

# A Review of the Comparative Development of Atlantic Cod (*Gadus morhua* L.) and Haddock (*Melanogrammus aeglefinus* L.) Based on an Illustrated Series of Larvae and Juveniles from Georges Bank

Peter J. Auditore, R. Gregory Lough and Elisabeth A. Broughton  
Northeast Fisheries Science Center, Woods Hole Laboratory, National Marine Fisheries Service  
NOAA, Woods Hole, MA 02543, USA

## Abstract

Developmental series for Atlantic cod, (*Gadus morhua* L.) and haddock, (*Melanogrammus aeglefinus* L.) are described, illustrated and compared for larvae through demersal juveniles (about 4–100 mm in length) from specimens collected in the Georges Bank area. Early life history stages include a yolk sac/first-feeding larva, preflexion/postflexion larva, and the pelagic and demersal juvenile. Early larvae of cod and haddock differ in development in their pigmentation patterns, fin formation, fin ray counts and overall fin size. Larval haddock by 8–9 mm develop larger pectoral fins and undergo pelvic fin formation earlier than larval cod. Haddock complete pelvic fin formation as postflexion larvae and maintain larger pectoral fins through the postflexion larvae and pelagic juvenile stages. Haddock also possess a greater mean total number of caudal, anal and dorsal fin rays than cod which altogether may provide greater swimming maneuverability. The sequencing of developmental characters coincide with the transition from pelagic to demersal habitats and the switch to associated prey fields. Morphological differences between cod and haddock can be related to differences in larval-juvenile feeding behavior, and prey preference manifest in the adult fish. Cod are considered a pursuit-type predator feeding on larger, more active prey. Haddock, which may be adapted for greater swimming maneuverability, are considered as a forage-type feeder preying on smaller, slower moving or sedentary organisms.

*Key words:* Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus* L.), early life history, Georges Bank, juveniles, larvae

## Introduction

Atlantic cod, (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) support important commercial and recreational fisheries in the North-west Atlantic (Hennemuth *et al.*, 1980). Both species are characterized as shelf spawners (Sherman *et al.*, 1984). The spawning seasons of cod and haddock overlap off northeastern United States, although cod have a protracted spawning often beginning in late-autumn and lasting until April or May the next year and haddock has a peak spawning in April. Planktonic eggs and larvae from spawnings on northeastern Georges Bank, are transported in the clockwise mean flow around the bank and drift to the southwest (Lough, 1984; Smith and Morse, 1985). During late-April and May, high concentrations of larvae occur on eastern Georges Bank and along the southern flank between the 60 and 100 m isobaths. Pelagic juvenile cod and haddock are widespread over Georges Bank during June and July, but high concentrations still remain on eastern part of the Bank. By August the recently-settled juveniles are most abundant on the north-

eastern part of the Bank (Grosslein and Hennemuth, 1973; Lough *et al.*, 1989).

Surprisingly, fragmentary detail is published on the early development and behavior of northwestern Atlantic cod and haddock (Hardy, 1978; Fahay and Markle, 1984). Although cod and haddock, like most species of the subfamily Gadinae, undergo a similar sequence of developmental events during their ontogeny, an examination of Georges Bank specimens has revealed some distinct differences in morphological development which may be related to reported behavioral differences. The objective of this paper is to present a more comprehensive description of the comparative morphology of cod and haddock integrating Georges Bank specimens with other regional descriptions in the literature. Also an attempt is made to relate morphology with specific behaviors such as swimming, feeding, vertical migration and settlement.

## Materials and Methods

Cod and haddock were collected on eight cruises in the Georges Bank and Nantucket Shoals

area during the springs of 1981, 1983 and 1984, and summers of 1985, 1986 and 1987 (Table 1). Larval fish were sampled using a 1 m<sup>2</sup> Multiple Opening/Closing Net Environmental Sensing System (MOCNESS), each of the nine nets fitted with 0.333 mm mesh (Lough, 1984). Pelagic juvenile fish were collected using a 10 m<sup>2</sup> MOCNESS equipped with five 3.0 mm mesh nets (Potter *et al.*, 1990). Demersal juvenile fish were sampled with a Yankee 36 bottom trawl fitted with a special 13.0 mm mesh cod-end liner (Azarovitz, 1981).

All larvae and juvenile fish were fixed in either 4% formaldehyde-seawater, or 95% ethanol within 20 min of gear retrieval. In the laboratory, morphometric and meristic observations were made with the aid of a Wild M5-A stereomicroscope (at 10–50x), fitted with polarizing filters and an ocular micrometer. Standard osteological clearing and staining techniques were used to enhance meristic structures for counts, measurements and observation of developmental characters (Potthoff, 1983). A survey of selected meristic and morphological characters was made from a developmental series (3–100 mm) of 740 larval and juvenile cod and haddock specimens. Observation of developmental characters representing specific size-classes routinely involved the selection and examination of 10 or more individuals per 2 mm length increase in good condition from different spawning seasons. Comparisons of larval and juvenile cod and haddock morphometric and meristic characters were based on a mean representative of specific size classes, year-class and sample.

Examination of fin ray development involved the counting of dorsal, caudal, anal, pectoral and pelvic fin rays, and evaluation of their development and size. Observations and illustrations of pigmentation patterns were also based on individuals from several year-classes. Illustrations of larval and ju-

venile fish were made with the aid of a camera lucida, and were based on a total of 300 individuals representing different year-classes. Morphometric measurements, including standard length, skull width, body height and maxillary length were measured to the nearest 0.1 mm. The standard length of all larval and juvenile fish reported here was corrected for fixation shrinkage to live length using Theilacker's equations as discussed in Bolz and Lough (1983).

## Results and Discussions

### Review of cod and haddock development

Atlantic cod and haddock spawn small planktonic eggs (1.2–1.6 mm) with larvae hatching at 3–4 mm notochord length (Dunn and Matarese, 1984). They follow a typical course of Gadinae ontogeny through a series of larval and juvenile stages (Table 2, Fig. 1): yolk sac larva, preflexion larva, postflexion larva, pelagic juvenile and demersal juvenile (Dunn and Matarese, 1984; Fahay, 1983). Larvae develop a relatively large head and moderately slender tapered body. Major characteristics of gadid larvae are: (a) coiled gut, (b) three dorsal fins and two anal fins, (c) pelvic fin insertion anterior of pectoral fin insertion, (d) peculiar hypural bones, and (e) lack of notochord flexion. Instead of true flexion, there is a shortening of the notochord in cod and haddock larvae. We have retained the term flexion as a stage demarcation since notochord shortening occurs at that point in development when flexion would occur in other species.

