

# Diet changes in Scotian Shelf haddock during the pelagic and demersal phases of the first year of life

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**ABSTRACT:** The diet of haddock *Melanogrammus aeglefinus* from the southern Scotian Shelf was studied during their first year of life. While haddock were pelagic, copepods were the numerically dominant component in the diet, with a significant benthic contribution (amphipods, polychaetes) first occurring in late summer. Examination of gut contents indicated that the transition from pelagic to demersal life occurred relatively suddenly. Catch rates did not vary with diel periodicity and gut contents of demersal fish had few occurrences of pelagic prey, indicating that diel migration was likely not an important aspect of the ecology of age 0 fish. Dietary changes during the months subsequent to the pelagic-demersal transition were minor relative to those associated with the transition itself, although some trends in importance of dietary items were observed, notably with copepods and mysids. Such trends did not appear to be related to the size of age 0 haddock.

## INTRODUCTION

Haddock *Melanogrammus aeglefinus* stocks typically exhibit highly variable recruitment (Mahon 1987). Although late juvenile and adult life-history stages are found in the vicinity of the sea bottom, younger fish occur near the ocean surface. In the north-west Atlantic, the pelagic phase lasts about 4 to 5 mo, with fish moving to the bottom in August and September at a length of 9 to 10 cm (Miller et al. 1963). The transition from the pelagic to demersal environment appears to be relatively rapid, taking place over a period of about 4 wk in July and August (Koeller et al. 1986). Most attempts to explain the high recruitment variability of haddock have focussed on the effects of the environment and food supply during the relatively short pelagic phase. However, several authors maintain that the period of transition to the demersal habit and the winter following are critical in determining the size of the year-class (Walford 1938, Chase 1955, Sissenwine 1984).

As part of a larger study of the ecology of all life-history stages of haddock off southwestern Nova Scotia, we describe here the diet of pelagic and demersal (age 0) juvenile haddock. Whereas other authors (Pálsson 1980, Robb & Hislop 1980, Bowman 1981,

Robb 1981) have reported the diets from specific stages of juvenile gadoids' life history, this is the first time the diet has been studied throughout their first year.

In addition to describing the diet of age 0 haddock, we were interested in whether haddock experienced an abrupt transition of feeding and other behaviour during the ontogenetic vertical migration. Therefore, we also classified the prey organisms by habitat. We could thus explore the possibility that diel migrations between pelagic and demersal habitats reduced the abruptness of the transition.

## METHODS

Haddock juveniles of age 0 were sampled on 7 surveys conducted off southwestern Nova Scotia, Canada, throughout the year (20 to 30 Jun 1983; 1 to 12 Aug 1983; 30 Aug to 9 Sept 1983; 12 to 26 Oct 1982; 12 to 26 Jan 1983; 5 to 15 Apr 1983; 10 to 26 May 1982). Sampling locations are shown in Fig. 1. As there were relatively few fish sampled on the May survey, it was combined with the April survey. On the first 2 cruises, while the juveniles were pelagic, an International Young Gadoid Pelagic Trawl (IYGPT) was used. During the first cruise when the IYGPT was employed, the

