.1	1.5	0.2		0.1	3.1	4.8	1.9	5.6
Pseudo adult	49.6	58.9	51.7	37.1	80.2	27.1	83.2	24.7	3.7	4.7	6.8	12.1	1.5		3.6		11.3	6.8	5.3	11.1
Oithona n1-3		2.2		12.2				0.6	1.3	1.1		1.0	1.6	3.0	0.9	4.2		0.2	0.1	0.2
Oithona n4-6	0.2	6.7		6.5			2.0	1.8	3.6	2.5	2.3	2.2	6.8	3.0		3.8	0.5	2.9	0.8	3.4
Oithona c1-3		1.9	0.6			0.6		0.1	1.9	2.3	1.8	2.2	4.6	0.5	1.4	0.6		1.5	0.4	1.1
Oithona c4-5		1.4				0.5		0.5	1.8	3.7	1.2	3.8			1.1	0.1	0.7	1.6	1.3	1.2
Oithona adult		9.9				29.9		42.4	8.9	7.2	5.8	7.1	6.9		23.2		7.9	10.8	8.6	6.5
Copepoda n1-3			0.1	1.4			0.7	2.0	11.5	0.2	0.8	0.2				4.7	0.0	0.7	0.1	6.1
Copepoda n4-6				1.0	6.3	1.1	4.2	3.5	2.1		1.0	0.8				2.2	0.0	3.8	0.2	10.4
Copepoda c1-3												0.4					0.2	1.4	0.3	18.2
Copepoda c4-5						10.5		4.7									0.3	0.4		2.2
Copepoda adult						22.8		3.1												

Table 2, continued. Yearly Chesson's α values for each prey category for mixed site cod (cm), stratified site cod (cs), mixed site haddock (hm) and stratified site haddock (hs). 4.8 is neutral selection. Gray shading indicates positive selection. cod = *Gadus morhua* haddock = *Melanogrammus aeglefinus*.

9-13mm	1993				1994				1995				1997				1999			
	cm	cs	hm	hs	cm	cs	hm	hs	cm	cs	hm	hs	cm	cs	hm	hs	cm	cs	hm	hs
9-13mm																				
Calanus n1-3												0.2								
Calanus n4-6																				
Calanus c1-2			3.1							7.9		4.5					0.5			0.8
Calanus c3-4		3.3	2.0						10.3								0.2	0.2		0.0
Calanus c5																				0.1
Calanus adult																				
Pseudo n1-3		1.4		0.6		0.5		0.7	2.0	0.9	5.5	1.7					0.1	0.2	0.4	1.9
Pseudo n4-6	0.1	1.4		3.2		1.7	0.3	0.4	11.1	8.7	11.8	8.8					0.1	0.5	0.4	1.0
Pseudo c1-3	0.5	4.8	0.5	4.5				0.5	9.3	28.1		17.2					1.8	16.6	4.8	14.6
Pseudo c4-5	3.2	14.9	0.6	2.8	3.4	0.6		0.2	8.8	32.5	15.6	17.5					1.4	6.1	2.4	7.1
Pseudo adult	94.6	55.0	93.3	72.2	96.6	11.5	96.7	26.0	26.9	14.2	25.3	27.9					7.3	9.8	7.5	9.4
Oithona n1-3																				0.0
Oithona n4-6												0.4	0.4					0.1	0.1	0.4
Oithona c1-3	0.3	0.4		0.9			3.0	0.5		1.1	2.7	2.8						0.9	0.4	0.7
Oithona c4-5		1.1						0.5	3.2	3.0	16.1	4.6						2.5	1.7	2.2
Oithona adult		17.8		15.4		35.5		36.6	19.7	3.5	22.6	9.4					3.0	13.6	15.1	10.2
Copepoda n1-3				0.4		1.2						0.2						0.2	0.0	1.3
Copepoda n4-6						3.6						0.2						0.7	0.1	3.9
Copepoda c1-3												3.3						0.7	0.6	17.9
Copepoda c4-5	1.3		0.6									1.4						0.2	0.1	2.6
Copepoda adult																				0.0

Table 3. Interannual niche overlap values (PS) for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) at the mixed and stratified site. Gary shading indicates niche overlap values greater than 0.50.

by prey species											
3-5m cod	93	94	95	97	99	3-5m had	93	94	95	97	99
93		0.62	0.78	0.46		93		0.54	0.51	0.20	0.37
94			0.56	0.55		94			0.67	0.40	0.59
95				0.56		95				0.32	0.60
97						97					0.62
99						99					
3-5s cod	93	94	95	97	99	3-5s had	93	94	95	97	99
93		0.35	0.61	0.27	0.21	93		0.47	0.31	0.14	0.39
94			0.38	0.66	0.52	94			0.47	0.65	0.90
95				0.32	0.33	95				0.30	0.53
97					0.83	97					0.65
99						99					
6-8m cod	93	94	95	97	99	6-8m had	93	94	95	97	99
93		0.89	0.11	0.08	0.74	93		0.94	0.26	0.07	0.47
94			0.14	0.15	0.69	94			0.31	0.09	0.48
95				0.20	0.20	95				0.49	0.55
97					0.12	97					0.28
99						99					
6-8s cod	93	94	95	97	99	6-8s had	93	94	95	97	99
93		0.60	0.41	0.14	0.23	93		0.57	0.30	0.27	0.46
94			0.30	0.17	0.30	94			0.39	0.27	0.62
95				0.30	0.43	95				0.15	0.43
97					0.11	97					0.27
99						99					
9-13m cod	93	94	95	97	99	9-13m had	93	94	95	97	99
93		0.94	0.31		0.90	93		0.98	0.42		0.59
94			0.26		0.85	94			0.43		0.60
95					0.40	95					0.69
97						97					
99						99					
9-13s cod	93	94	95	97	99	9-13s had	93	94	95	97	99
93		0.60	0.33		0.42	93		0.84	0.34		0.31
94			0.19		0.53	94			0.47		0.43
95					0.51	95					0.71
97						97					
99						99					

Table 4. Annual niche overlap values (PS) for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae from each size class. Values account for both prey species and life stage.