Selected developmental characters of larval and juvenile cod and haddock are listed in Table 3. From hatching (3–4 mm) to about 7–8 mm standard length there appear to be only minor differences in development between the two species. Haddock

TABLE 1. Station information for Atlantic cod and haddock specimens collected for illustration and developmental comparison by 1-m<sup>2</sup> MOCNESS (0.333-mm mesh), 10-m<sup>2</sup> MOCNESS (3-mm mesh) and Yankee-36 otter trawl (Y-36 O-Trawl) on Georges Bank during 1981, and 1983–87 early life history surveys.

Year	Vessel	Cruise	Date	Gear	Depth (m)	No. of specimens examined
1981	<i>Albatross IV</i>	81-03	28–29 Apr	1-m <sup>2</sup> MOCNESS	67–79	190
1981	<i>Albatross IV</i>	81-05	25–26 May	1-m <sup>2</sup> MOCNESS	77–80	120
1983	<i>Albatross IV</i>	83-03	13–16 May	1-m <sup>2</sup> MOCNESS	40–79	80
1983	<i>Albatross IV</i>	83-03	18–19 May	10-m <sup>2</sup> MOCNESS	34–52	60
1984	<i>Albatross IV</i>	81-05	13–21 Jun	10-m <sup>2</sup> MOCNESS	35–75	50
1985	<i>Albatross IV</i>	85-06	06–13 Jul	10-m <sup>2</sup> MOCNESS	80–84	40
1985	<i>Albatross IV</i>	85-06	06–13 Jul	Y-36 O-TRAWL	80–84	80
1986	<i>Albatross IV</i>	86-03	10–21 Jun	10-m <sup>2</sup> MOCNESS	39–73	60
1987	<i>Albatross IV</i>	87-04	03–07 Jun	10-m <sup>2</sup> MOCNESS	43–81	60

TABLE 2. Early life history stages of Atlantic cod and haddock with approximate size and age post hatching.

Developmental stage	Size (mm)	Age (days)	Transition phase
Pelagic egg	1.2–1.6 (diameter)	–	developing egg
Hatched larva	3–4	0	hatching
Yolksac larva	4–5	4–7	yolksac absorption
Preflexion larvae	5–10	30	flexion
Postflexion larva	10–17	52	fin ray completion
Pelagic juvenile	17–60	106	demersal lifestyle
Demersal juvenile	60–100	138	
Immature	ca 200	365	

TABLE 3. Selected developmental early life history characters of larval-juvenile cod and haddock.

Character	<i>Gadus morhua</i>	<i>Melanogrammus aeglefinus</i>	Source
Caudal fin rays	begin 5–6 mm complete 18–20 mm total # 52–55	begin 5–6 mm complete 15–18 mm total # 53–56	This study This study Markle (1982)
Dorsal fin rays	begin 9–10 mm complete 18–20 mm total # 51–62	begin 9–10 mm complete 15–18 mm total # 56–67	Fahay (1983) This study Markle (1982)
Anal fin rays	begin 9–10 mm complete 18–20 mm total # 39–48	begin 9–10 mm complete 15–18 mm total # 45–53	Fahay (1983) This study Markle (1982)
Pectoral fin rays	begin (hatching) complete 10–12 mm total # 19–20	begin (hatching) complete 10–12 mm total # 19–23	This study This study This study
Pelvic fin rays	begin 10–12 mm complete 19–22 mm total # 6	begin 8–9 mm complete 15–17 mm total # 6	This study This study This study
Flexion	10–17 mm	10–15 mm	Dunn & Matarese (1984)
Scales	55–60 mm	60–65 mm	This study
Teeth	15–17 mm	15–17 mm	This study
Swimbladder	well formed 4.0 mm oval at 9.0 mm	well formed 4.0 mm oval at 9.0 mm	Schwartz (1971) Ellertsen <i>et al.</i> (1980)
Barbel	25–30 mm	none	This study
Eyes	pigmented at hatching	unpigmented at hatching	Fahay (1983)
Neuromast organs	well-developed by 5–6 mm ca 3 weeks	no information	Blaxter (1984)

hatch yolksac larvae with unpigmented eyes, and have a slightly deeper body during the preflexion stage (5–10 mm) than cod, which hatch with pigmented eyes and have a more fusiform body shape (Fahay, 1983). Both species possess a well formed swimbladder at 4 mm, undergo gut coiling and vent development at approximately 5 mm, and begin

caudal fin ray formation at 5–6 mm (Ellertsen *et al.*, 1981). Neuromast organs, precursors of the lateral line, are reported by Blaxter (1984) to be well developed in cod larvae by 5–6 mm.

The pectoral fins are located high on the body and the pelvic fins are located in a high thoracic

