

**Abstract.**—Predation and cannibalism during larval life are potential determinants of recruitment and year-class strength in marine fish. We studied predation by larval Atlantic mackerel, *Scomber scombrus*, 3–14 mm in length, on conspecifics and other fish larvae over Sable Island Bank (Scotian Shelf) in July 1991. With increasing length, the diet of mackerel larvae shifted from copepod nauplii to copepods and fish larvae. Mackerel <5 mm selected strongly for copepod nauplii. Mackerel ≥6 mm preyed indifferently on copepods (i.e. in proportion to their abundance in the plankton) but selected strongly for fish larvae. The larval fish prey of Atlantic mackerel larvae comprised conspecifics (66%), yellowtail flounder, *Limanda ferruginea* (18%), silver hake, *Merluccius bilinearis* (12%), and redfish, *Sebastes* spp. (4%) larvae. Predation was stage-specific: only the newly hatched larvae of a given species were ingested. Based on a conservative estimate of the transit time of fish larvae in the gut (24 h), estimates of prey mortality by Atlantic mackerel larvae ranged from 7% to 57%/d (average 31%) of the standing stock of newly hatched larvae of suitable prey size. Piscivory was limited at densities of fish larvae <0.1/m<sup>3</sup>. Predation on fish larvae by Atlantic mackerel larvae declined with increasing density of nauplii in the environment and with increasing number of alternative copepod prey ingested. Because the capacity of Atlantic mackerel larvae to digest fish larvae was limited, cannibalism was density independent and predation on other species was compensatory. Hence, despite its potential importance during the first days after hatching, cannibalism and predation by Atlantic mackerel larvae 3–14 mm long do not appear to contribute to the density-dependent regulation of Atlantic mackerel and other prey species.

## Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment\*

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Several lines of indirect evidence suggest that predation is a major determinant of early survival in marine fish (Bailey and Houde, 1989): 1) the high mortality rate of eggs and yolk-sac larvae in the field (Fossum, 1988; Incze and Campbell, 1989); 2) the high estimates of predation mortality obtained by subtracting starvation mortality from total mortality (Hewitt et al., 1985; Leak and Houde, 1987); 3) the vulnerability of fast-growing, healthy larvae to predators in mesocosm experiments (Øiestad, 1985); 4) the wide range of potential predators of prerecruit fish in the sea (Hunter, 1984; Bailey and Houde, 1989); and 5) the variety of spawning strategies that can be interpreted as reducing the vulnerability of eggs and larvae to predators (Bailey and Houde, 1989). A recent field study comparing concurrent measurements of predation mortality and total mortality confirmed that predators such as medusae can have a significant impact on the early survival of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay (Purcell et al., 1994). Yet, in most ecosystems, the actual predators of fish larvae, the trophodynamics between predators and fish larvae, and the role of predation in regulating year-class strength remain unclear (Hunter, 1984; Ander-

son, 1988; Bailey and Houde, 1989; Heath, 1992).

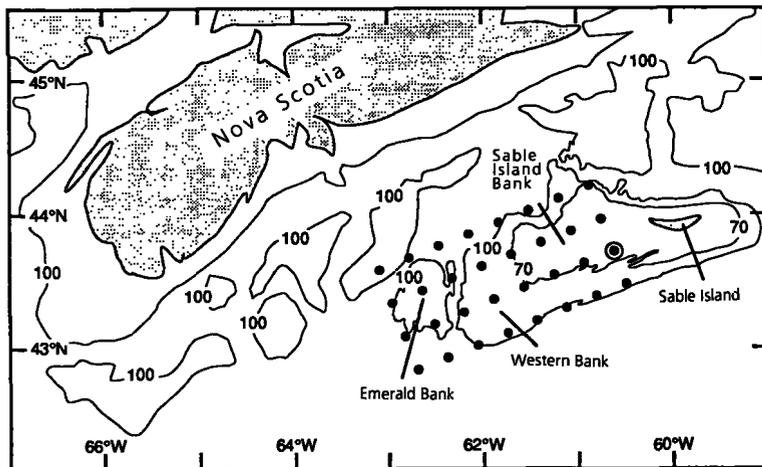
Scomid larvae often prey on the larval stages of their own and other fish species (Hunter and Kimbrell, 1980; Jenkins et al., 1984; Finucane et al., 1990; Young and Davis, 1990). In particular, Atlantic mackerel, *Scomber scombrus*, larvae capture fish larvae sometimes more than half their own length (Grave, 1981). The diet of Atlantic mackerel larvae changes markedly during ontogeny. First-feeding larvae may be phytophagous, young post-yolk-sac larvae feed primarily on copepod nauplii and copepodites, and Atlantic mackerel >6.5 mm in length add conspecifics and other fish larvae to their diet (Grave, 1981; Peterson and Ausubel, 1984; Ware and Lambert, 1985).

Because the probability of encounter between planktonic larvae increases with increasing density, Grave (1981) proposed that intracohort cannibalism could be a simple mechanism for the density-dependent regulation of year-class strength in Atlantic mackerel. In the present study, we examined the diet of Atlantic mackerel larvae and their selectivity for prey on Sable Island Bank (Scotian Shelf) in July

1991. Cannibalism and predation on other fish larvae were studied in relation to larval fish density and the availability and consumption of alternative invertebrate prey. In particular, we searched for evidence that cannibalism and piscivory by Atlantic mackerel larvae were density dependent. Finally, we evaluated the potential impact of predation by Atlantic mackerel larvae on the early survival of fish larvae.

## Methods

In spring, the northern component of the Northwest Atlantic stock of Atlantic mackerel migrates from the New England Continental Shelf and the Scotian Shelf towards the southern Gulf of St. Lawrence where the bulk of spawning takes place from early June to mid-August (Sette, 1943, 1950). Some spawning also takes place along the coast of Nova Scotia (Sette, 1943; Berrien et al., 1981). During a 27-month series of monthly ichthyoplankton surveys on Emerald, Western, and Sable Island banks (Fig. 1), Atlantic mackerel larvae were captured offshore, primarily over Sable Island Bank, in June, July, and August of 1991 and 1992. The larvae ranged from 2.7 to 13.7 mm standard length (SL)(unpreserved), corresponding to an approximate age span of 4 to 16 days (D'Amours et al., 1990). These lengths and ages indicate that the shallow waters west of Sable Island constitute a spawning ground for the species. The present study focuses on the trophodynamics of Atlantic mackerel larvae sampled in July 1991.