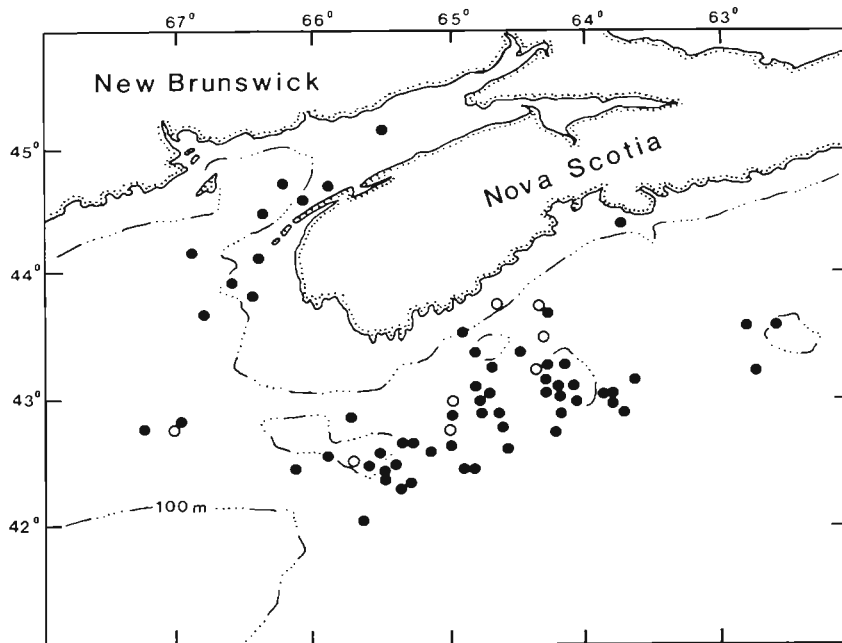


Fig. 1. Distribution of sets where age 0 haddock were captured and subsequently examined for gut contents, southern Scotian Shelf, eastern Canada, 1982 to 1983. (○) Pelagic sets; (●) demersal sets

entire water column was fished during a 3-step oblique haul of 30 min duration, 10 min at each depth. However, based on depth-stratified sampling which indicated that the majority of age 0 haddock were caught in the uppermost 50 m of the water column (Koeller et al. 1986), the subsequent cruise sampled only that depth interval. The tow speed during pelagic trawls was 3.5 knots and depth was monitored using a head-rope transducer. Based on their size, all fish caught in the pelagic trawl surveys were assumed to be age 0.

For the remaining cruises after the juveniles had descended to the bottom, a Western IIA trawl equipped with rollers was used. Sets were 30 min in duration, and towing speed was also 3.5 knots. Station locations were selected according to a depth-stratified random sampling design (Halliday & Koeller 1981). For bottom trawl samples, individuals comprising the mode nearest the origin of the length-frequency histogram were assumed to be age 0.

A length-stratified subsample of age 0 fish was kept from large catches, otherwise all individuals were retained. They were either frozen whole or the body cavity opened and the whole fish preserved in dilute formalin. The prey of each fish were identified to the lowest taxonomic level possible for the state of digestion, and enumerated. To compare type of prey selected by haddock among cruises, we also assigned each prey item to one of 3 habitat groups: planktonic, benthic and intermediate according to descriptions by Gosner (1971). The last group was assigned where the organisms were known to occur throughout the water column or where the level of identification did not permit more precise classification. An exception was

*Calanus finmarchicus* which we classified as intermediate on the basis of recent studies on the Scotian Shelf (D. Wildish, St. Andrews Biological Station, New Brunswick, Canada, pers. comm.). Two prey categories, Copepoda unidentified and Amphipoda unidentified were divided among the groups in the proportions shown by the identifiable planktonic, intermediate and benthic individuals in those categories.

Juvenile haddock have been observed to undertake diel vertical migrations, being on the bottom during the day and in the water column at night (Woodhead 1964, Bailey 1975). If such fish were feeding in the water column at night and returning to the bottom with planktonic prey in an advanced state of digestion, it is possible that the results from individuals sampled on bottom during the day might overemphasize the abruptness of the transition to benthic feeding. We explored this possibility by looking for differences in prey composition, feeding intensity, proportion of unidentified organic material and availability to demersal trawls, which might be related to time of day.

Ideally, the possible occurrence of diel migrations would be investigated by discrete depth sampling at intervals from the bottom to the surface within a confined geographical area. In practice, owing to the need to switch from a bottom trawl to a pelagic trawl, this would require more than one vessel or a large number of replicate tows. Due to the costs of such an experiment we have combined the information from 2 sets of surveys, one pelagic, the other demersal, as did Koeller et al. (1986).

The distribution of abundance in trawl tows is often

Table 1. *Melanogrammus aeglefinus*. Length-frequency distributions of 0-group haddock sampled for stomach content analysis, Scotian Shelf, 1982-83