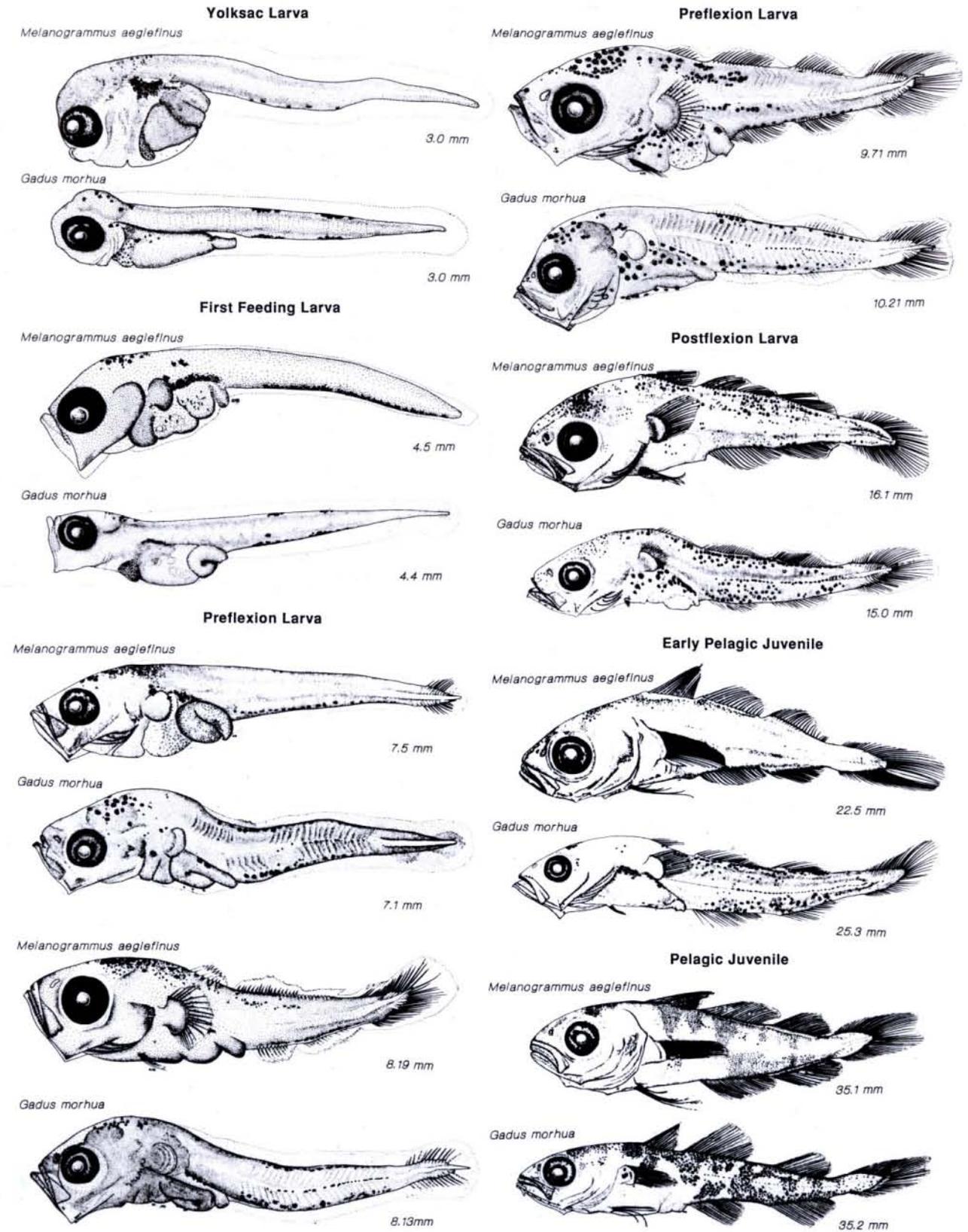
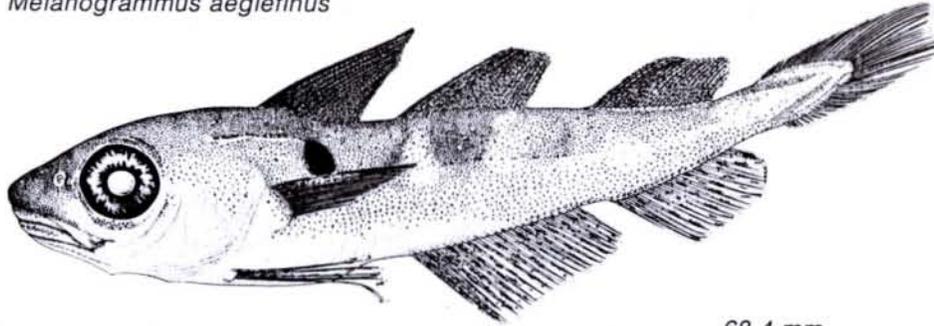


Fig. 1. Comparative developmental series of haddock and cod, from yolk sac larva through to demersal juvenile, illustrated from specimens collected on Georges Bank.