**Figure 1**

Location of the 32 rectangular midwater trawl (RMT) stations sampled for Atlantic mackerel, *Scomber scombrus*, larvae and their prey from 18 to 23 July 1991 on Emerald, Western, and Sable Island banks (Scotian Shelf). The vertical distribution of fish larvae was studied with the multi-net sampler on 24 and 25 July at the station marked with a circled black dot. Isobaths are in meters.

## Sampling

Atlantic mackerel larvae and their prey were sampled from 18 to 23 July 1991 over a grid of 32 stations covering part of Emerald, Western, and Sable Island banks (Fig. 1). Three different plankton nets mounted on a rectangular midwater trawl (RMT) were used to collect young fish and zooplankton simultaneously. A main net (8-m<sup>2</sup> sweeping section, 1,600- $\mu$ m mesh) captured juvenile fish; an intermediate net (2-m<sup>2</sup> sweeping section, 333- $\mu$ m mesh) collected fish larvae and mesozooplankton; and a small net (0.0075-m<sup>2</sup> mouth, 64- $\mu$ m mesh) sampled the microzooplankton prey of fish larvae. The RMT was towed once at each station in a multiple oblique trajectory from 0 to 75 m (or 5 m from the bottom at stations shallower than 75 m) for an average ( $\pm$  standard deviation [SD]) of 17 ( $\pm$ 5) min at a speed of approximately 2 knots (1 m/s). A CTD (conductivity, temperature, and depth) probe and flowmeters linked to a computer allowed real-time monitoring of depth, water column temperature and salinity, and the volume of water filtered by each net.

On 24 July, a multi-net sampler (Eastern Marine Services E-Z-Net) mounted with 10 identical nets (1-m<sup>2</sup> mouth, 333- $\mu$ m mesh) was used to determine the vertical distribution of fish larvae at the grid station (52-m depth) where the greatest density of fish larvae was found with the RMT (Fig. 1). Six casts were made at intervals of approximately four hours from 2115 h on 24 July to 2000 h on 25 July 1991. For each cast, 4 depth intervals of 10 m were sampled twice in the following order: 40–30, 30–20, 20–10, 10–0, 0–10, 10–20, 20–30, and 30–40 m. Nets were also opened on the downward (0–40 m) and upward (40–0 m) trajectories of the cast, providing two depth-integrated samples. The multi-net system was equipped with the same real-time monitoring system as that used on the RMT.

Most fish larvae (70%) were sorted immediately at sea and preserved in 95% ethanol. The remainder of the plankton sample, including undetected fish larvae, was preserved in 4% buffered formalin. A subset of 50 Atlantic mackerel larvae were videotaped on the ship for determination of morphometrics before preservation. Twenty-six of these (3.3 to 13.7 mm fresh SL) were preserved in ethanol and 24 (3.3 to 13.3 mm fresh SL) in formalin.

In the laboratory, all fish larvae remaining in the preserved samples were sorted and identified. All undamaged mackerel

larvae ( $n=1,667$ ) were measured to the nearest 0.1 mm SL. Standard length of mackerel larvae preserved in ethanol and formalin was corrected for shrinkage by using the relationships between fresh and preserved measurements obtained from the subset of larvae videotaped at sea ( $r^2=0.98$ ). The standard length of a random subset of the 3 other dominant larval fish species (51 silver hakes, 467 yellowtail flounders, 200 redfishes, preserved in ethanol) was measured. Mackerel lengths represent fresh measurements except those used for comparison with other species, in which case all lengths are ethanol-preserved measurements.

### Gut content analysis

Undamaged Atlantic mackerel larvae were selected for gut content analysis. The digestive tract was separated from the body and dissected under a light microscope. Whenever possible, prey were identified and measured. The position of the prey in the tractus (foregut, midgut, and reargut) and the state of digestion of the prey (slightly, partly, and well digested) were noted. Because crustacean prey were flattened dorso-ventrally, cephalothorax length, rather than width, was measured. Fish larvae were particularly damaged by digestion and only a small proportion of them (36 out of 710) could be identified and measured directly under the light microscope.

Indirect identification of some digested fish larvae was based on discriminant analysis of their otoliths. To establish the discriminant function, between 18 and 29 ethanol-preserved specimens of each of the four dominant larval fish species sampled in July 1991 (Atlantic mackerel, silver hake, yellowtail flounder, and redfish), ranging in size from hatching length to 10 mm, were selected from the plankton collections and measured. The sagittae and lapilli of each fish were extracted and 8 measurements were taken on each of the 4 otoliths: longest and shortest diameter (LD and SD); longest and shortest radius (LR and SR); surface and perimeter (SU and PE); and longest and shortest diameter of nucleus (LN and SN). The discriminant function used 15 measures and ratios of measures ( $LR_S/LR_L$ ,  $LN_S/SU_L$ ,  $PE_S/SU_S$ ,  $PE_S/LD_L$ ,  $SN_S/LN_L$ ,  $SR_S/SD_L$ ,  $LD_S/LR_L$ ,  $SD_S/SD_L$ ,  $LR_S/SU_L$ ,  $SD_S/SR_S$ ,  $SD_S/SN_L$ ,  $SD_L/LN_S/SN_L$ ,  $SR_S/SU_L$ ), in order of decreasing discriminatory power, where the subscripts *S* and *L* refer to the sagitta and the lapillus, respectively (from the same side of the fish). The discriminant function, which was validated by using the known larvae, correctly classified between 67% and 89% of the larvae of each species (Table 1).

The discriminant function was used to identify an additional 38 (out of 710) digested fish larvae for

**Table 1**

Validation of the linear discriminant function used to identify fish larvae found in the gut of larval Atlantic mackerel, *Scomber scombrus*, sampled from 18 to 23 July 1991, southwest of Sable Island (Scotian Shelf). The discriminant function is based on the morphometry of the otoliths of known larvae (see text). Successful identification is the percentage of larvae of a given species correctly identified by the discriminant function. Type-1 error is the proportion of fish larvae incorrectly assigned to another species ( $H_0$  rejected when it is true). Type-2 error is the proportion of fish larvae identified as a given species that were actually of another species ( $H_0$  accepted when it is false).

	Silver hake	Yellowtail flounder	Atlantic mackerel	Redfish
Successful identification (%)	78	89	71	67
Type-1 error (%)	22	11	29	33
Type-2 error (%)	8	29	28	31
Sample size	54	38	58	36

which one undamaged sagitta and one undamaged lapillus (from the same side of the fish) were recovered. The length of identified fish larvae was back-calculated on the basis of the best polynomial regression between one of the otolith dimensions and the ethanol-preserved standard length for the known specimens of the species ( $LD_S$ ,  $r^2=0.87$  for Atlantic mackerel;  $LD_S$ ,  $r^2=0.93$  for silver hake;  $SR_S$ ,  $r^2=0.80$  for yellowtail flounder;  $SD_S$ ,  $r^2=0.75$  for redfish).