Cod vs Haddock						
	1993	1994	1995	1997	1999	mean
3-5mm mixed	0.57	0.41	0.61	0.79		0.60
3-5mm stratified	0.47	0.69	0.66	0.97	0.59	0.68
6-8mm mixed	0.96	0.93	0.48	0.80	0.61	0.75
6-8mm stratified	0.56	0.73	0.75	0.90	0.64	0.72
9-13mm mixed	0.93	0.98	0.57		0.71	0.80
9-13mm stratified	0.83	0.72	0.62		0.90	0.77
mean	0.72	0.74	0.61	0.86	0.69	

Table 5. Yearly niche overlap values (PS) between larvae from each size category from the mixed and the stratified sites. cod = *Gadus morhua* had = *Melanogrammus aeglefinus*.

Mixed vs Stratified site						
	1993	1994	1995	1997	1999	mean
3-5mm cod	0.66	0.88	0.65	0.77		0.74
3-5mm had	0.43	0.76	0.57	0.97	0.79	0.70
6-8mm cod	0.61	0.82	0.67	0.86	0.40	0.67
6-8mm had	0.33	0.65	0.42	0.88	0.79	0.61
9-13mm cod	0.86	0.58	0.59		0.41	0.61
9-13mm had	0.82	0.81	0.68		0.65	0.74
mean	0.62	0.75	0.60	0.87	0.61	

0.69 mean
0.11 std

Table 6. The probability that the differences in the median values being compared are due to random sampling not larval capture site or 10 m depth binning. Probability <0.025 is significant and shaded gray. COD = *Gadus morhua* HAD = *Melanogrammus aeglefinus*.

Mann-Whitney Rank Sum Test: probability <0.025 is significant
Mixed vs Stratified Site

	prey count	stomach biomass	mean prey biomass
A	3-5mm COD	0.581	0.014
	3-5mm HAD	0.005	0.013
	6-8mm COD	<0.001	0.412
	6-8mm HAD	<0.001	<0.001
	9-13mm COD	<0.001	0.095
	9-13mm HAD	<0.001	0.006

Kruskal-Wallis Anova on ranks: probability <0.025 is significant
Mixed vs Depth

	prey count	stomach biomass	mean prey biomass
B	3-5mm COD	0.358	0.924
	3-5mm HAD	0.557	0.371
	6-8mm COD	0.128	0.158
	6-8mm HAD	0.669	0.006
	9-13mm COD	0.950	0.886
	9-13mm HAD	0.055	0.114

Kruskal-Wallis Anova on ranks: probability <0.025 is significant
Stratified vs Depth

	prey count	stomach biomass	mean prey biomass
C	3-5mm COD	0.152	0.880
	3-5mm HAD	0.024	0.011
	6-8mm COD	<0.001	0.006
	6-8mm HAD	<0.001	<0.001
	9-13mm COD	<0.001	<0.001
	9-13mm HAD	<0.001	<0.001

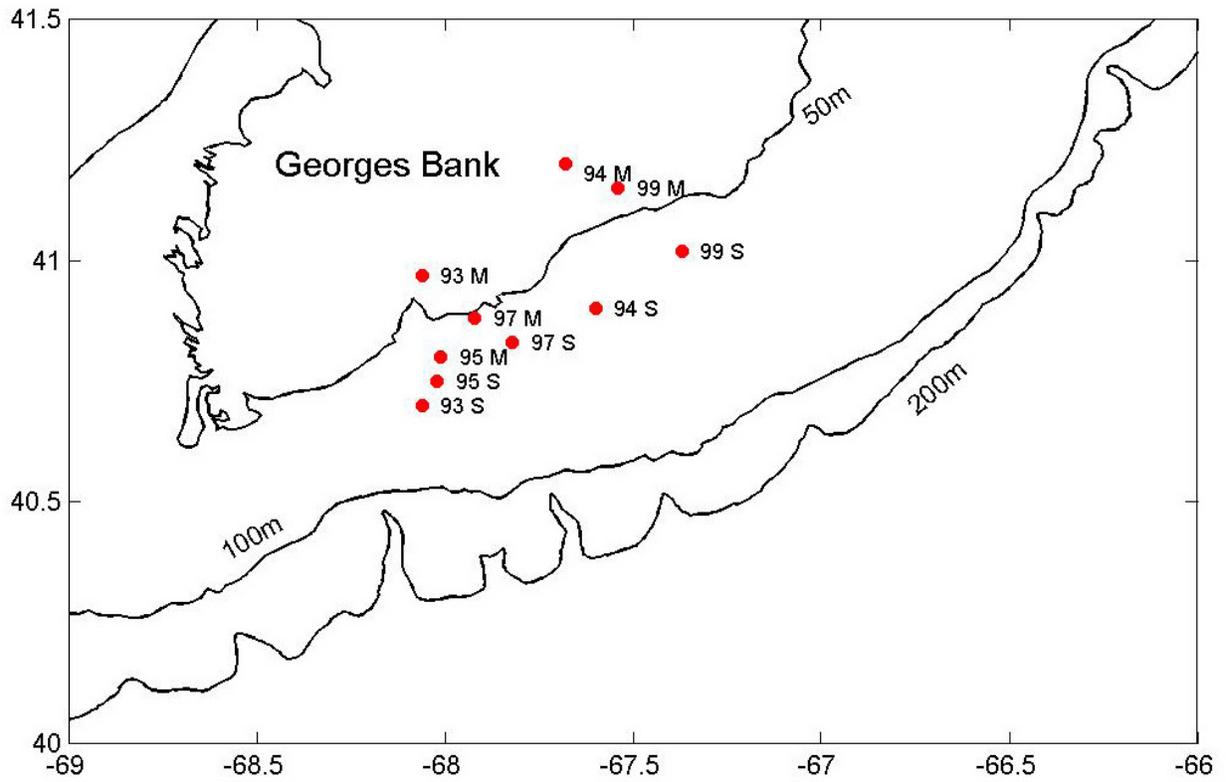


Figure 1. Map of the southern flank of Georges Bank showing the locations of the mixed (M) and stratified (S) sites in May for all years of the study.