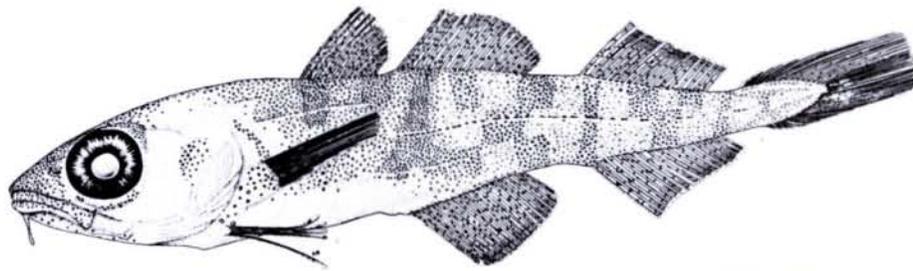
**Demersal Juvenile**

*Melanogrammus aeglefinus*



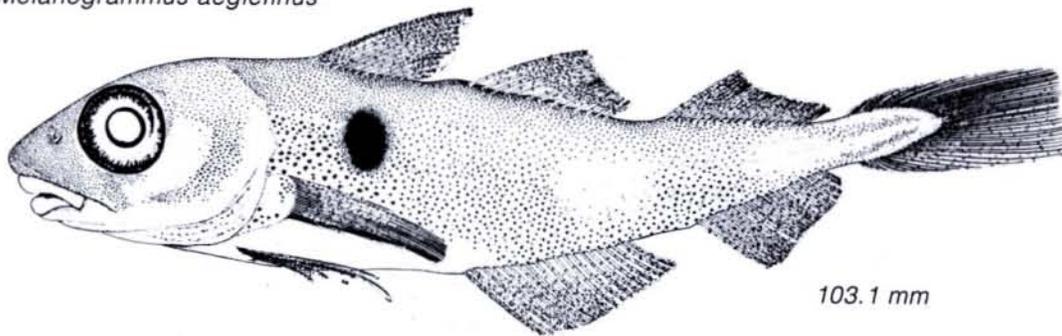
68.4 mm

*Gadus morhua*



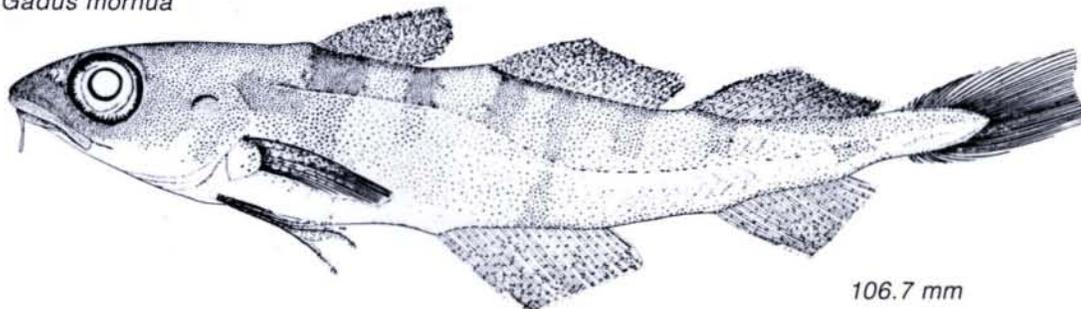
67.7 mm

*Melanogrammus aeglefinus*



103.1 mm

*Gadus morhua*



106.7 mm

Fig. 1. (Continued). Comparative developmental series of haddock and cod, from yolk sac larva through to demersal juvenile, illustrated from specimens collected on Georges Bank.

position typical of gadiform development. Their three dorsal and two anal fins have numerous rays and long bases, with posterior dorsal and anal rays separate from the caudal rays (Fahay and Markle, 1984). Approaching the point of notochord flexion at 8–9 mm, haddock develop large pectoral fins and begin development of pelvic fin buds. Cod possess smaller pectoral fins at this size and do not begin pelvic fin development until 10 mm. The illustrations of preflexion larvae in Fig. 1 clearly contrast paired fin development between the two species. Larval haddock have more advanced notochord shortening, earlier fin ray development, and undergo transformation to the pelagic juvenile stage smaller and earlier than cod.

Comparisons of the morphological and meristic characters of the two species suggest that differential development continues through the early pelagic juvenile stage. Although both species share the same complement, location and sequential formation of paired and unpaired fins, postflexion haddock have a higher number of fin rays and complete formation of pelvic, caudal, dorsal and anal rays sooner than postflexion cod. The total number of fin rays usually determines the overall size of a fin, which would account for the notable difference in fin size between the two species.

The pelagic juvenile stage (17–60 mm) is marked by the completion of fin ray formation. The juveniles

then begin to develop adult characteristics, including teeth and scales. Some distinct morphological features of haddock at this stage include a deep, stocky body shape with a large blunt head, and an elongation of the first dorsal and pelvic fins. Cod at this stage maintain a streamline, fusiform body shape and relatively small overall fin size (Fig. 1).

Both species undergo transformation from pelagic to demersal juvenile stage at 40–60 mm. Formation of scales occurs at about 55–60 mm and pelvic fins begin to shorten. Cod develop a distinct barbel on the lower jaw at this size, which is first noticeable at 25–30 mm. The illustrations of early demersal stage cod and haddock in Fig. 1 contrast these characters in addition to differences in the overall size of the first anal fins, dorsal fins, pelvic fin lengths and body depth.

The two species begin to resemble each other morphologically as they approach the onset of a demersal lifestyle, however, an elongation of the second pelvic fin ray of the demersal juvenile haddock becomes pronounced at 70–80 mm. Both species, as shown in Fig. 1 at >100 mm have a re-orientation of the mouth to a ventral position.

The developing pigment patterns of cod and haddock are shown in Table 4. Both species have well developed pigment patterns at hatching (Fahay, 1983). Their larvae can be distinguished easily from

TABLE 4. Developing pigmentation patterns of cod and haddock larvae and juveniles in relation to standard length.

Cod pigmentation	Standard length (mm)	Haddock pigmentation
2 dorsal postanal patches 2 ventral postanal patches	3	ventral, postanal row of individual melanophores
	4	continuous ventral postanal melanophores
dorsal and ventral double body contour pigment	5	individual ventral postanal melanophores
melanophores on midline	7	
	9	pectoral fin rays pigmented
	11	first dorsal fin pigmented
	15	dorsal, pelvic and pectoral fins well pigmented
abdominal iridocytes		
opercular iridocytes	20	
dorsal fins sparsely pigmented	25	abdominal iridocytes
medium melanophores in an irregular cryptic pattern	30	small, dense, evenly distributed pigment pattern
	35	shoulder patch developing
	40	distinct black shoulder patch

one another by comparing dorsal and ventral post-anal pigmentation (Fig. 1). Larval haddock hatch with a single ventral row of stellate melanophores, which range from the vent to the notochord tip and proliferate eventually to form a line at about 10 mm. Recently hatched cod have two dorsal and ventral post-anal patches which form bars that eventually spread longitudinally from the vent to the notochord. At approximately 8 mm, cod develop a distinctive series of melanophores along the mid-lateral line. Cod and haddock from 8 to 40 mm can be distinguished from each other by these midline melanophores; in cod they are present, in haddock they are absent. Both species develop a dense screen-like pattern of stellate melanophores over the dorsal peritoneal cavity during the preflexion state. These melanophores coalesce over the stomach and hind gut as both species develop through the postflexion-pelagic juvenile stages, and eventually they are obscured by abdominal iridocytes that form a silvery cover over the stomach area. Formation of melanophores on pectoral and pelvic fin rays begins at about 8–10 mm in larval haddock, with both fins appearing densely pigmented by 15 mm. Haddock dorsal and anal fin melanophores develop at approximately 14–20 mm, and by 40 mm all dorsal and anal fins display some degree of pigmentation. Pelagic juvenile cod begin forming melanophores on the bases of pectoral fin rays at about 20 mm; dorsal, anal and pelvic fin pigmentation begin at 25–30 mm; and by 50 mm all dorsal and anal fins are moderately pigmented (Fig. 1). Haddock develop a distinct black “shoulder patch” of pigment at 35–40 mm.