Zooplankton were identified, enumerated, and measured in the RMT collections (64- $\mu$ m and 333- $\mu$ m net samples) that contained Atlantic mackerel larvae. The selectivity of Atlantic mackerel larvae for a category of prey was estimated by using Chesson's  $\alpha$  (Chesson, 1978):

$$\alpha_j = (d_j / p_j) / \left( \sum d_i / p_i \right), \text{ for } i = 1, \dots, N,$$

where  $\alpha_j$  is the selectivity for prey taxon *j*, *N* is the number of prey taxa,  $d_j$  and  $p_j$  are the frequencies of prey taxon *j* in the diet and the plankton respectively, and  $d_i$  and  $p_i$  are the same frequencies for the *i*th prey taxon. Copepod eggs in the diet of large fish larvae may have reflected the ingestion of egg-bearing females and, accordingly, eggs were not considered in the calculation of selectivity indices. Following Fortier and Harris (1989),  $\alpha_j$  was first computed for each individual Atlantic mackerel larva captured in the RMT and then averaged by length classes (<5, 5 to <6, 6 to <7, 7 to <8,  $\geq 9$  mm). Variations in  $\alpha$  reflect changes in the preference of the predator.  $\alpha$  is not

affected by changes in the abundance of potential prey and is thus suitable for describing ontogenetic variations in prey selectivity and for comparing or averaging selectivity among stations with different prey densities (Pearre, 1982). A value of  $\alpha_j > 1/N$  indicates that prey  $j$  is selected for, whereas  $\alpha_j < 1/N$  indicates that the prey is rejected.

All dissected mackerel larvae (feeding and non-feeding) were included in the determination of diurnal patterns of feeding activity. Larvae with empty guts occurred primarily during late-night and early-morning hours (0000–0800 h). These larvae were excluded from the calculations of feeding ratios (mean number of prey organisms per gut of feeding mackerel) or of piscivory (proportion of feeding mackerels with at least one fish larva in the gut). Note that the calculation of a feeding ratio for Atlantic mackerel larvae feeding on fish larvae was meaningless because the gut of mackerel larvae seldom (3% of all cases) contained more than one fish larva.

## Results

### Zooplankton and fish larvae

Copepods numerically dominated the zooplankton (Table 2). The cyclopoid *Oithona similis*, harpacticoid copepods, and the calanoid *Pseudocalanus* sp. were particularly abundant. The low mean densities of copepod eggs and nauplii ( $< 2/L$ ) may reflect the wide depth interval sampled by the RMT (0–75 m) because these organisms are often concentrated at the pycnocline or in the surface mixed layer.

Representatives of at least 18 genera of fish were collected (Table 2). Silver hake, yellowtail flounder, Atlantic mackerel, and redfish made up the bulk (98%) of the larval fish assemblage. Atlantic mackerel, silver hake, and yellowtail flounder larvae were found primarily over the shallow area of Sable Island Bank (Fig. 2). Redfish larvae were more evenly distributed in the sampling area than were the other species. Vertically, Atlantic mackerel, yellowtail flounder, and redfish larvae aggregated in the surface layer ( $< 20$  m) at night and moved deeper in the water column during the day (Fig. 3). In the morning and afternoon, Atlantic mackerel were concentrated in the thermocline at 10–20 m, whereas yellowtail flounder and redfish were found in or below the thermocline. At 2000 h, all four species were most abundant in the thermocline. During the day, the newly-hatched silver hake larvae were found primarily in the surface layer (0–20 m). Too few larvae were captured at night to confirm any diel migration pattern in this species.

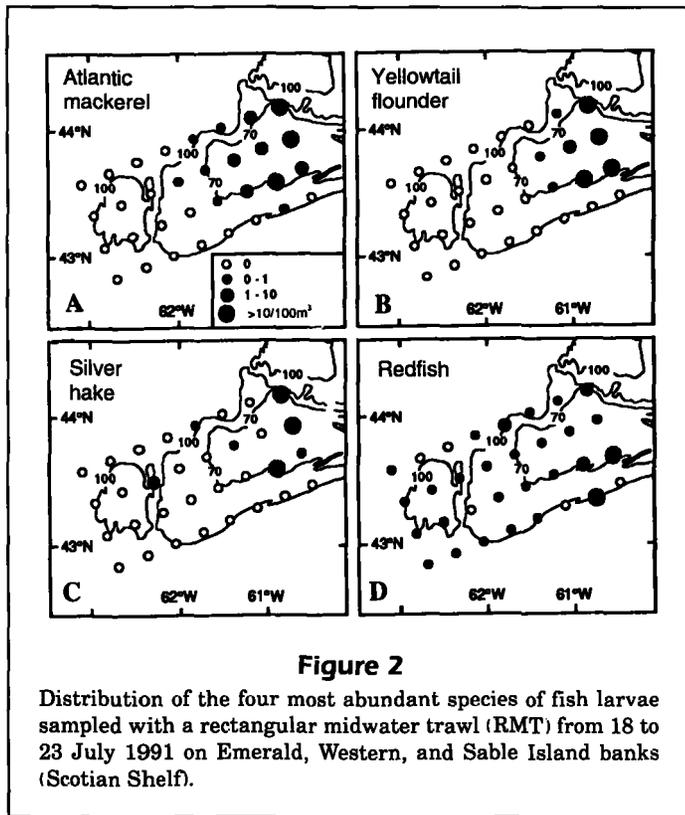
**Table 2**

Mean density ( $\pm$  standard deviation) and percent composition of the zooplankton and larval fish assemblages at stations where Atlantic mackerel larvae, *Scomber scombrus*, were captured ( $n=14$ ) from 18 to 23 July 1991, southwest of Sable Island (Scotian Shelf).