| Length (cm) | Pelagic surveys |                  | Demersal surveys |            |            |                |
|-------------|-----------------|------------------|------------------|------------|------------|----------------|
|             | June (1983)     | Early Aug (1983) | Aug/Sep (1983)   | Oct (1982) | Jan (1983) | Apr/May (1982) |
| 3           | 22              |                  |                  |            |            |                |
| 4           | 58              |                  |                  |            |            |                |
| 5           | 31              |                  |                  |            |            |                |
| 6           | 27              | 1                |                  |            |            |                |
| 7           | 16              | 5                | 1                |            |            |                |
| 8           | 2               | 7                | 2                | 3          |            |                |
| 9           |                 | 5                | 4                | 14         | 1          |                |
| 10          |                 |                  | 4                | 12         | 10         |                |
| 11          |                 |                  | 2                | 27         | 22         | 1              |
| 12          |                 |                  |                  | 22         | 26         | 8              |
| 13          |                 |                  |                  | 16         | 26         | 3              |
| 14          |                 |                  |                  | 13         | 12         | 5              |
| 15          |                 |                  |                  | 9          | 8          | 10             |
| 16          |                 |                  |                  | 4          | 5          | 6              |
| 17          |                 |                  |                  | 3          | 10         | 5              |
| 18          |                 |                  |                  | 5          | 3          | 4              |

highly skewed, with a relatively large proportion of zeros (Smith 1981). Consequently we used the non-parametric, Kruskal-Wallis statistic (Conover 1980) to test for differences in numbers caught-per-tow between 4 time blocks (0001 to 0600 h, 0601 to 1200 h, 1201 to 1800 h, 1801 to 0000 h).

## RESULTS

The contents of 480 stomachs were examined. The lengths of the sampled fish showed the progression in size which would be expected for age 0 haddock (Table 1). On the basis of catch rates presented by Koeller et al. (1986) we considered the transition from pelagic to demersal existence to have taken place over the period covered by the second (early Aug) and third (August/September) cruises.

The juvenile haddock fed upon a wide variety of prey

items (Appendix 1) which, for the purposes of examining changes in feeding over time, we have aggregated by habitat and taxon. Aggregation by habitat showed a distinct transition from planktonic to benthic feeding as the juveniles became demersal (Table 2). After the juveniles became demersal, the frequency of occurrence of planktonic prey continued to decline gradually.

Aggregation by major taxon showed that the shift from planktonic to demersal feeding involves substantial changes in the type of prey consumed (Table 3). Copepods and pteropods became increasingly insignificant components of the diet, whereas ophiuroids and polychaetes became major components. Amphipods remained relatively important through the first year, but there is a shift from the planktonic hyperiideans to benthic species (e.g. *Leptocheirus* spp., *Unciola* spp.).

The comparison of numbers caught-per-tow did not reveal any significant differences among the 4 time blocks comprising the 24 h day in any of the surveys (Table 4). To further explore the possibility of a diel migration off bottom to feed on planktonic prey after the transition to a demersal existence, we compared the percentage contribution of unidentified organic matter to total stomach weight in each of the 4 time blocks for the 4 bottom trawl surveys (Table 5). Kruskal-Wallis tests on the proportions of unidentified organic matter indicated that there were no significant ( $p > 0.05$ ) differences among the time blocks. Therefore, it does not appear likely that the fish were feeding off bottom during some period and returning with a large proportion of digested food which may have been different in composition from that observed.

After the juvenile haddock became demersal, there was a continued change in diet through the first year, though less marked than the change which accompanied the transition (Table 3). The most evident trends are an increasing contribution of ophiuroids and a decreasing contribution of copepods. These trends may have been related to the increasing mean size of the fish in successive surveys or to seasonal changes in

Table 2. *Melanogrammus aeglefinus*. Percent contribution by numbers of planktonic, benthic and intermediate prey to the diet of age 0 haddock during their first year, Scotian Shelf, 1982-83. The number of stomachs examined and prey items classified is also shown

|                          | Pelagic surveys |                  | Aug/Sep (1983) | Demersal surveys |            |                |
|--------------------------|-----------------|------------------|----------------|------------------|------------|----------------|
|                          | Jun (1983)      | Early Aug (1983) |                | Oct (1982)       | Jan (1983) | Apr/May (1982) |
| Planktonic               | 62.6            | 8.8              | 5.1            | 5.3              | 5.1        | 0              |
| Intermediate             | 38.2            | 20.6             | 5.6            | 5.4              | 2.9        | 18.9           |
| Benthic                  | 0.2             | 70.6             | 89.3           | 89.3             | 92.0       | 81.1           |
| Total no. of prey items  | 5627            | 70               | 215            | 1255             | 341        | 307            |
| No. of stomachs examined | 156             | 18               | 13             | 128              | 123        | 42             |