### Implications of comparative development

Mean size at age is equivalent for both species as shown by a recent study of the comparative growth of cod and haddock larvae in the Gulf of Maine by Campana and Hurley (1989). They showed that neither species had a substantial growth difference within the temperature range of 3° to 7°C, at least through 30 days of age. Further, Bolz and Lough (1988) found no significant difference in the estimated mean standard length of cod (10.1 mm) and haddock (10.3 mm) at 30 days of age based on otolith aging analysis and even at 140 days the difference was negligible (107 vs 103 mm).

**Morphology.** Despite similar body shape and developmental stages, cod and haddock differ significantly during their early life histories. Morphologically they vary in early larval details of fin formation and fin ray counts and overall fin size. The functional importance of this variability may be a factor in vertical migration and feeding behavior which depends on swimming performance. Larval haddock by 8–9 mm develop larger pectoral fins

and undergo pelvic fin formation earlier than larval cod.

Haddock complete pelvic fin formation as postflexion larvae, and maintain larger pectoral fins through the postlarval and pelagic juvenile stages. Haddock also possess a greater total number of caudal, anal and dorsal fin rays than cod. In a survey of early developmental morphological characters of northwestern Atlantic gadids, Markle (1982) also found haddock (and pollock *Pollachius virens*) to have the highest caudal fin ray count among the Gadinae.

The formation of abdominal iridocytes and pigmentation patterns in early pelagic juveniles are well suited for both the pelagic and demersal life style. Dense abdominal cavity pigmentation, iridocytes and dorsal countershading serve to camouflage pelagic juveniles. Variable “checker board” pigmentation patterns make it possible for the demersal cod and haddock to closely resemble their natural habitat. Recently-settled juvenile cod and haddock aggregate on an extensive lag pebble-gravel deposit located on the northeastern edge of Georges Bank and mimic the mottled appearance of the bottom (Lough *et al.*, 1989). This coloration may function as camouflage and aid the juvenile fish in predator avoidance as well as in the capture of prey.

**Swimming behavior.** The caudal fin serves as the main thruster of locomotion and is assisted by the dorsal and anal fins (Cohen, 1984). The dorsal and anal fins function primarily passively as keels, aiding in stabilization and braking, and may also function as rudders (Gosline, 1973). Pectoral and pelvic fins also act as rudders and serve an important function during vertical migration (Fig. 2). The lift and downward movement, and braking can be generated through orientation of pectoral and pelvic fins during forward movement (Aleev, 1969; Blaxter, 1986; Gosline, 1973; Webb and Weihs, 1986).

Lough and Potter (1993) have summarized available field data on the vertical distribution patterns of cod and haddock larvae through the pelagic juvenile and recently-settled demersal juvenile stages on Georges Bank. Diurnal migration appears to be well established in 9–13 mm cod and haddock larvae and may have been initiated at the smaller size of 6–8 mm. The larvae of both species generally reside deeper by day and shallower by night. The larger fish have a greater vertical range. When the water column was thermally-stratified, the smaller larvae were confined more closely to the thermocline region. The more advanced fin development of haddock at 8–9 mm, compared to cod, may give them a greater maneuverability earlier than cod.