	Density	Percent
<b>Invertebrates (no./m<sup>3</sup>)</b>		
Copepods		
<i>Oithona similis</i>	2,048 $\pm$ 1,226	29
Copepod nauplii	1,642 $\pm$ 978	23
Harpacticoids	973 $\pm$ 565	14
Copepod eggs	606 $\pm$ 597	8
<i>Pseudocalanus</i> sp.	506 $\pm$ 452	7
<i>Temora longicornis</i>	168 $\pm$ 278	2
<i>Calanus finmarchicus</i>	153 $\pm$ 163	2
<i>Centropages</i> sp.	85 $\pm$ 107	1
<i>Metridia lucensis</i>	12 $\pm$ 20	<1
<i>Eurytemora hirundoides</i>	2 $\pm$ 5	<1
<i>Acartia</i> sp.	1 $\pm$ 2	<1
<i>Calanus hyperboreus</i>	<1	<1
<i>Metridia longa</i>	<1	<1
Tintinnids	690 $\pm$ 838	10
Bivalve larvae	198 $\pm$ 306	3
Gastropods	64 $\pm$ 60	1
Appendicularians	29 $\pm$ 39	<1
Polychaete larvae	6 $\pm$ 15	<1
Chaetognaths	2 $\pm$ 3	<1
Euphausiids	2 $\pm$ 3	<1
Amphipods	1 $\pm$ 3	<1
Decapod larvae	1 $\pm$ 1	<1
Gelatinous zooplankton	<1	<1
<b>Ichthyoplankton (no. 100/m<sup>3</sup>)</b>		
<i>Merluccius bilinearis</i> , silver hake	17 $\pm$ 52	37
<i>Limanda ferruginea</i> , yellowtail flounder	12 $\pm$ 30	27
<i>Scomber scombrus</i> , Atlantic mackerel	11 $\pm$ 23	24
<i>Sebastes</i> spp., <sup>1</sup> redfish	4 $\pm$ 10	10
<i>Glyptocephalus cynoglossus</i> , witch flounder	<1	<1
<i>Melanogrammus aeglefinus</i> , haddock	<1	<1
<i>Scophthalmus aquosus</i> , spotted flounder	<1	<1
<i>Mallotus villosus</i> , capelin	<1	<1
<i>Ammodytes</i> sp., sand lance	<1	<1
<i>Hippoglossoides platessoides</i> , American plaice	<1	<1
<i>Lophius americanus</i> , goosefish	<1	<1
<i>Stichaeus punctatus</i> , Arctic shanny	<1	<1
<i>Urophycis</i> sp., hake	<1	<1
<i>Ulvaria subbifurcata</i> , radiated shanny	<1	<1
Others <sup>2</sup>	1 $\pm$ 1	2

<sup>1</sup> Includes *Sebastes mentella* and *Sebastes fasciatus*.

<sup>2</sup> Includes unidentified fish larvae, pleuronectids, gonostromatids, stichaeids, and *Cyclopterus lumpus* (lumpfish) in order of decreasing average density.



### Diet and feeding patterns in Atlantic mackerel larvae

The diet of Atlantic mackerel larvae changed markedly during early ontogeny (Table 3). Small larvae (<5 mm) fed almost exclusively on copepod nauplii. With increasing length, their diet shifted from nauplii to copepods (copepodites and adults) and fish larvae. Copepod eggs did not contribute substantially (<1% of the prey) to the diet of mackerel larvae <7 mm that preyed mainly on copepod nauplii. The increased proportion of copepod eggs in the diet of larvae  $\geq 7$  mm may have reflected the ingestion of egg-bearing female copepods such as *O. similis* or *Pseudocalanus* sp. Appendicularians were present in small proportion (<5%) in the diet of all length classes of larvae. The importance of fish larvae in the diet increased with the length of Atlantic mackerel larvae. The smallest Atlantic mackerel larva that had preyed on another fish larva was 3.3 mm (fresh SL).

The mean cephalothorax length of the copepod prey of Atlantic mackerel larvae increased threefold over the range of lengths studied (<5 to  $\geq 9$  mm, Table 3). Feeding incidence was high ( $\geq 75\%$ ) in all length classes of mackerel. The feeding ratio (all prey types considered) tended to decrease with length, a reflection of the increasing frequency of large prey such as fish larvae. The incidence of predation on fish lar-

vae increased with larval mackerel size, from 12% in the smallest length class (<5 mm) to 69% in the largest length class ( $\geq 9$  mm).

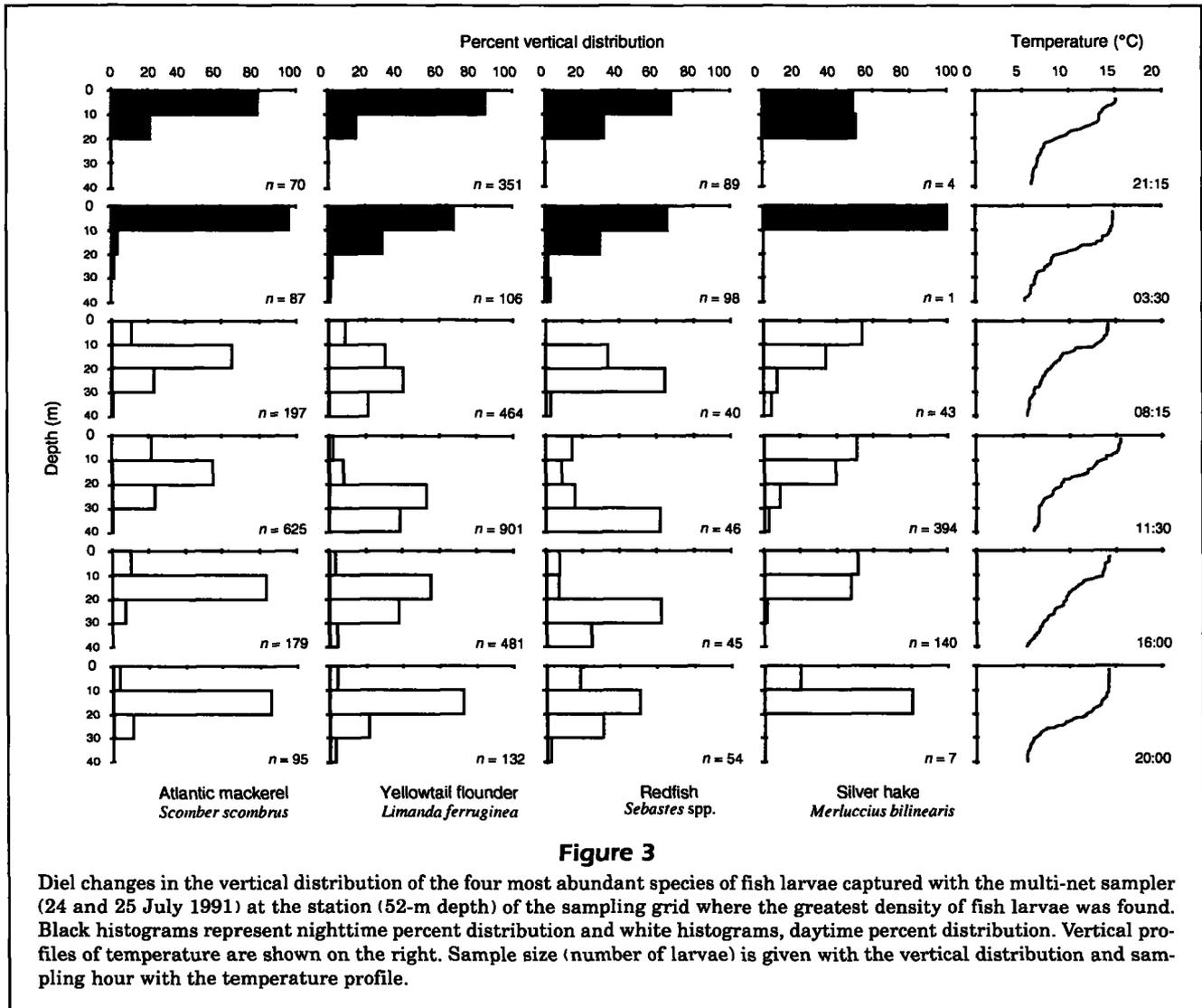
The mean number of invertebrate prey in the gut of Atlantic mackerel larvae was relatively constant from the second half of the night to late afternoon (1.9–3.5 prey per gut) and then jumped to 13 prey at dusk or soon after (Fig. 4A). This sharp increase in the number of invertebrate prey at dusk may represent an increase in copepod availability as the latter pass through the layer containing mackerel larvae during their nycthemeral migration towards the surface. The percentage of dissected Atlantic mackerel larvae with at least one fish larva in the gut tended to increase from the morning (<30%) to the afternoon and late evening (40–60%) (Fig. 4B).