Table 3. *Melanogrammus aeglefinus*. Percent contribution by numbers (above) and percent frequency of occurrence of each prey category (below) in the diet of age 0 haddock on each cruise, Scotian Shelf, 1982–83

| Prey group       | Pelagic surveys     |                     |                     | Demersal surveys    |                     |                     |
|------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
|                  | Jun<br>(1983)       | Early Aug<br>(1983) | Aug/Sep<br>(1983)   | Oct<br>(1982)       | Jan<br>(1983)       | Apr/May<br>(1982)   |
| Echinoids        | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>1.5</u><br>4.1   | <u>0.3</u><br>2.4   |
| Ophiuroids       | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.5</u><br>3.9   | <u>15.8</u><br>22.0 | <u>11.4</u><br>21.4 |
| Bivalves         | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.2</u><br>1.6   | <u>0.9</u><br>1.6   | <u>0.7</u><br>4.8   |
| Pteropods        | <u>3.1</u><br>8.3   | <u>1.4</u><br>5.6   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   |
| Other gastropods | <u>0.2</u><br>3.2   | <u>0.0</u><br>0.0   | <u>0.5</u><br>7.7   | <u>0.2</u><br>1.6   | <u>5.9</u><br>6.5   | <u>0.3</u><br>2.4   |
| Polychaetes      | <u>0.0</u><br>0.0   | <u>1.4</u><br>5.6   | <u>45.1</u><br>30.8 | <u>7.1</u><br>28.9  | <u>28.7</u><br>38.2 | <u>12.4</u><br>33.3 |
| Cumaceans        | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>4.7</u><br>7.7   | <u>2.1</u><br>7.0   | <u>5.0</u><br>5.7   | <u>10.7</u><br>26.2 |
| Copepods         | <u>92.3</u><br>69.2 | <u>27.1</u><br>50.0 | <u>17.7</u><br>30.8 | <u>4.0</u><br>4.7   | <u>4.1</u><br>4.1   | <u>0.0</u><br>0.0   |
| Amphipods        | <u>4.1</u><br>24.4  | <u>50.0</u><br>38.9 | <u>26.5</u><br>53.8 | <u>79.7</u><br>61.7 | <u>29.9</u><br>33.3 | <u>44.6</u><br>57.1 |
| Mysids           | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>5.1</u><br>15.4  | <u>0.2</u><br>1.6   | <u>0.3</u><br>0.8   | <u>0.0</u><br>0.0   |
| Euphausiids      | <u>0.0</u><br>0.6   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>4.2</u><br>25.8  | <u>1.2</u><br>3.3   | <u>15.3</u><br>21.4 |
| Crabs            | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.0</u><br>0.0   | <u>0.2</u><br>2.3   | <u>1.8</u><br>3.3   | <u>0.0</u><br>0.0   |
| Shrimps          | <u>0.1</u><br>3.2   | <u>8.6</u><br>11.1  | <u>0.5</u><br>7.7   | <u>0.5</u><br>3.9   | <u>1.8</u><br>4.1   | <u>0.7</u><br>4.8   |
| Miscellaneous    | <u>0.2</u><br>5.8   | <u>11.4</u><br>27.8 | <u>0.0</u><br>7.7   | <u>1.2</u><br>3.9   | <u>3.2</u><br>9.8   | <u>3.6</u><br>9.5   |

Table 4. *Melanogrammus aeglefinus*. Chi-squared ( $\chi^2$ ) comparison of the catch-per-tow of age 0 haddock among 4 time blocks using the Kruskal-Wallis non-parametric test. Mean and standard deviation (given in brackets) are reported for each time block. Pelagic and demersal surveys, Scotian Shelf, 1982–83