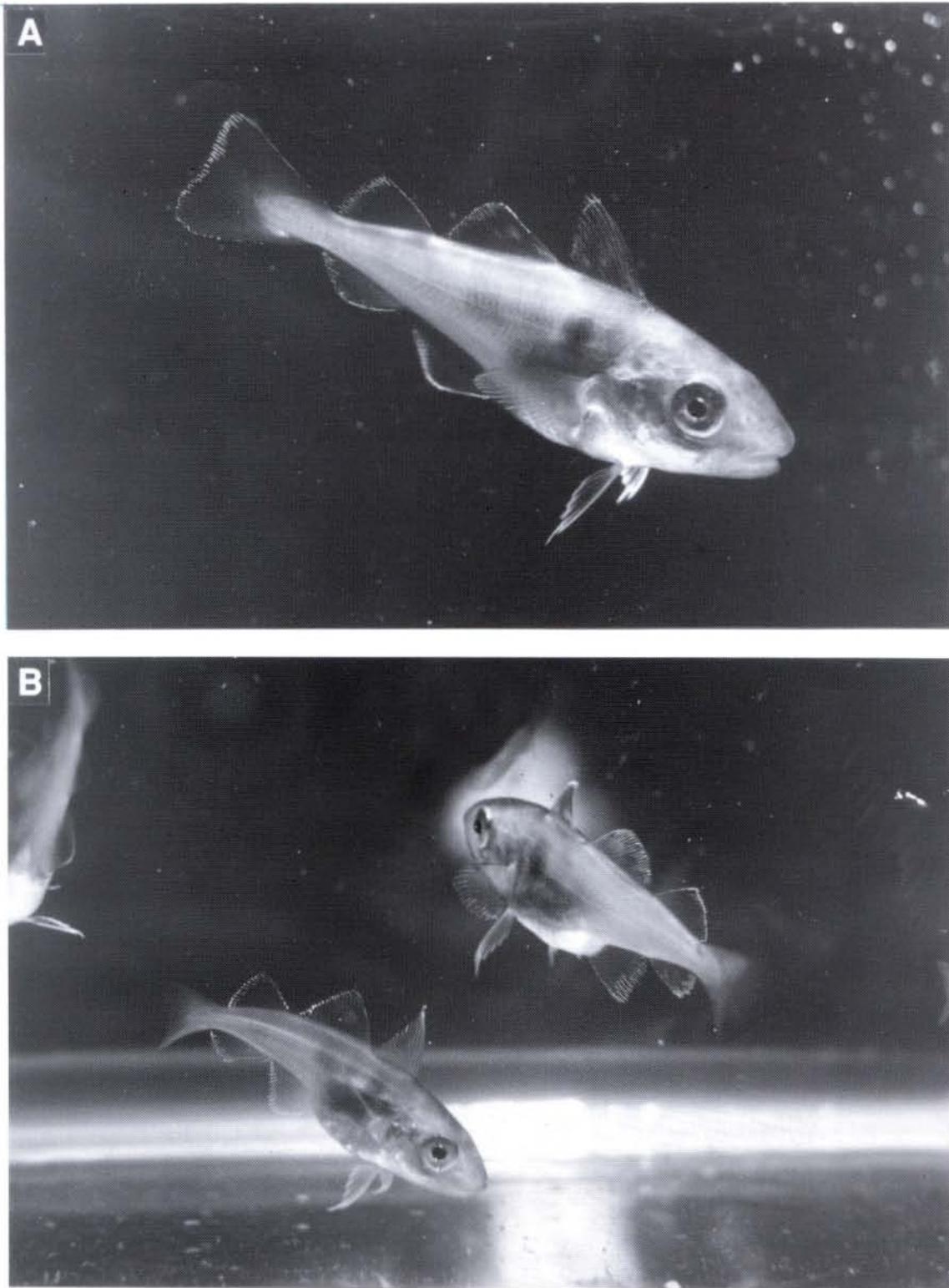


Fig. 2. Aquarium photographs of swimming juvenile haddock, about 9 cm in length, showing positioning of fins. **(A)** Fish swimming in slightly downward position with pelvic fins pulled back towards the body and a more ventral orientation of the pectoral fins. **(B)** Rear and side perspectives of two fish swimming near bottom. Note fan-like arrangement and rotation of pectoral fins to provide lift and maneuverability.

By the onset of the pelagic juvenile phase (about 17 mm) the fish generally are found in the lower part of the water column both day and night on eastern Georges Bank (Lough and Potter, 1993). Both species may assume a demersal life style at a size of about 60 mm, but the transition may begin as early as 30–40 mm. Demersal stage juvenile cod and few haddock were observed from submersibles on eastern Georges Bank in late-July and early-August to reside within a few centimetres of the bottom during the day, more or less stationary, swimming into the current (Lough *et al.*, 1989). At night they were observed near bottom as well as several meters off the bottom drifting with the current. The strong tidal currents characteristic of Georges Bank are reduced considerably within a meter of the bottom because of friction. As the submersible encountered the juvenile fish, the typical escape response was a quick thrust off the bottom up into the stronger current. This was followed by an extension of the pectoral and pelvic fins which allowed the fish to drift quickly in higher velocity current of the sheared bottom boundary layer. In the evening, juvenile fish were often observed drifting with the current in random orientations, apparently feeding on near-bottom invertebrates that were active at night.

Vertical distribution patterns of cod and haddock larvae appear to be similar based on available data, however, differences begin to appear during the pelagic juvenile stage. Perry and Neilson (1988) studied the vertical distributions of pelagic juvenile cod and haddock (about 30–50 mm) on eastern Georges Bank in June 1985 and found that cod had a wider vertical distribution range than haddock, and vertical migrations of cod were related to the diel light cycle, whereas migrations of haddock were more variable. Haddock at a stratified site remained near the thermocline, while at a shoal mixed site they were found mostly near bottom except before noon and midnight when they were caught throughout the water column. Cod, at both sites, were mostly near bottom during the day and in midwater at night, their upward migration apparently limited by the thermocline. During the transition period from pelagic to demersal life between 3–10 cm, juvenile cod and haddock stay close to bottom during the day and migrate off bottom at night, the vertical range of these night excursions decreasing with size of fish (Lough *et al.*, 1989). Lough and Potter (1993) concluded that haddock assume a more demersally-oriented life at a smaller size than cod, i.e. a shorter transition period. This is consistent with reported adult behaviour as adult haddock tend to remain close to the bottom at night as well as during the day, whereas adult cod make extensive migrations into the water column at night (Beamish, 1966; Woodhead, 1966). Differences in their vertical distribution patterns may be related to different feeding behavior and prey preference.

**Feeding behavior.** The prey of larval cod and haddock consists of the developing zooplankton on Georges Bank. The categorized prey selection of cod and haddock is compared in Fig. 3 redrawn from Auditore *et al.* (MS 1988). As they develop from pelagic larvae through the demersal juvenile stages they undergo a series of feeding transitions. Increasingly larger and more mobile prey characteristic of their transitional habitats are utilized: (1) Yolk sac and first-feeding larvae prey primarily on small plankton such as copepod nauplii, phytoplankton and lamellibranch larvae. Both species eat diatoms and *Peridinium* sp. although they represent a larger percentage of the diet of haddock than cod. (2) Preflexion and postflexion stage larvae begin selecting larger prey, principally calanoid copepod, copepodites and adults of the dominant copepods *Pseudocalanus* sp., *Calanus* sp., and *Centropages* sp. (3) Pelagic juveniles select various benthic epifauna such as mysids, amphipods, vertically migrating species of chaetognaths and adult copepods. (4) Recently-settled demersal juveniles feed on epibenthic amphipods, euphausiids and decapods. (5) Older demersal juveniles (>80 mm) gradually begin selecting more benthic prey like polychaetes, isopods, brachyura and benthic amphipods.

With the exception of the yolk sac stage, both cod and haddock feed on the same species of prey throughout their early life history and select prey that are numerically abundant (Kane, 1984; Buckley and Lough, 1987). Prey size plays an important role as larger size prey are generally selected as the fish grow larger. We found results similar to the study by Kane (1984), that cod larvae consumed larger prey types than haddock larvae of the same size (<11 mm SL), but haddock compensated by consuming more of the smaller prey. Cod larvae were considered by Kane (1984) to be active predators that fed on large prey shortly after yolk sac absorption. Haddock larvae in contrast, were more of a forager type depending largely on less motile prey such as copepod eggs and nauplii, and phytoplankton. Our findings show that differences in prey selection between cod and haddock occur prior to yolk sac absorption. From the view point of functional morphology, the haddock larva with larger fin area may be adapted for greater swimming maneuverability to set up precise feeding strikes. In contrast, a cod larva, with its smaller fin area, may be more adapted for pursuit-type predation, i.e. longer range, darting feeding strikes. It also is possible that the fins have a chemosensory function, taste buds for detecting food material in close proximity (Hasler, 1954). The early development of fins in haddock larvae may be related to this function. As pelagic and recently-settled juveniles, they shift prey selection to epibenthic prey, swarming populations that also undergo diel vertical migrations such as mysids