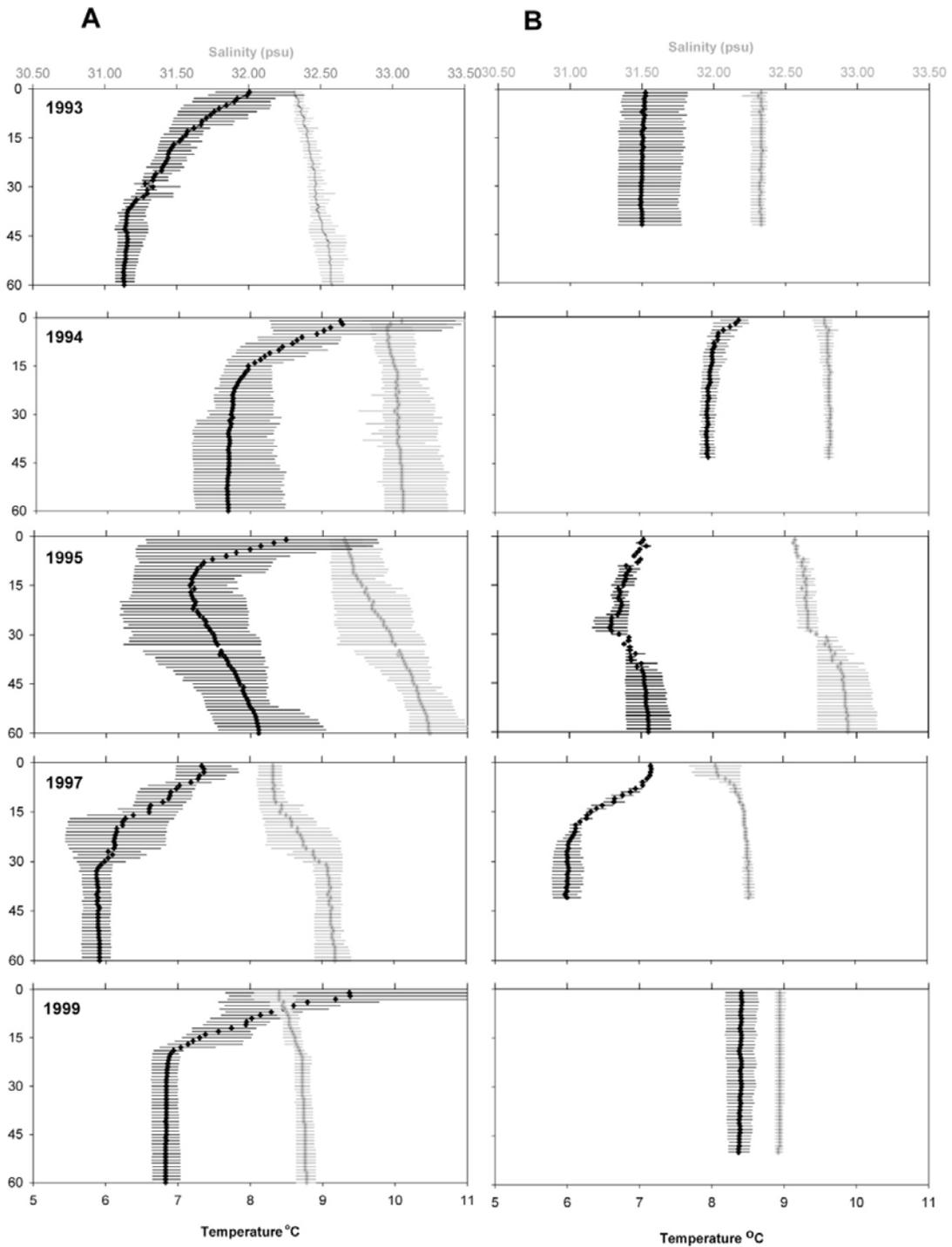


Figure 2. Mean water column conditions at each site during the study. Values are based on oceanographic data from the 1/4m MOCNESS (multiple opening and closing net environmental sensing system) binned in 1m depth intervals. Horizontal bars represent the range of temperature in degrees Celsius (black) and salinity in practical salinity units (gray) present during the sampling period. Mean temperature is shown in bold black and mean salinity is shown in dark gray.