The gut of Atlantic mackerel larvae usually contained no more than one fish larva (97% of cases). Forty-four percent (314 out of 710) of mackerel larvae containing a larval fish prey also contained at least one invertebrate prey. Most fish larvae were found in the midgut of Atlantic mackerel larvae throughout the diurnal period (Fig. 5A). The frequency of fish larvae in the foregut remained relatively constant during daylight hours, increased at dusk, and decreased in the second half of the night. Occurrence in the reargut was maximum in the early morning hours. In general, fish larvae in the gut of mackerel larvae were either partly or well digested (Fig. 5B). The percentage of Atlantic mackerel containing slightly digested fish larvae was low and relatively constant throughout the day. The frequency of partly digested fish larvae was high and tended to increase from early morning to late afternoon, whereas the frequency of well digested fish larvae declined.

### Prey selectivity in Atlantic mackerel larvae

Atlantic mackerel larvae of all lengths fed selectively, but selectivity for a given prey type changed during ontogeny (Table 4). Selection for copepod nauplii was high in small larvae (<5 mm) but declined rapidly as predator size increased; larvae  $\geq 7$  mm selected against this prey. Despite their numerical importance in the diet, copepods were either selected against by larvae <7 mm or consumed in rough proportion to their availability in the plankton by larger larvae. Selection for fish larvae increased steadily with the length of Atlantic mackerel larvae and preference for this prey type was particularly strong in larvae  $\geq 9$  mm (Table 4).

When analyzed by size categories, copepod prey (nauplii + copepodites + copepods) <300  $\mu\text{m}$  in cephalothorax length were selected (among the copepods) by larvae <7 mm, whereas copepods in the range 300–600  $\mu\text{m}$  were selected against or consumed in near



proportion to their availability in the plankton by larvae of all lengths. Copepods  $\geq 600 \mu\text{m}$  were selected for by larvae  $\geq 7 \text{ mm}$  (Table 5).

Out of the 710 fish larvae found in the gut of Atlantic mackerel larvae, 36 were identified visually and 38 were identified by discriminant analysis of their otoliths (Table 6). The species composition of the prey identified by either method was similar (Table 6). Assuming that the species composition of the 74 fish larvae identified represented the true composition of the assemblage ingested, conspecifics made up the majority (66%) of the fish larvae preyed upon by Atlantic mackerel larvae. Selectivity for a given species of larval fish prey was calculated for stations where  $\geq 10$  larvae were identified in the gut of Atlantic mackerel larvae. The results indicated little selection by mackerel larvae for any species of fish larvae ( $\alpha \approx 1/N = 0.25$ , where  $N = 4$  species) (Table 6).

Atlantic mackerel larvae preyed primarily on newly hatched larvae despite the availability of larger larvae in the plankton (Fig. 6). Only one conspecific prey  $> 5 \text{ mm}$  was found in the gut of mackerel larvae despite the availability of conspecifics in the plankton. Except for one larva 9 mm long, yellowtail flounder prey were  $< 6.5 \text{ mm}$ . The three redfish prey for which measurements are available were  $< 5.5 \text{ mm}$ . Atlantic mackerel apparently did not capture silver hakes  $> 2.5 \text{ mm}$ . The lengths of conspecifics, redfish, and silver hake prey corresponded to the range of lengths at hatching for these species (Fig. 6).

#### Predation by Atlantic mackerel larvae in relation to prey density

There was no consistent relationship between predation on invertebrates by Atlantic mackerel larvae

**Table 3**

Percent composition of diet and feeding statistics by length classes for larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991.

Prey taxa	Length class (mm)					
	<5	5-6	6-7	7-8	8-9	≥9
Copepod eggs	<1	<1	<1	18	46	37
Copepod nauplii	89	63	56	23	2	8
Copepods <sup>1</sup>	5	21	30	41	34	34
Appendicularians	4	7	4	5	2	1
Fish larvae	2	9	9	12	14	16
Others <sup>2</sup>	<1	<1	<1	1	2	4
Total number of prey	742	1,655	2,913	1,350	570	227
Total number of mackerel larvae	172	444	523	322	144	62
Feeding incidence (%)	75	87	92	88	88	86
Mean feeding ratio (prey per gut)	5.8	4.3	6.0	4.8	4.5	4.3
Incidence of piscivory (%)	12	39	54	57	63	69
Mean length of copepod prey (μm) <sup>3</sup>	190	253	289	405	657	597

<sup>1</sup> Copepodites and adult copepods.

<sup>2</sup> Include euphausiids, chaetognaths, gastropods, phytoplankton cells, cladocerans, amphipods, euphausiid nauplii, and crab larvae in order of decreasing frequency.

