Transition from pelagic to benthic prey for age group 0–1 Atlantic cod, *Gadus morhua*

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Atlantic cod, *Gadus morhua* L., settle to the bottom early in life at standard lengths of 30 to 40 mm (Bowman, 1981; Hawkins et al., 1985; Hop et al., 1994; Methven and Bajdik, 1994). After settlement into benthic habitats, Atlantic cod continue to feed on pelagic prey but then shift to benthic prey. The rate at which cod make this transition has not been quantified at a level usable in trophic dynamic studies. To quantify the rate at which this shift in diet occurs, the volumetric proportion of pelagic prey in the diet of 98 juvenile Atlantic cod (age group 0 and 1) was measured. The data were used to evaluate a method that enables the calculation of food quantities with high accuracy for incorporation in trophic studies.

Materials and methods

Juvenile Atlantic cod (ages 0 and 1) were collected at Bellevue, Trinity Bay, Newfoundland, from July to December 1989 and from August to October 1991. Refer to Methven and Bajdik (1994) for additional information on fish collection and the collection site. A sample of 98 group-0 (40.2–100.1 mm standard length [SL]) and group-1 (85.1–192.0 mm SL) cod were used. Stomach contents were analyzed by using prey volume to quantify the transition from pelagic to benthic prey.

For each individual, prey were identified to the lowest taxon possible, then counted. Displacement volume was measured for each taxon with a 5-mL graduated cylinder or a 200-µL micropipette. Prey volume was estimated as a proportion of the total volume of the pipette by using a millimeter ruler (200 µL measured 90.5 mm, i.e. 1 mm=approx. 2.2 µL). If a prey group was too small for volumetric displacement, measurements of length, width, and depth were taken for each individual prey item by using a dissecting microscope with an ocular micrometer. Measurements were made by using eye piece units and converted to millimeters to calculate volumes with geometric formulae (Table 1).

To evaluate the accuracy of calculated volumes, both displacement volume and calculated volume were measured for various prey items. Calculated volume tended to be higher than displacement volume by a constant rate, therefore linear regression was used to calibrate calculated volume against displacement volume. The intercept was not significantly different from zero ($P=0.1453, F_{[1,33]}=116.43$), therefore the parameters were re-estimated without the intercept ($P=0.0001$, $F_{[1,33]}=258.02$). The regression equation was

$$\textit{Displacement volume} = (0.72)(\textit{calculated volume}).$$

A correction factor of 0.72 was applied to all calculated volumes to obtain estimated displacement volumes.

The following references were used to identify invertebrate prey items and to determine whether they were benthic or pelagic with respect to habitat: Smith, 1964; Allen, 1967; Russell-Hunter, 1969; Schultz, 1969; Feeley and Wass, 1971; Meglitsch, 1972; Naylor, 1972; Bousfield, 1973; and Gardner and Szabo, 1982. Scott and Scott (1988) was used to identify vertebrate prey.

Percent pelagic prey in the diet was plotted against standard length to determine the relation between the two.

Results

Both group-0 and group-1 cod fed on a broad range of prey. However, few occurred in large amounts

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Table 1

Prey shapes and volume formulae used in the study. spl = species length; spw = species width; spd = species depth.

Prey type and species	Shape	Formula
Copepoda, Polychaeta, and shrimp and crab zoea	cylinder	$V = 3.14\ r^2 \times spl$ $r = spw/2$
Amphipoda (straight) and Mysidicae	cylinder	$V = 3.14 \times r^2 \times spl$ $r = [(spw + spd)/2]/2$ or $r = spw/2$
Amphipoda (curved)	1/2 cylinder	$V = 3.14 \times r^2 \times spw$ $r = spl/2$
Crab (adult)	disc	$V = 3.14 \times r^2 \times spd$ $r = [(spl + spw)/2]/2$
Crab (megalopa), Isopoda, and Ostracoda	box	$V = spl \times spw \times spd$
Crustacean eggs and eyes	sphere	$V = 4/3 \times 3.14\ r^3$ $r = spl/2$
Snail	circular cone	$V = 1/3 \times 3.14\ r^2 \times spd$ $r = [(spl + spw)/2]/2$

Table 2

Prey of age group 0–1 cod based on two measurement methods. B = Benthic, P = Pelagic, U = Unknown, Unid. = Unidentified. Mean number = number of individuals per stomach; mean volume = microliters per stomach.

Method	Group 0		Group 1	
Mean number	Calanoida (P)	22.7	*Jaera marina* (B)	37.9
	Harpacticoida (B)	3.6	Eggs (U)	17.7
	Unid. Copepoda (U)	3.2	*Gammarus oceanicus* (B)	3.0
	Jaera marina (B)	2.7	*Pontogeneia inermis* (P)	3.0
	Pontogeneia inermis (P)	2.1	Harpacticoida (B)	1.2
	Other (U)	5.7	Other (U)	5.8
Mean volume	Unid. Gammaridae (B)	27.4	*Crangon septemspinosa* (B)	297.7
	Gammarus oceanicus (B)	24.9	*Gammarus oceanicus* (B)	98.4
	Unid. Mysidacea (U)	12.9	*Jaera marina* (B)	84.0
	Calliopius laeviusculus (P)	12.3	*Urophycis tenuis* (B)	62.5
	Pontogeneia inermis (P)	11.2	Unid. Teleostei (U)	42.6
	Unid. Copepoda (U)	10.7	Unid. Decapoda (U)	40.9
	Calanoida (P)	6.5	Unid. Crustacea (U)	31.1
	Jaera marina (B)	6.1	Unid Polychaeta	28.9
	Other (U)	100.0	Other (U)	317.1

(Table 2). Group-0 cod fed predominately on amphipod taxa (*Pontogeneia inermis*, *Gammarus oceanicus*, *Calliopius laeviusculus*, and unidentified Gammaridae) and copepod taxa (Calanoida and Harpacticoida). Predominate prey of group-1 cod were more diverse, including two amphipod taxa, an isopod (*Jaera marina*), invertebrate eggs, a shrimp (*Crangon septemspinosa*), white hake (*Urophycis tenuis*), and other unidentified teleosts, decapods, and polychaete worms.