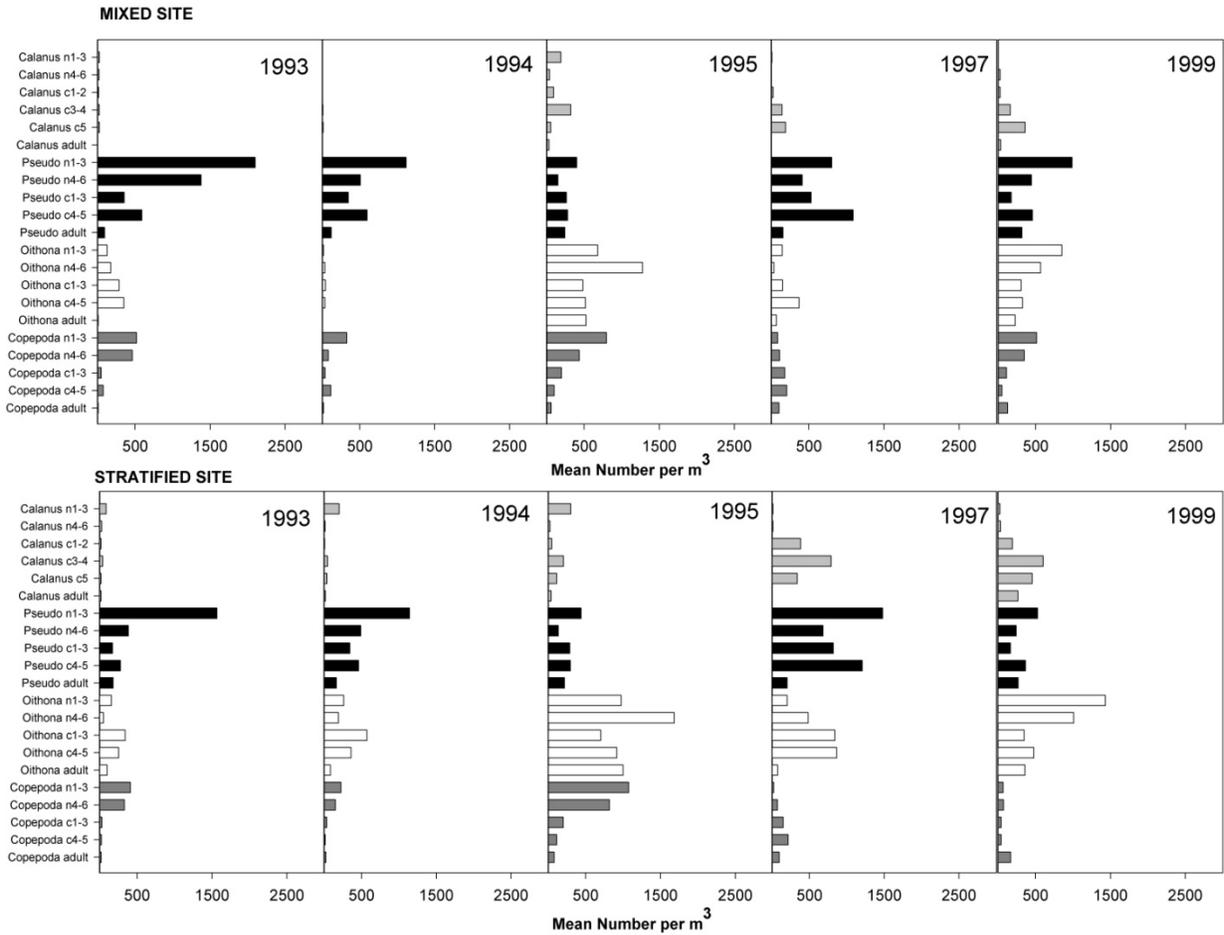


Figure 3. Yearly mean zooplankton prey field concentrations (number per m^3) for the mixed and stratified sites based on the 1/4m MOCNESS (multiple opening and closing net environmental sensing system) samples. The prey fields depicted include only zooplankton in the size range that could be captured and ingested by 5-13mm SL gadid larvae.

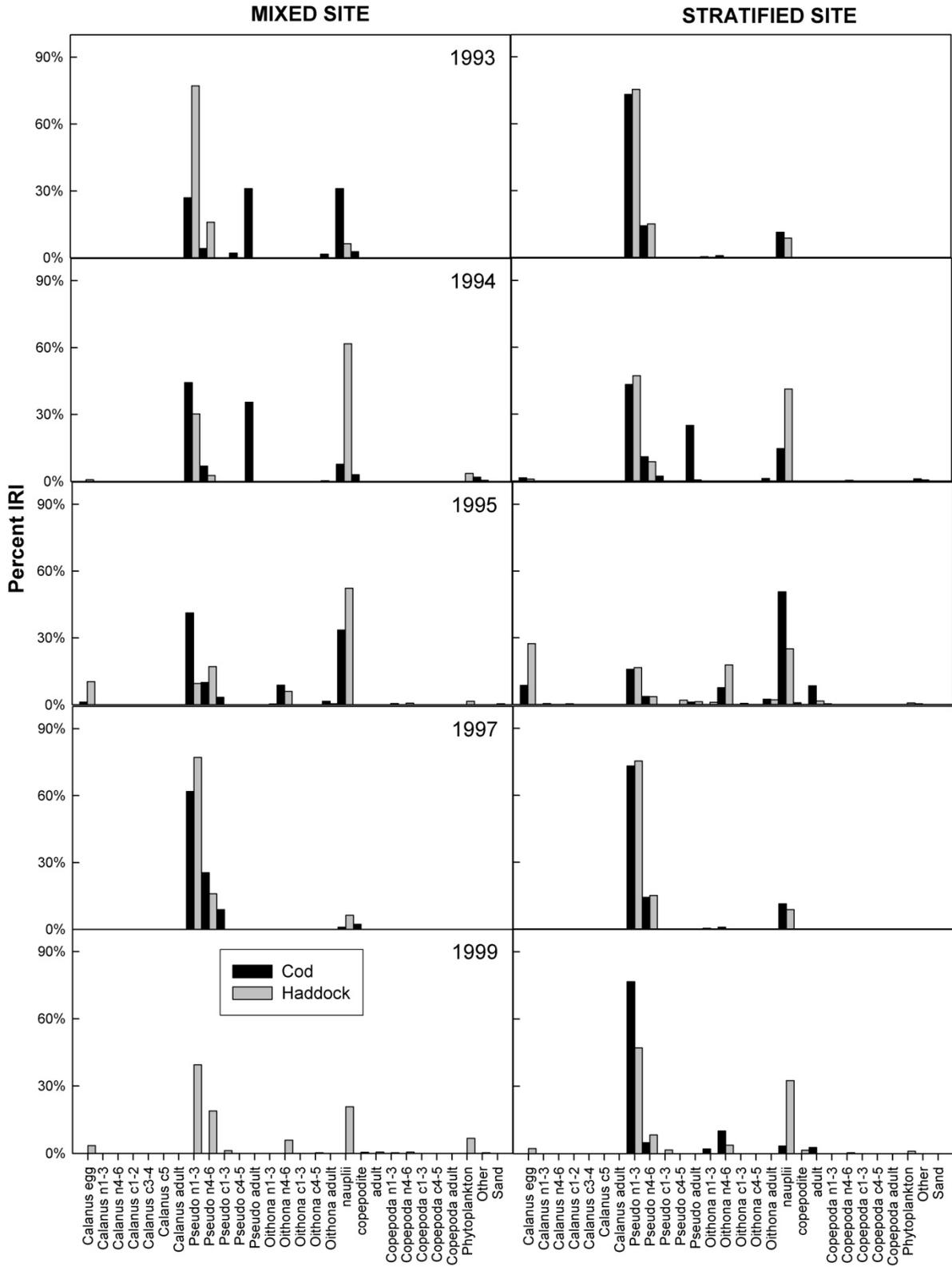


Figure 4. Yearly percent index of relative importance (%IRI) for 3-5mm cod, *Gadus morhua*, (black) and haddock, *Melanogrammus aeglefinus*, (gray) for 28 prey categories.