| Survey    |          | 0001–<br>0600 h   | 0601–<br>1200 h  | 1201–<br>1800 h  | 1801–<br>0000 h  | $\chi^2$ | p    | n  |
|-----------|----------|-------------------|------------------|------------------|------------------|----------|------|----|
| Jun       | Pelagic  | 16.60<br>(33.81)  | 5.50<br>(8.06)   | 6.05<br>(13.96)  | 6.10<br>(10.86)  | 0.97     | 0.81 | 71 |
| Early Aug |          | 0.92<br>(1.70)    | 1.76<br>(5.27)   | 0.11<br>(0.47)   | 1.13<br>(2.87)   |          |      |    |
| Aug/Sep   | Demersal | 21.23<br>(34.16)  | 41.90<br>(65.29) | 22.18<br>(44.47) | 26.47<br>(57.65) | 0.61     | 0.89 | 78 |
| Oct       |          | 13.04<br>(41.43)  | 14.96<br>(30.23) | 5.90<br>(14.13)  | 1.68<br>(4.42)   |          |      |    |
| Jan       |          | 32.06<br>(122.30) | 16.07<br>(31.75) | 21.23<br>(49.10) | 19.00<br>(28.18) |          |      |    |
| Apr/May   |          | 25.23<br>(56.07)  | 11.50<br>(21.22) | 7.00<br>(16.91)  | 4.67<br>(11.63)  |          |      |    |

Table 5. *Melanogrammus aeglefinus*. Chi-squared ( $\chi^2$ ) comparison of the percent unidentified organic material in stomachs of age 0 haddock among 4 time blocks for each demersal survey using the Kruskal-Wallis non-parametric test, Scotian Shelf, 1982–83

| Survey  | Average percent unidentified organic materials |                 |                 |                 | $\chi^2$ | p    | n   |
|---------|--|-----------------|-----------------|-----------------|----------|------|-----|
|         | 0001–<br>0600 h                                | 0601–<br>1200 h | 1201–<br>1800 h | 1801–<br>0000 h |          |      |     |
| Aug/Sep | 0  | 6.25            | 0               | 0               | 5.5      | 0.14 | 13  |
| Oct     | 13.29  | 13.08           | 13.05           | 13.21           | 1.10     | 0.78 | 128 |
| Jan     | 11.71  | 13.74           | 12.61           | 13.00           | 0.66     | 0.88 | 101 |
| Apr     | 5.43   | 6.75            | 6.95            | 3.25            | 0.63     | 0.89 | 42  |

Table 6. *Melogrammus aeglefinus*. Comparison of diet of 'large' and 'small' demersal age 0 haddock in each bottom trawl survey (0 = less than 1%; – = not present), Scotian Shelf, 1982–83

| Prey          | Aug/Sep (1983) |         | Oct (1982) |         | Jan (1983) |         | Apr/May (1982) |         |
|---------------|----------------|---------|------------|---------|------------|---------|----------------|---------|
|               | < 10 cm/       | ≥ 10 cm | < 13cm/    | ≥ 13 cm | < 13 cm/   | ≥ 13 cm | < 15 cm/       | ≥ 15 cm |
| Echinoids     |                |         | 0/0        |         | 1/2        |         | 1/–            |         |
| Ophuroids     |                |         | 0/0        |         | 12/21      |         | 10/12          |         |
| Bivalves      |                |         | –/0        |         | 1/0        |         | –/1            |         |
| Gastropods    |                | 1/0     | –/0        |         | 7/5        |         | 1/–            |         |
| Polychaetes   |                | 31/56   | 11/4       |         | 35/20      |         | 8/15           |         |
| Cumaceans     |                | 10/0    | 4/1        |         | 4/6        |         | 4/13           |         |
| Copepods      |                | 40/4    | 7/2        |         | 5/3        |         |                |         |
| Amphipods     |                | 17/34   | 68/89      |         | 28/32      |         | 62/36          |         |
| Mysids        |                | 0/9     | 0/0        |         | 0/–        |         |                |         |
| Euphausiids   |                | 0/1     | 6/3        |         | 2/0        |         | 9/18           |         |
| Crabs         |                |         | 0/0        |         | 2/1        |         |                |         |
| Shrimps       |                |         | 0/0        |         | –/4        |         | 1/0            |         |
| Miscellaneous |                |         | 2/0        |         | 4/3        |         | –/5            |         |

availability of prey. We addressed the first possibility by comparing the diet composition of 'large' and 'small' haddock in each survey, with these size categories divided at the median length (Table 6). In August, copepods were still a significant component of the diet of small fish, whereas in large fish, polychaetes and amphipods were dominant. However, after August there was no consistent pattern of size-related preference across surveys at the level of taxonomic aggregation used here. Regarding the possibility that seasonal trends in the abundance of prey accounted for changes in diet composition, no data were available to permit an examination of that hypothesis.