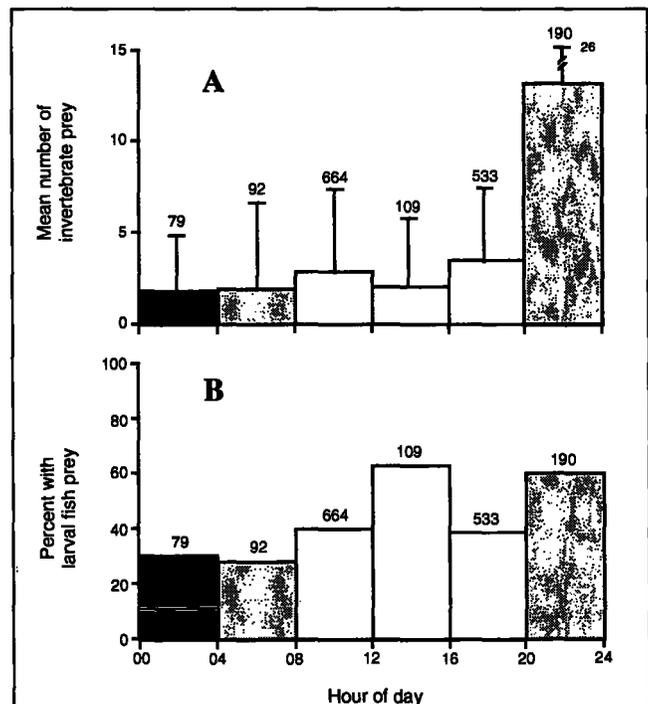
<sup>3</sup> Nauplii, copepodites, and adult copepods.

and the density of these prey in the environment. The feeding ratio for copepod nauplii (mean number of nauplii per gut) was not correlated with the density of nauplii in situ for any length class of Atlantic mackerel larvae ( $P \geq 0.33$ ). The feeding ratio for copepods (copepodites and adults) was negatively correlated with the density of this prey for Atlantic mackerel larvae 6 to <7 mm ( $P = 0.03$ ,  $n = 7$ ) but not significantly correlated with prey density for other length classes (5 to <6 and  $\geq 7$  mm,  $P \geq 0.67$ ).

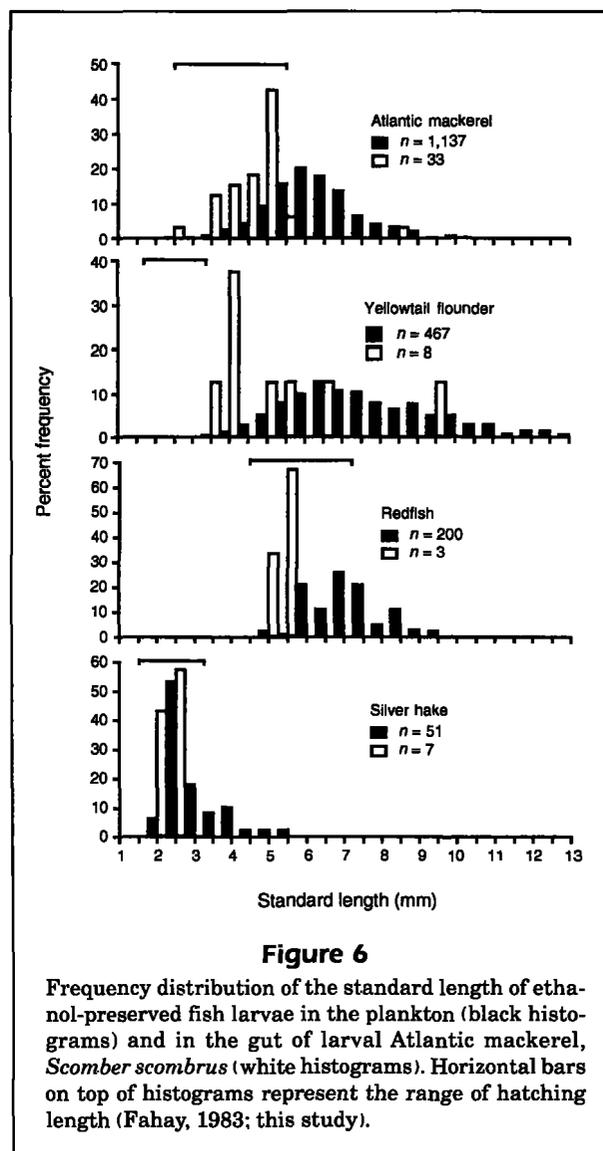
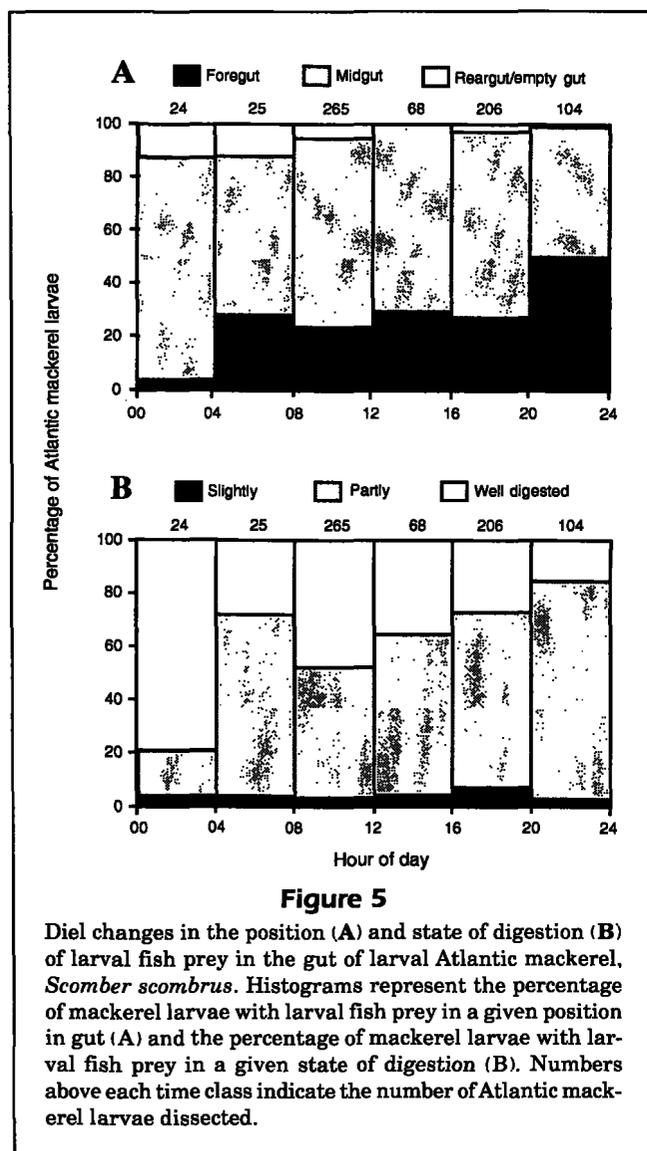
In RMT collections, the relationship between the incidence of piscivory (proportion of feeding Atlantic mackerel with at least one fish larva in the gut) and the density of fish larvae of suitable prey size (sum of Atlantic mackerels and redbishes  $\leq 5.5$  mm, yellowtail flounders  $\leq 6.5$  mm, and silver hakes  $\leq 2.5$  mm) was adequately described by an Ivlev equation (Fig. 7, A-C). Incidence of piscivory was limited at densities of larval fish prey  $< 0.1$  larvae/m<sup>3</sup> and quickly reached a plateau as availability increased. The height of the plateau (maximum incidence of piscivory) increased with predator length. The parameters of the Ivlev equation varied little when the data from the multi-net collections were added to the RMT data set (Fig. 7, D-F).