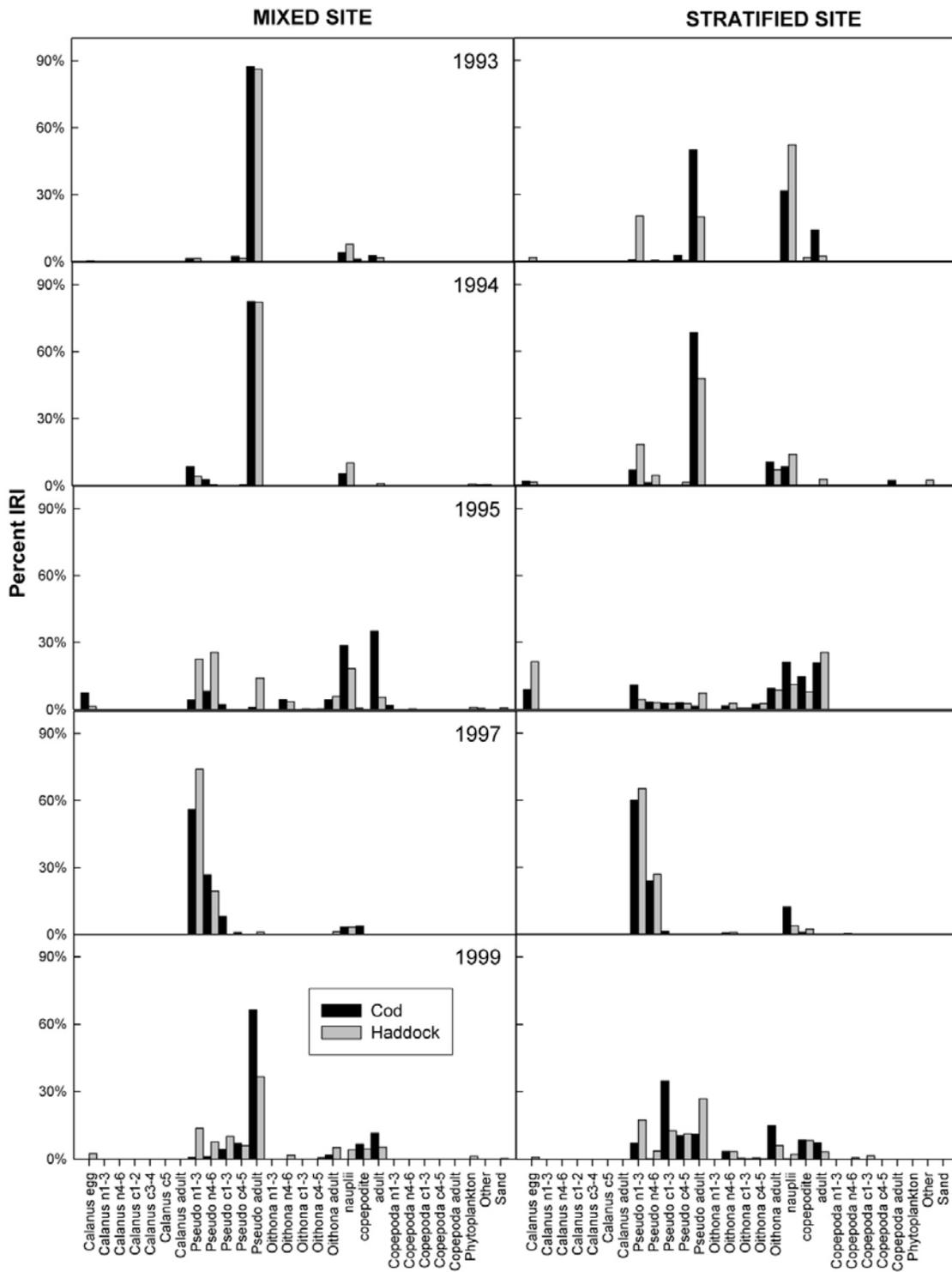


Figure 5. Yearly percent index of relative importance (%IRI) for 6-8mm cod, *Gadus morhua*, (black) and haddock, *Melanogrammus aeglefinus*, (gray) for 28 prey categories.