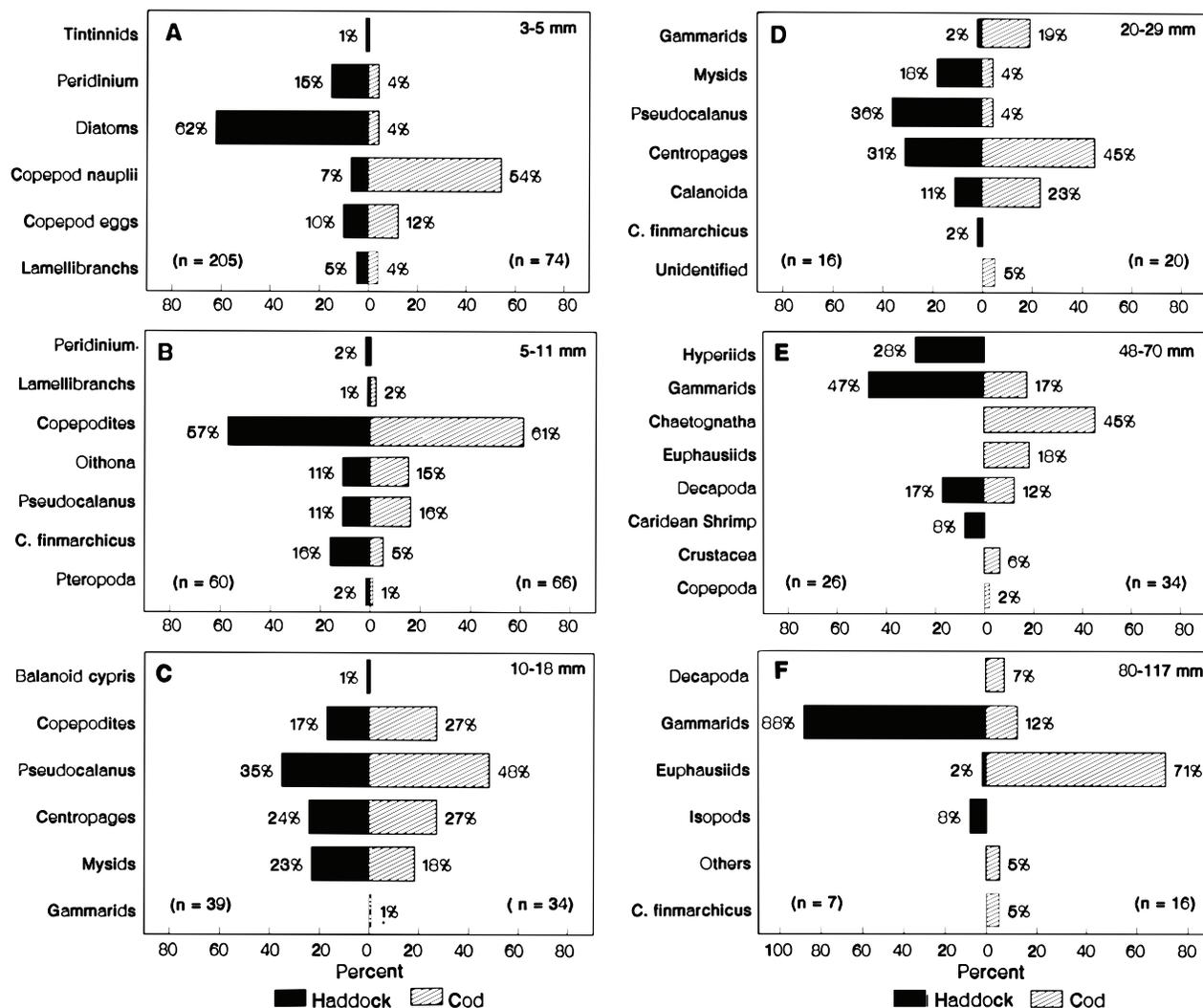


Fig. 3. Comparative prey selection of haddock and cod, (A) Yolksac larva, (B) Preflexion larva, (C) Postflexion larva, (D) Early pelagic juvenile, (E) Pelagic juvenile, (F) Demersal juvenile, from Georges Bank specimens. The number (n) for each species represents the total fish stomachs examined for the stage size range. The percentage prey composition was calculated for the total number of fish stomachs analyzed within the length range of the stage.

(*Neomysis americana*), amphipods (*Gammarus annulatus*, *Themisto gaudichaudii*), and euphausiids (*Meganyctiphanes norvegica*) (Auditore *et al.*, MS 1988; Perry and Neilson, 1988; Lough *et al.*, 1989). In the northern North Sea, Robb (1981) studied diel feeding of pelagic 0-group gadids and also found different feeding behavior for cod and haddock. Cod juveniles preyed on larger, active organisms, while haddock selected smaller, slower moving or sedentary organisms. Northwest Atlantic feeding studies by Bowman (1981a, b), and Mohn and Neilson (1987) indicated that demersal juvenile cod and haddock begin selecting benthic prey at about 70 mm. The prey of juvenile cod and haddock larger

than 70 mm consisted primarily of polychaetes and bottom dwelling crustaceans. The switch by cod and haddock to more benthic prey is at this size, when the mouth re-orientes to a ventral position.

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### References

ALEEV, Yu. G. 1969. Function and gross morphology in fish. Israel Program for Scientific Translations Ltd.,