### Effect of alternative invertebrate prey on piscivory

In the present study, the absolute predation rate could not be assessed because the transit time for fish larvae

**Figure 4**

Daily feeding activity of larval Atlantic mackerel, *Scomber scombrus*. (A) Mean number (and standard deviation) of invertebrate prey per dissected gut. (B) Percentage of dissected mackerel larvae with at least one fish larva in the gut. Black histograms represent nighttime, gray histograms twilight, and white histograms daytime. Number above time class indicates the number of dissected mackerel larvae.



in the gut of Atlantic mackerel larvae is unknown. However, assuming a digestion time of 24 hours, a relative daily predation rate (PR, in %/d) was defined as the proportion of all fish larvae of suitable prey size in a sample that was found in the gut of Atlantic mackerel larvae:

$$PR = (NP_g \times 100) / (NP_g + DP),$$

where  $NP_g$  = the density of fish larvae in mackerel gut per  $m^3$  of water; and

$DP$  = the density of larvae of suitable prey size in the plankton per  $m^3$ .

Predation rate by Atlantic mackerel larvae 3–14 mm long ranged from 7% to 57%/d (average of 31%/d) of the standing stock of the newly hatched fish

larvae of suitable prey size (or 2% to 27%/d of all fish larvae). Daily predation declined linearly with increasing density of copepod nauplii (Fig 8A), the only other prey strongly selected for by Atlantic mackerel larvae (Table 4). Sample size for the regression was low (8) because few RMT collections (for which estimates of zooplankton density are available) contained enough Atlantic mackerel larvae to calculate a reliable index. Daily predation was not significantly correlated with the density of copepods ( $P=0.991$ ) or the combined density of nauplii and copepods ( $P=0.658$ ). Daily predation on fish larvae of suitable prey size decreased asymptotically as the average number of alternative copepod prey (nauplii + copepodites + adults) consumed by Atlantic mackerel larvae increased (Fig. 8B). The relationship was best described by a reciprocal model; 24% of the variance in daily

**Table 4**

Prey selectivity ( $\alpha$ , Chesson, 1978) in larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991.  $\alpha$  was calculated for each Atlantic mackerel larvae and averaged over length classes. A plus sign (+) indicates positive selection for prey ( $\alpha > 1/N = 0.2$ , where  $N = 5$  prey taxa). Only samples containing at least 10 Atlantic mackerel larvae were considered in the calculations.

Prey taxa	Length class (mm)					
	<5	5-6	6-7	7-8	8-9	≥9
Copepod nauplii	+0.70	+0.33	+0.27	0.06	0.01	—
Copepods <sup>1</sup>	0.02	0.12	0.14	+0.24	+0.32	+0.28
Appendicularians	+0.22	+0.29	0.14	0.14	0.08	0.04
Fish larvae	0.05	+0.26	+0.44	+0.49	+0.53	+0.61
Others <sup>2</sup>	0.01	<0.01	0.01	0.07	0.06	0.07
No. of mackerel larvae	98	203	183	184	113	44

<sup>1</sup> Copepodites and adult copepods.

<sup>2</sup> Includes euphausiids, chaetognaths, gastropods, cladocerans, amphipods, euphausiid nauplii, and crab larvae in order of decreasing frequency.

**Table 5**

Selectivity for copepod (nauplii, copepodites, and adults) prey size in larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991.  $\alpha$  (Chesson, 1978) was calculated for each Atlantic mackerel larva and averaged over length classes. A plus sign (+) indicates positive selection for size ( $\alpha > 1/N = 0.2$ , where  $N = 5$  size categories). Only samples containing at least 10 Atlantic mackerel larvae were considered in the calculations.

Copepod size ( $\mu\text{m}$ )	Length class (mm)					
	<5	5-6	6-7	7-8	8-9	≥9
< 300	+0.94	+0.64	+0.40	0.10	0.01	0.02
300 < 400	0.04	+0.22	+0.26	0.14	0.03	0.04
400 < 500	0.02	0.08	0.12	0.08	0.05	<0.01
500 < 600	—	0.04	0.11	+0.25	0.16	+0.28
≥600	—	0.02	0.11	+0.43	+0.75	+0.66
No. of mackerel larvae	93	165	129	101	61	17

predation rate was explained by the consumption of alternative copepod prey. When one outlier point was removed, the fraction of the variance explained by the model increased to 46% (Fig. 8B).

## Discussion

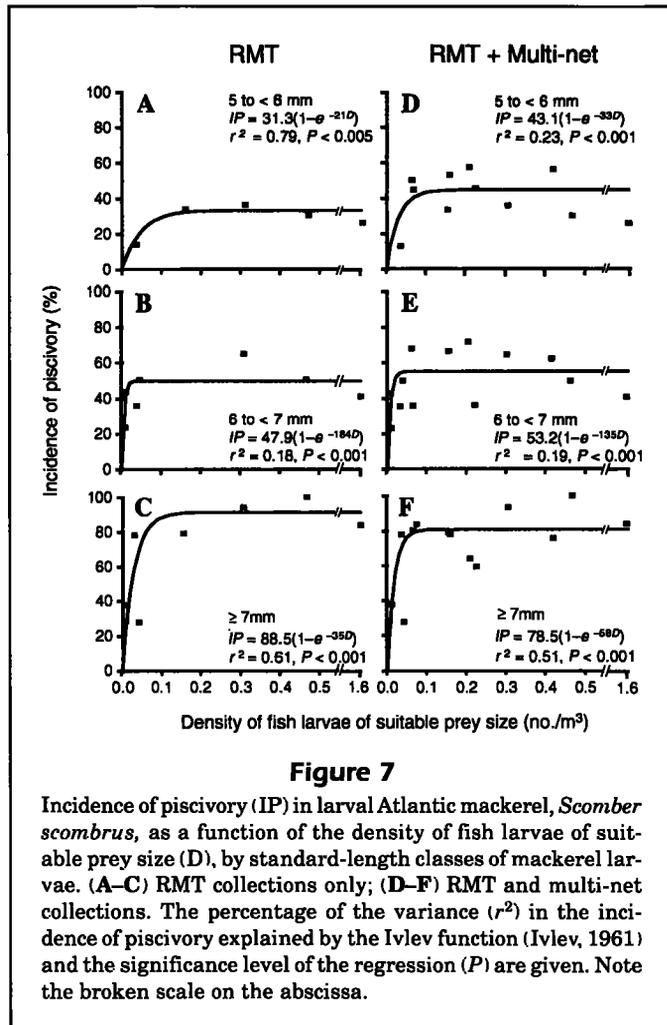
### Selectivity for fish larvae in Atlantic mackerel larvae