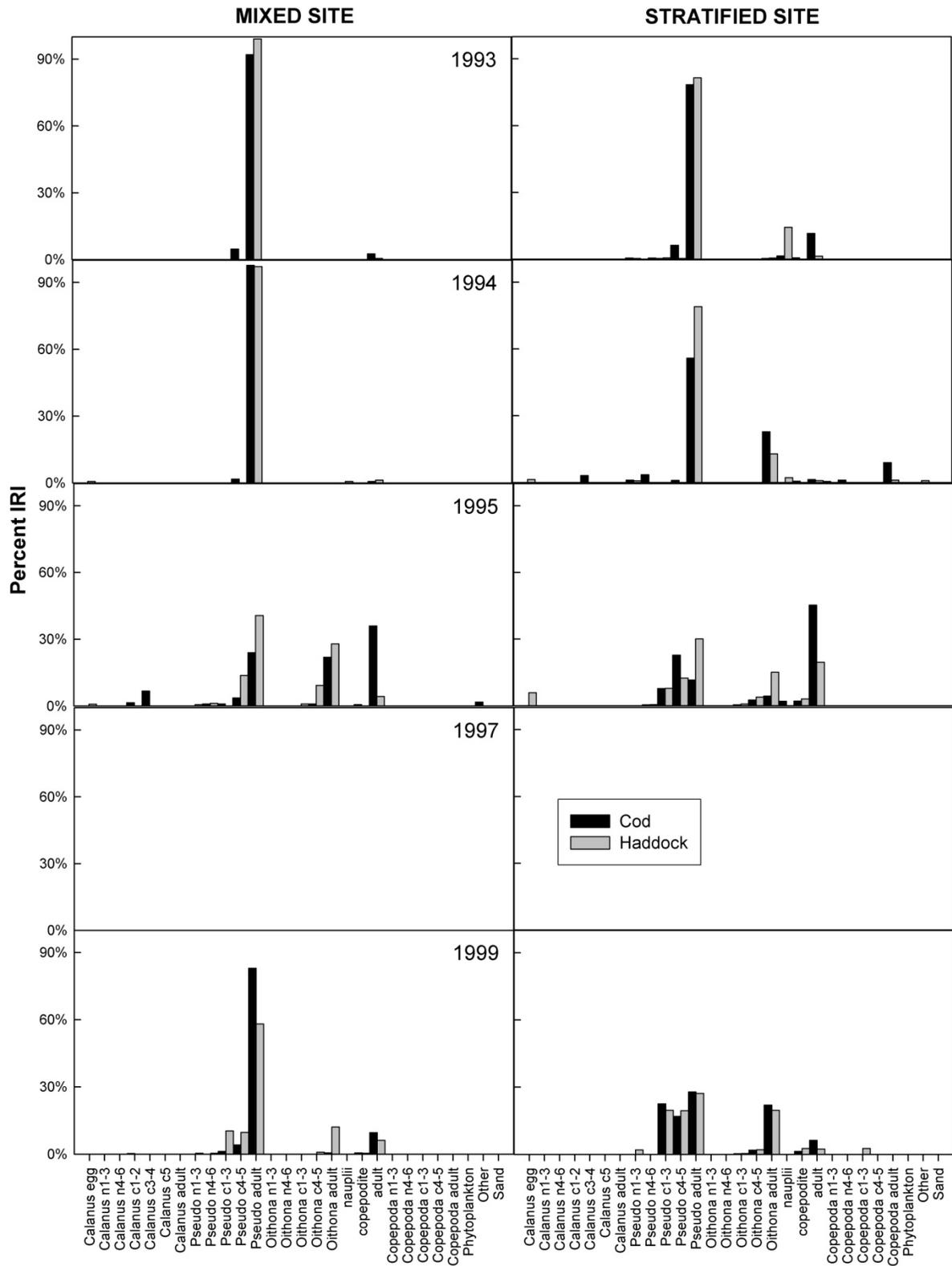


Figure 6. Yearly percent index of relative importance (%IRI) for 9-13mm cod, *Gadus morhua*, (black) and haddock, *Melanogrammus aeglefinus*, (gray) for 28 prey categories.

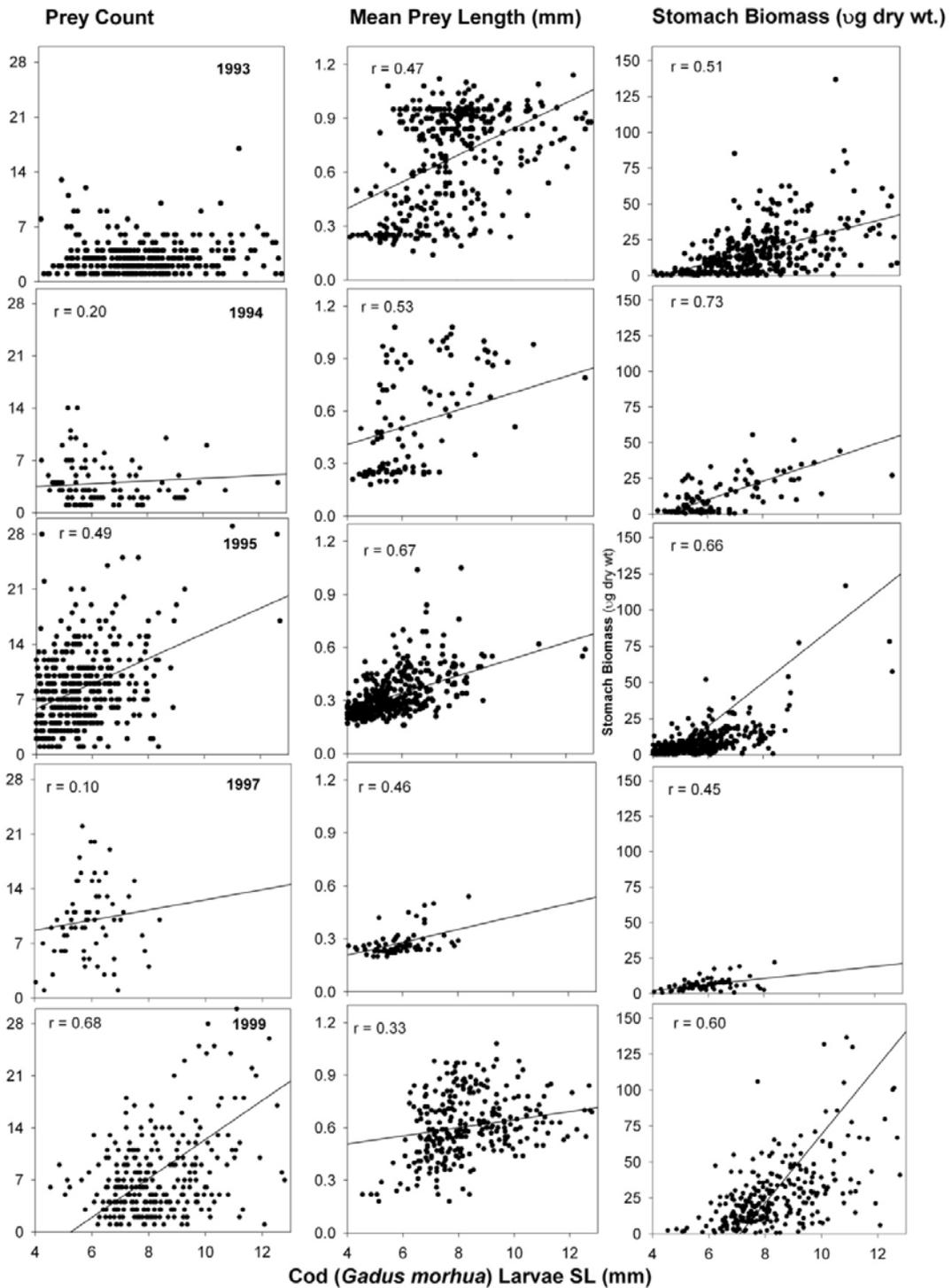


Figure 7. Yearly prey counts, mean prey lengths and total stomach biomass for cod (*Gadus morhua*) larvae. Each point represents the value for an individual larva. Plots are fitted with a simple regression showing the correlation (r) between increasing larval standard length (SL) and the three sets of data. 1993 prey counts had no meaningful correlation.