Figure 1 indicates a rapid shift from pelagic to benthic prey at standard lengths of 60 to 100 mm. Four group-0 fish, represented by triangles in Figure 1, had <5% pelagic prey. Prey of these fish consisted of a large volume of unidentified prey and a single benthic prey item (e.g. one ostracod or one amphipod head). These fish were omitted in the calculation of the mean proportion of pelagic prey for the three size groups of cod in Table 3.

The rapid shift to benthic prey by juvenile Atlantic cod was related to body size. This change was quantified for use in food web computations. The diet of cod 40–59.9 mm SL was 98% pelagic prey, that of cod 60–100 mm SL was 39% pelagic prey, and the diet of cod greater than 100 mm SL was 13% pelagic prey by volume. A simple explanation for this rapid shift is that the mouth opening of smaller size classes is too small to enable predation upon many benthic prey species. However, it is important for juvenile cod to settle to benthic habitats as soon as possible to find protection against predators. Therefore, they quickly shift to a benthic diet as soon as their gape size is large enough.

A series of hypotheses were examined to decide whether the rapid shift in diet was associated with conditions of the study: time of day, time of year, and breakdown of the thermocline. The pattern of change in Figure 1 was not due to time of day, because cod were captured primarily at night (18:10 to 04:30 hours). Data were then replotted by month of capture, which proved not to be responsible for the rapid shift in diet. Data were then replotted by date to investigate relation to the breakdown of the thermocline in mid-October. It was hypothesized that the thermocline keeps pelagic and benthic prey well separated (i.e. pelagic prey are unavailable to demersal juveniles). After the breakdown of the thermocline, the pelagic prey may occur lower in the water column. However, the change in percentage of pelagic prey did not change suddenly at the time of thermocline breakdown.

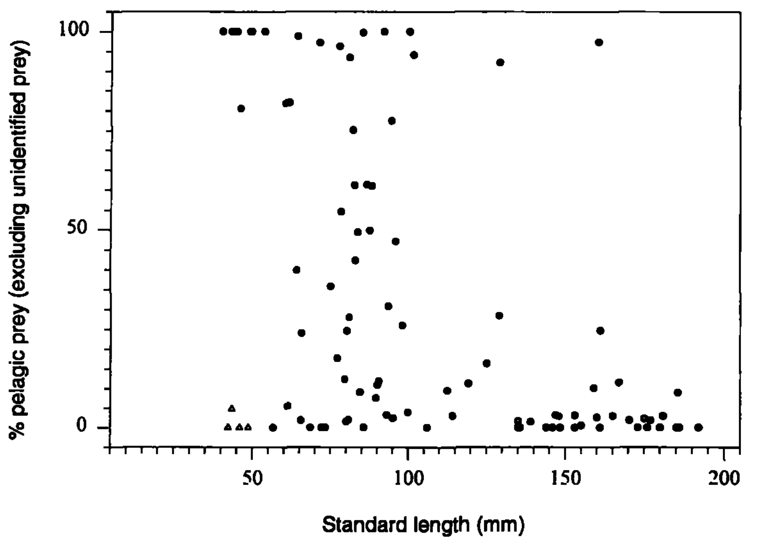

Figure 1
Percent pelagic prey (excluding unidentified prey) as a function of standard length (mm) for juvenile Atlantic cod. Four fish, indicated by the four triangles at the bottom left, had a single prey item identified.

Table 3
Percent pelagic prey in the diet of three size groups of juvenile Atlantic cod.

Size group (mm)	Mean % pelagic prey	Standard error	Number of stomachs
40–59	97.56	2.44	8
60–100	38.5	5.32	45
>100	13.06	4.43	41

Conclusions

The diets of group-0 and group-1 Atlantic cod at Trinity Bay, Newfoundland, are comparable to those of other areas (Daan, 1973 [northeastern Atlantic]; Arntz, 1974 [western Baltic]; Pálsson, 1980 [Iceland]; Bowman, 1981 [western Atlantic]; Keats et al., 1987 [eastern Newfoundland]; Paz et al., 1991 [Flemish Cap]; Keats and Steele, 1992 [eastern Newfoundland]; Hop et al., 1992, 1994 [northeastern Atlantic]). Demersal group-0 cod fed on both pelagic and benthic organisms, whereas group-1 cod fed more on benthic organisms as the principal components of the diet. The diets of group-0 and group-1 cod overlapped within a narrow range of body size (85.1 to 100.1 mm SL). Small pelagic prey, such as calanoid copepods, became less important in the diet of group-1 cod, whereas larger benthic prey items, such as decapods, amphipods, teleost fish, and polychaetes, became more important.

Results of the present study indicate that the ontogenetic shift from pelagic to benthic prey occurs within a narrow size range (from 60 to 100 mm SL) and hence more rapidly than previously believed (Daan, 1973; Bowman, 1981). This rapid shift may have been overlooked in previous studies that did not examine the diet of small cod in as much detail as in our study (i.e. volume in microliters of individual prey taxa). However, results of our study do not indicate that all cod less than 100 mm rely solely on benthic food. For example, it is well documented (e.g. Kohler and Fitzgerald, 1969) that, at particular times of the year, large juvenile and adult cod can forage far off the bottom on pelagic prey. One implication of this finding is that any investigation of cod recruitment variability, in relation to food supply, should include postsettlement stages.

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