- IPST Cat. 1773, Weiner Bindery Ltd., Jerusalem, Israel.
- AUDITORE, P. J., G. R. BOLZ, and R. G. LOUGH. MS 1988. Juvenile haddock, *Melanogrammus aeglefinus*, and Atlantic cod, *Gadus morhua*, stomach contents and morphometric data, from four recruitment surveys (1984–1986) in the Georges Bank-Nantucket Shoals area. *NMFS/NEFC Woods Hole Lab. Ref. Doc.*, No. 88–05, 105 p.
- AZAROVITZ, T. R. 1981. A brief historical review of the Woods Hole Laboratory Trawl survey time series. *In: Bottom trawl surveys*. W. G. Doubleday and D. Rivard (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.*, **58**: 62–67.
- BEAMISH, F. W. H. 1966. Vertical migration by demersal fish in the Northwest Atlantic. *J. Fish. Res. Board Can.*, **23**: 109–139.
- BLAXTER, J. H. S. 1984. Neuromasts and cupular growth of cod larvae. *In: The propagation of cod *Gadus morhua** L. E. Dahl, D. S. Danielssen, E. Moksness, P. Solemdal (ed.) *Flodevigen rapportser*, **1**: 183–188.
1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Trans. Amer. Fish. Soc.*, **115**: 98–114.
- BOLZ, G. R., and R. G. LOUGH. 1983. Growth of larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), on Georges Bank, spring 1981. *Fish. Bull. U.S.*, **81**: 827–836.
1988. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. *Fish. Bull. U.S.*, **86**: 223–235.
- BOWMAN, R. E. 1981a. Food and feeding of 0-group haddock in the Northwest Atlantic. *ICES Rapp. Proc.-Verb.*, **178**: 322–323.
- 1981b. Food of 10 species of Northwest Atlantic juvenile groundfish. *Fish. Bull. U.S.*, **79**: 200–206.
- BUCKLEY, L. J., and R. G. LOUGH. 1987. Recent growth, biochemical composition and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. *Can. J. Fish. Aquat. Sci.*, **44**: 14–25.
- CAMPANA, S. E., and P. C. HURLEY. 1989. An age- and temperature-mediated growth model for cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, larvae in the Gulf of Maine. *Can. J. Fish. Aquat. Sci.*, **46**: 603–613.
- COHEN, D. M. 1984. Gadiformes: Overview. *In: Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, W. J. Richardson (ed.). *Amer. Soc. Ichth. and Herp., Spec. Pub.*, **1**: 259–265.
- DUNN, J. R., and A. C. MATARESE. 1984. Gadidae: Development and relationships. *In: Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, W. J. Richardson (ed.). *Amer. Soc. Ichth. and Herp., Spec. Pub.*, **1**: 283–299.
- ELLERTSEN, B., P. SOLEMDAL, S. TILSETH, and T. WESTGARD. 1980. Some biological aspects of cod larvae *Gadus morhua* L. *Fiskeridir. Skr. Havunders*, **17**: 29–47.
- FAHAY, M. P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *J. Northw. Atl. Fish. Sci.*, **4**: 1–423.
- FAHAY, M. P., and D. F. MARKLE. 1984. Gadiformes: Development and relationships. *In: Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, W. J. Richardson (ed.). *Amer. Soc. Ichth. and Herp., Spec. Pub.*, **1**: 265–283.
- GOSLINE, W. A. 1973. Functional morphology and classification of teleostean fishes. The University Press of Hawaii, Honolulu, p. 42–49.
- GROSSLEIN, M. G., and R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. *ICES Rapp. Proc.-Verb.*, **164**: 77–88.
- HARDY, J. D. 1978. Development of fishes of the Mid-Atlantic Bight. *U.S. Fish Wildl. Serv.*, Vol. II, p. 219–337.
- HASLER, A. D. 1954. Odour perception and orientation in fishes. *J. Fish. Res. Board Can.*, **11**: 107–129.
- HENNEMUTH, R. C., J. E. PALMER, and B. E. BROWN. 1980. A statistical description of recruitment in eighteen selected fish stocks. *J. Northw. Atl. Fish. Sci.*, **1**: 101–111.
- KANE, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. *Mar. Ecol. Prog. Ser.*, **16**: 9–20.
- LOUGH, R. G. 1984. Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results. *In: The propagation of cod *Gadus morhua** L. E. Dahl, D. S. Danielssen, E. Moksness, P. Solemdal (ed.) *Flodevigen rapportser*, **1**: 395–434.
- LOUGH, R. G., and D. C. POTTER. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. *Fish. Bull. U.S.*, **91**: 281–303.
- LOUGH, R. G., P. C. VALENTINE, D. C. POTTER, P. J. AUDITORE, G. R. BOLZ, J. D. NEILSON, and R. I. PERRY. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Mar. Ecol. Prog. Ser.*, **56**: 1–12.
- MAHON, R., and J. D. NEILSON. 1987. Diet changes in Scotian Shelf haddock during pelagic and demersal phases of the first year of life. *Mar. Ecol. Prog. Ser.*, **37**: 123–130.
- MARKLE, D. F. 1982. Identification of larval and juvenile Canadian Atlantic gadoids with comments on the systematics of gadid subfamilies. *Can. J. Zool.*, **60**: 3420–3438.
- PERRY, R. I., and J. D. NEILSON. 1988. Vertical distributions and trophic interactions of the age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Mar. Ecol. Prog. Ser.*, **49**: 199–214.
- POTTER, D. C., R. G. LOUGH, R. I. PERRY, and J. D. NEILSON. 1990. Comparison of the MOCNESS and IYGPT pelagic samplers for the capture of 0-group cod (*Gadus morhua*) on Georges Bank. *ICES J. Cons.*, **46**: 121–128.
- POTTHOFF, T. 1983. Clearing and staining techniques. *In: Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, W. J. Richardson (ed.). *Amer. Soc. Ichth. and Herp., Spec. Pub.*, **1**: 35–37.
- ROBB, A. P. 1981. Observations on the food and diel feeding behavior of pelagic 0-group gadoids in the northern North Sea. *Fish. Biol.*, **18**: 183–194.
- SCHWARTZ, A. 1971. Swimbladder development and func-

- tion in the haddock, *Melanogrammus aeglefinus* L. *Bio. Bull. Mar. Biol. Lab. Woods Hole, Mass.*, **141**: 176–188.
- SHERMAN, K., W. SMITH, W. MORSE, M. BERMAN, J. GREEN, and L. EJSYMONT. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production and pulses in zooplankton off the Northeast United States. *Mar. Ecol. Prog. Ser.*, **18**: 1–19.
- SMITH, W. G., and W. W. MORSE. 1985. Retention of larval haddock, *Melanogrammus aeglefinus*, in the Georges Bank region, a gyre-influenced spawning area. *Mar. Ecol. Prog. Ser.*, **24**: 1–13.
- WEBB, P. W., and D. WEIHS. 1986. Functional locomotor morphology of early life history stages of fishes. *Trans. Amer. Fish. Soc.*, **115**: 115–127.
- WOODHEAD, P. M. J. 1966. The behavior of fish in relation to light in the sea. *Oceanogr. Mar. Biol. A. Rev.*, **4**: 337–403.
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