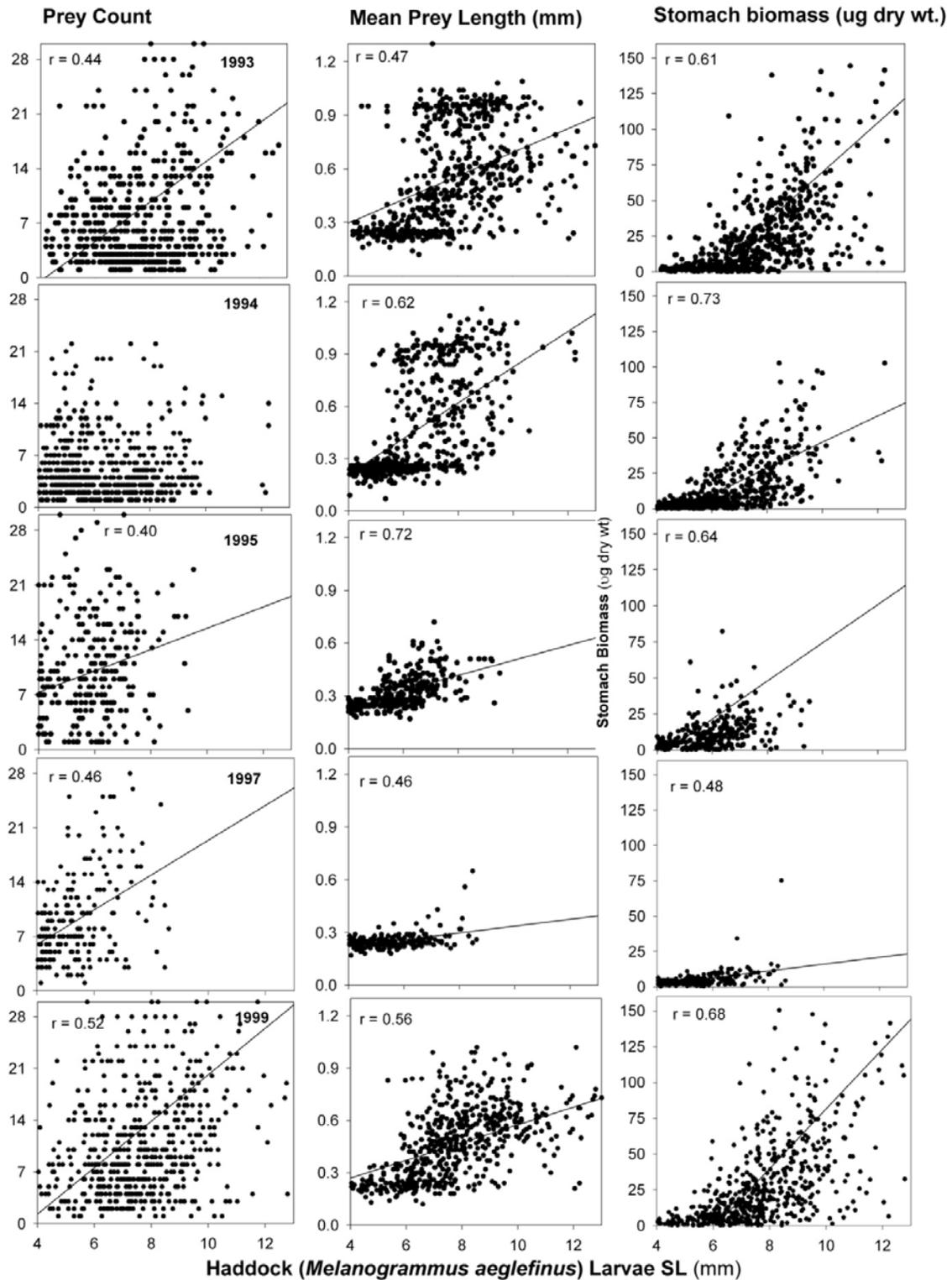


Figure 8. Yearly prey counts, mean prey lengths and total stomach biomass for haddock (*Melanogrammus aeglefinus*) larvae. Each point represents the value for an individual larva. Plots are fitted with a simple regression showing the correlation (r) between increasing larval standard length (SL) and the three types of data. 1994 prey counts had no meaningful correlation.