## DISCUSSION

This paper attempts to reconstruct the diet of juvenile haddock during their first year of life. To achieve this, it was necessary to combine collections of the 1982 and 1983 year-classes of haddock. Such a procedure might invalidate our conclusions if there were significant interannual differences in haddock size-at-age or in prey availability. The length-fre-

quency distributions (Table 1) indicate a reasonable progression of mean length-at-age through the first year. Therefore, by the criterion of no significant interannual differences in size-at-age, pooling of data from 1982 and 1983 year-classes is probably appropriate. Interannual variability in the abundance of prey would be expected for some prey types (D. Wildish pers. comm.). Unfortunately, the relative importance of interannual variability in abundance of haddock prey is not documented. However, at the level of taxonomic aggregation in Table 3, the contribution of prey groups is relatively consistent across the sequence of bottom trawl surveys.

We also attempted to evaluate the abruptness of the transition from pelagic to demersal existence. Koeller et al. (1986) have already demonstrated that the transition period for a cohort is about 4 wk. We were more concerned with the transition period of individual fish and whether diel vertical migration could be a mechanism for diminishing the impact of adjusting to a new habitat. We concluded on the basis of the gut contents examination that the movement from pelagic to demersal habitats occurred relatively suddenly (Tables 2 & 3).

A previous study of the diet of northwest Atlantic haddock found that fish greater than 8 cm (fork length) fed largely on benthic prey including amphipods, decapods and polychaetes, whereas smaller fish selected pelagic organisms such as copepods and euphausiids (Bowman 1981). Those findings are generally consistent with ours, but Bowman noted that benthic amphipods and cumaceans were also found in the diet of the smallest haddock (2 cm fork length), and inferred that the transition from pelagic to demersal life must be gradual.

Another study of demersal haddock during their first year in Icelandic waters (Pálsson 1980) showed that ophiuroids and bivalves increased in importance with time. However, in contrast to our study, the contribution of euphausiids to the diet of Icelandic haddock juveniles was higher just after the transition to the bottom than during the following winter. Since Pálsson considered euphausiids to be planktonic, he also concluded that the transition to benthic feeding was gradual. A problem with our interpretation of feeding habits during the transition period is that there were relatively few ( $n=31$ ) fish collected during late summer, which appeared to be the time at which fish were making the transition to bottom life.

Neither Bowman (1981) nor Pálsson (1980) addressed the possible role of diel migration in the ecology of age 0 haddock. However, as the diet of fish examined in those studies consisted of both benthos and plankton, the occurrence of diel vertical migrations was implied. Such migrations could relate to feeding or to predator avoidance, both of which would be likely to exhibit considerable geographical variation. Studies have differed in their conclusions as to the extent of vertical diel migration by juvenile haddock. For pelagic stages, Colton (1965) and Robb (1981) found no diel migration in Georges Bank and North Sea haddock, whereas Bailey (1975) observed extensive vertical migration in the latter area. For demersal juveniles, Colton (1965) found diel differences in catch rates by bottom trawls in 2 of 3 years. This was attributed to diel migration and net avoidance. Similarly, near Sable Island on the Scotian Shelf, there was a distinct diel pattern in catch rates of age 0 fish in bottom surveys (Scott 1982, 1984).

In our study, catch rates of demersal age 0 haddock did not vary with 24 h periodicity (Table 4), likely indicating that the fish were not undertaking significant diel vertical migrations. Further support for the absence of such migrations is found in the compara-

tively low abundance of planktonic organisms in the diet of the fish (Tables 2 & 5). Similarly, for the age 0 haddock caught in the midwater trawl in June, there was no significant diel variability in catch rate and the diet consisted largely of planktonic organisms (Table 2). Most of the intermediate organisms in the diet were *Calanus finmarchicus*, which is generally considered to be planktonic but which we assigned as intermediate on the basis of recent information that they were often taken in a suprabenthic sled. We consider this habitat assignment to be conservative with regard to our conclusions. Most surprising was the high proportion of benthic organisms in fish sampled in the midwater trawl in August (Table 2). These benthic organisms were mostly (73%) cyclopoid copepods and corophiid amphipods. Whereas the June cruise was well before the transition period described by Koeller et al. (1986), the August cruise was near the end. In view of this, it appears possible that just prior to becoming demersal, haddock undertake migrations to the bottom, possibly in search of suitable substrate. Unfortunately, the sample size in this cruise is relatively small. More intensive sampling within the transition period would help to resolve this hypothesis.