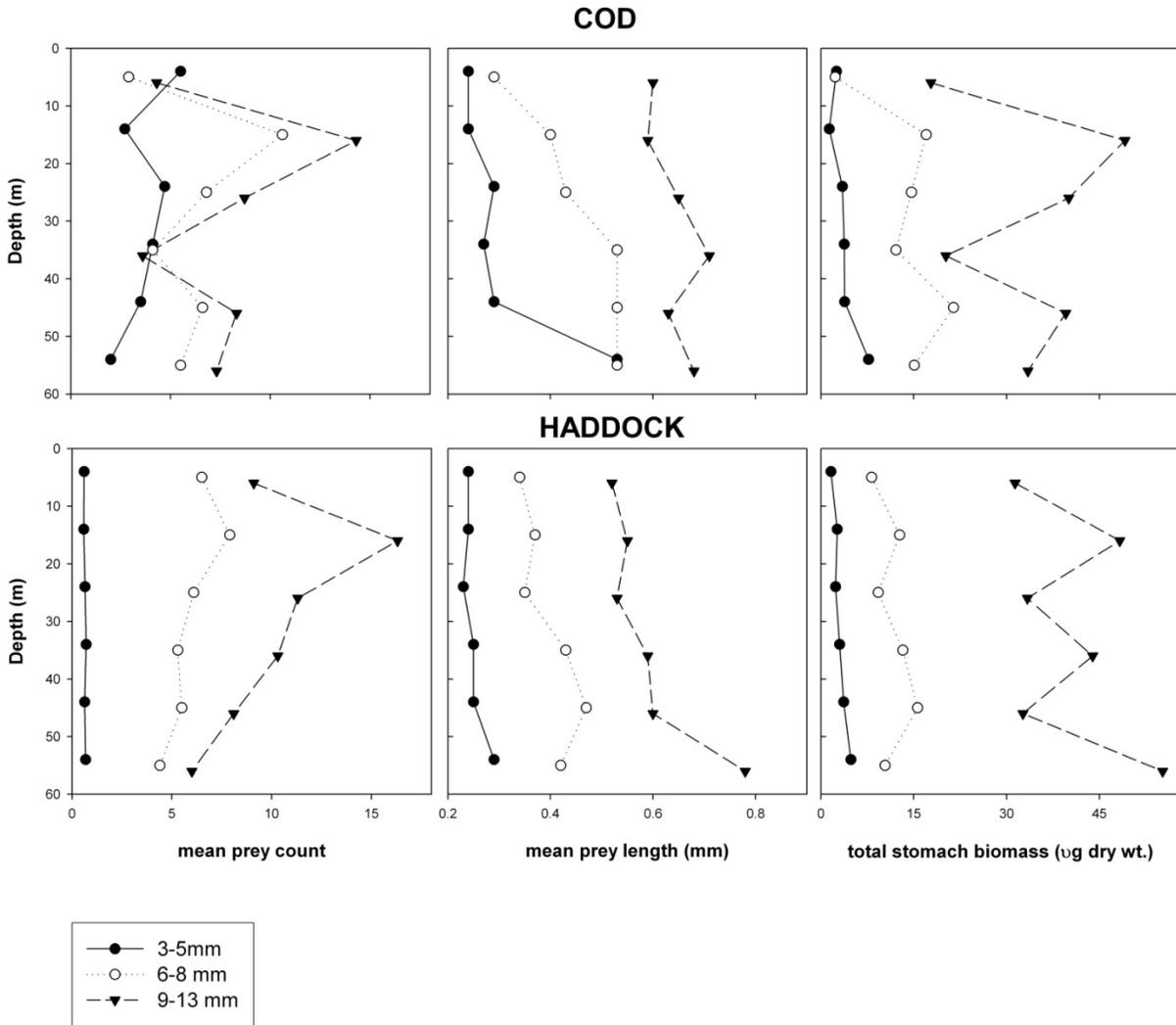


Figure 9. Mean prey count, mean stomach biomass and mean prey length for stratified site cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae sampled in 10m depth intervals. 3-5mm larval data is black circles (●), 6-8mm data is white squares (□) and 9-13mm data is gray triangles (▲).

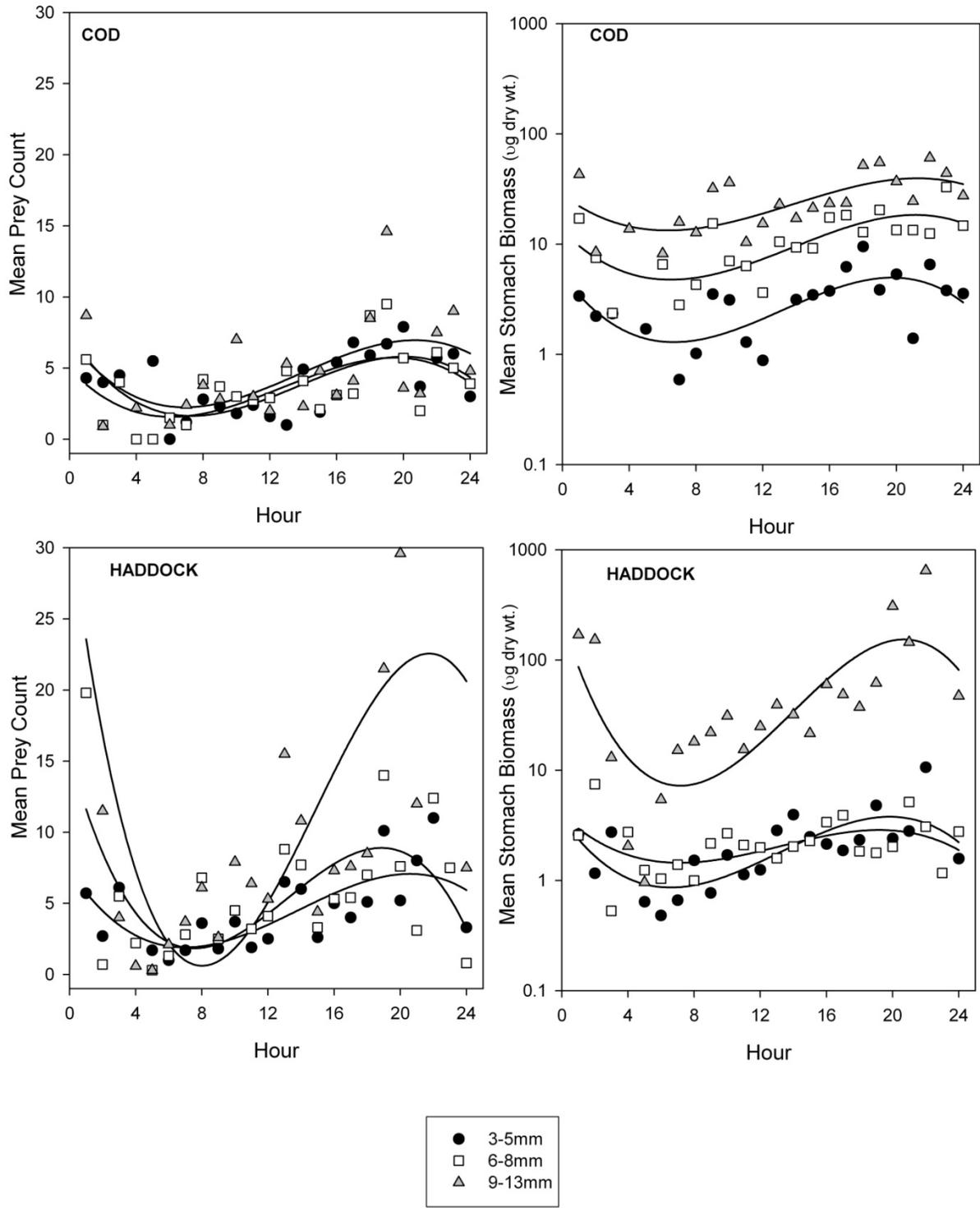


Figure 10. Hourly mean prey count and mean stomach biomass for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The 3-5mm larval data are depicted with black circles (●), 6-8mm larval data with white squares (□) and 9-13mm larval data with gray triangles (△). Values for each larval size class have been fitted with a 3rd order regression.

APPENDIX

Prey field and larval feeding data for all years categorized by sampling site, sampling depth, larval size class, and larval species.

Depths with no larvae and species categories without data have been removed from each table.

Gray "TOTAL" columns represent depth integrated data for each sampling site and year

Depth = mean depth of the net. Most nets sampled 10 m depth increments. Data with no depth value indicated integrate the entire water column.

Total # of nets = number of plankton samples processed in each data category

Total # of fish = number of larvae sampled in each data category

Count = *Zooplankton* mean number per m⁻³

Prey mean number per individual larva

Biomass = *Zooplankton* mean biomass (ug dry wt.) per m⁻³

Prey mean biomass (ug dry wt.) per individual larva

N1-N3 = copepod nauplii stages 1-3

N4-N6 = copepod nauplii stages 4-6

C1-C3 = copepod copepodite stages 1-3

C4-C5 = copepod copepodite stages 4-5

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