In conclusion, we suggest the following scenario: haddock juveniles live and feed in the epipelagic zone until they are almost ready to assume a demersal existence. At that point they make forays to the bottom during which they feed. When they have located suitable bottom, they become demersal, feeding almost exclusively on benthic prey. For the cohort, this transition may take about a month (Koeller et al. 1986) whereas for individual fish, it is probably much more abrupt.

If vertical migration is most pronounced during the transition period, apparent geographical differences in the abruptness of the transition to demersal habitat, accompanying changes in feeding behavior, and in the extent of vertical migration could result from the timing of sampling in relation to the transition period. For example, Bailey (1975) observed substantial vertical migration of pelagic juveniles during a 2 wk period in August, perhaps coincident with the transition period.

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**Appendix 1.** *Melanogrammus aeglefinus*. Diet of juvenile haddock during pelagic and demersal phases of their first year. Designation of habitat type is also indicated (B: benthic, I: intermediate; P: pelagic; Pr.: prorated to the various habitat preferences by proportions of identifiable specimen, as described in text). N: number of stomachs in which prey item was found

| Prey                        | Group         | Habitat | N  | Prey                             | Group         | Habitat | N  |
|-----------------------------|---------------|---------|----|----------------------------------|---------------|---------|----|
| <b>POLYCHAETA</b>           | Polychaetes   | B       | 22 | Isopoda                          | Miscellaneous | B       | 5  |
| Ampharetidae                | Polychaetes   |         |    | Amphipoda                        | Amphipods     | Pr.     | 73 |
| <i>Melinna cristata</i>     | Polychaetes   | B       | 42 | Corophiidae                      | Amphipods     | B       | 5  |
| Phyllodocidae               | Polychaetes   | B       | 9  | Caprellidae                      | Amphipods     | B       | 33 |
| Lumbrineridae               | Polychaetes   | B       | 9  | Aoridae                          | Amphipods     |         |    |
| Glyceridae                  | Polychaetes   |         |    | <i>Leptocheirus pinguis</i>      | Amphipods     | B       | 22 |
| <i>Glycera</i> sp.          | Polychaetes   | B       | 6  | <i>Unciola</i> sp.               | Amphipods     | B       | 55 |
| Onuphidae                   | Polychaetes   |         |    | Ampeliscidae                     | Amphipods     | B       | 18 |
| <i>Nothria conchylega</i>   | Polychaetes   | B       | 6  | Lysianassidae                    | Amphipods     | B       | 6  |
| Goniadidae                  | Polychaetes   | B       | 6  | <i>Anonyx</i> sp.                | Amphipods     | B       | 6  |
| <i>Goniada</i> sp.          | Polychaetes   |         |    | Oedicerotidae                    | Amphipods     |         |    |
| Opheliidae                  | Polychaetes   | B       | 4  | <i>Monoculodes</i> sp.           | Amphipods     | B       | 4  |
| <i>Ophelia limacina</i>     | Polychaetes   | B       | 2  | Gammaridae                       | Amphipods     | B       | 1  |
| Terebellidae                | Polychaetes   | B       | 2  | Melittidae                       | Amphipods     | B       |    |
| <i>Amphitrite</i> sp.       | Polychaetes   | B       | 1  | <i>Melita dentata</i>            | Amphipods     | B       | 3  |
| Aphroditidae                | Polychaetes   | B       | 2  | Pleustidae                       | Amphipods     |         |    |
| Maldanidae                  | Polychaetes   | B       | 2  | <i>Pleustes panoplus</i>         | Amphipods     | B       | 1  |
| Nereidae                    | Polychaetes   |         |    | Hyperiididae                     | Amphipods     | P       | 11 |
| <i>Nereis</i> sp.           | Polychaetes   | B       | 2  | <i>Parathemisto gaudichaudi</i>  | Amphipods     | P       | 37 |
| Nephtyidae                  | Polychaetes   |         |    | <i>Hyperia galba</i>             | Amphipods     | P       | 1  |
| <i>Nephtys</i> sp.          | Polychaetes   | B       | 1  | Euphausiacea                     | Krill         |         |    |
| Pectinariidae               | Polychaetes   |         |    | Euphausiidae                     | Krill         | I       | 6  |
| <i>Pectinaria granulata</i> | Polychaetes   | B       | 1  | <i>Meganyctiphanes norvegica</i> | Krill         | I       | 41 |
| Polynoidae                  | Polychaetes   | B       | 1  | Decapoda (larvae)                | Miscellaneous |         | 1  |
|                             |               |         |    | Shrimps unid.                    | Shrimps       | I       | 7  |
| <b>GASTROPODA</b>           | Gastropods    | B       | 12 | Pandalidae                       | Shrimps       |         |    |
| Buccinidae                  | Gastropods    | B       | 3  | <i>Pandalus montagui</i>         | Shrimps       | I       | 3  |
| Naticidae                   | Gastropods    |         |    | Hippolytidae                     | Shrimps       | B       | 5  |
| <i>Luniata heros</i>        | Gastropods    | B       | 1  | Cragonidae                       | Shrimps       | B       | 1  |
|                             | Pteropods     | P       | 28 | Axiidae                          | Shrimps       | B       | 4  |
| Polyplacophora              | Miscellaneous | B       | 2  | Paguridae                        | Crabs         | B       | 6  |
|                             |               |         |    | Majidae                          | Crabs         | B       | 1  |
| <b>PELECYPODA</b>           | Bivalves      |         |    | <b>ECHINOIDEA</b>                |               |         |    |
| Anomiidae                   | Bivalves      | B       | 1  | <i>Strongylocentrotus</i>        |               |         |    |
| Cardiidae                   | Bivalves      | B       | 1  | <i>droebachiensis</i>            | Echinoids     | B       | 3  |
| <i>Cardium</i> sp.          | Bivalves      | B       | 1  | <i>Echinarachnius parma</i>      | Echinoids     | B       | 3  |
| Pectinidae                  | Bivalves      | B       | 1  |                                  |               |         |    |
| <i>Chlamys islandica</i>    | Bivalves      | B       | 1  | <b>OPHIUROIDAE</b>               | Ophiuroids    | B       | 8  |
| <b>CRUSTACEA (unid.)</b>    | Bivalves      | ?       | 2  | Ophiactidae                      | Ophiuroids    |         |    |
| Ostracoda                   | Bivalves      | ?       | 2  | <i>Ophiopholis aculeata</i>      | Ophiuroids    | B       | 30 |
| Copepoda                    |               | P       | 13 | Ophiuridae                       | Ophiuroids    | B       | 3  |
| Calanoida                   | Copepods      | Pr.     | 78 |                                  |               |         |    |
| <i>Calanus finmarchicus</i> | Copepods      | I       | 95 | Eggs                             | Miscellaneous |         |    |
| <i>Temora longicornis</i>   | Copepods      | P       | 49 | Fish                             | Miscellaneous | ?       | 7  |
| <i>Centropages typicus</i>  | Copepods      | P       | 38 | Invertebrate                     | Miscellaneous | ?       | 4  |
| <i>Centropages</i> sp.      | Copepods      | P       | 29 |                                  |               |         |    |
| <i>Paracalanus parvus</i>   | Copepods      | P       | 29 | Cnidaria                         | Miscellaneous | B       | 1  |
| <i>Pseudocalanus</i> sp.    | Copepods      | P       | 27 | Chaetognatha                     | Miscellaneous | P       | 1  |
| Cyclopoida                  | Copepods      | B       | 3  | Rhynchocoela                     | Miscellaneous | ?       | 2  |
|                             |               |         |    | Sipuncula                        | Miscellaneous | B       | 2  |
| <b>MALACOSTRACA</b>         |               |         |    | Tunicate                         | Miscellaneous | ?       | 2  |
| Mysidacea                   | Miscellaneous | I       | 5  | Fish                             | Miscellaneous | ?       | 2  |
| Cumacea                     | Cumaceans     | B       | 28 | Thallophyta                      | Miscellaneous | B       | 1  |

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