Over 50% of feeding Atlantic mackerel  $\geq 6$  mm had captured at least one fish larva despite the absolute and relative (to other prey) scarcity of fish larvae of suitable prey size in the plankton (on average 0.14 fish larva/ $\text{m}^3$  vs. 5,920 nauplii and copepods/ $\text{m}^3$ ). By comparison, copepods were preyed upon in proportion to their relative abundance in the plankton. On the basis of the small percentage of larval fish prey that could be

**Table 6**

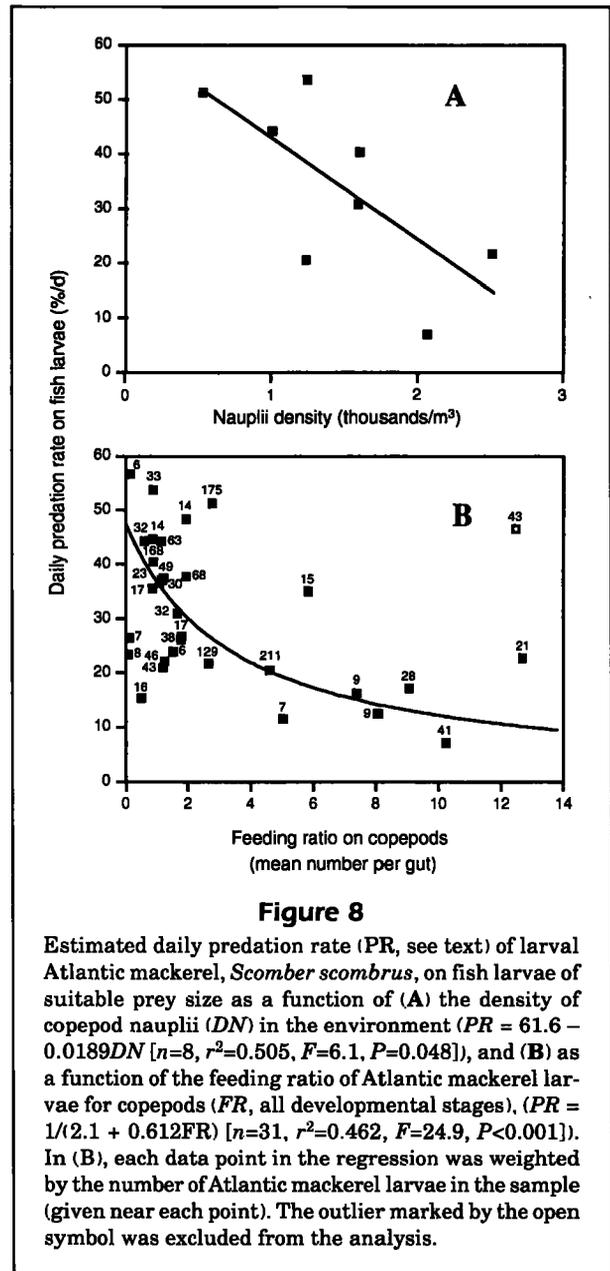
Species composition of larval fish prey found in the gut of larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991. Positive selection for prey ( $\alpha > 1/N = 0.25$ , where  $N = 4$  species of larval fish prey) is indicated by a plus sign (+).

	Silver hake	Yellowtail flounder	Atlantic mackerel	Redfish
Number identified visually	6	3	27	0
Number identified by otoliths	7	6	22	3
Total number identified	13	9	49	3
Percent of grand total	18	12	66	4
Selectivity index	0.18	+0.31	+0.34	0.21



identified (74 out of 710), Atlantic mackerel larvae exhibited little preference for any of the four dominant species of fish larvae available in July in the area studied.

Despite their relatively low frequency in the diet (2% to 16% by number), fish larvae represented an important fraction of the energy intake of Atlantic mackerel larvae. For example, most of the conspecifics ingested ranged from 3.0 to 5.5 mm in length, which translates into 20 to 200  $\mu\text{g}$  in dry weight (Table 3 in Peterson and Ausubel, 1984). By comparison, the approximate dry weight of copepod prey (0.1–0.6 mm in cephalothorax length) ranged from 0.006 to 2  $\mu\text{g}$  (Cohen and Lough, 1981). Thus, assuming that the nutritional value of copepods is four times that of fish larvae per unit biomass (Gotceitas and Brown, 1993), the energy intake represented by one fish larva corresponded to that of 2.5 to 25 of the largest copepods ingested. Pacific mackerel, *Scomber japonicus*, and Atlantic mackerel larvae are characterized by fast growth, high metabolism, and high food requirements (Hunter and Kimbrell, 1980; Peterson and Ausubel, 1984; Ware and



Lambert, 1985). The width of ingested fish larvae closely matches the mouth width of Atlantic mackerel larvae (Ware and Lambert, 1985), and fish larvae are the largest prey ingested (Grave, 1981; Ware and Lambert, 1985; this study). Hence, fish larvae probably represent the most profitable prey available in the plankton to satisfy the high food requirements of Atlantic mackerel larvae.

Piscivores generally select small prey in laboratory experiments and consistently ingest smaller than average prey in field situations, a potential reflection of an inability to capture larger prey (Juanes and Conover, 1994, and references therein). In the

present study, Atlantic mackerel larvae 3–14 mm long preyed primarily on newly hatched fish larvae (conspecifics and others). This suggests that in the days following hatching, fish larvae quickly acquire enough motility to escape attack from Atlantic mackerel larvae in this size range. Thus, the predation rates estimated in the present study (7% to 57%/d of the standing stock of larvae of suitable prey size) would apply only over the relatively short period before the development of an efficient escape response. Growth during this period would determine cumulative predation mortality from co-occurring Atlantic mackerel larvae 3–14 mm in length. In the laboratory, survival to metamorphosis in Pacific mackerel larvae was positively correlated with growth over the period during which sibling cannibalism occurred (Hunter and Kimbrell, 1980).

### Effect of prey density on predation by Atlantic mackerel larvae

Surprisingly few studies have related the feeding success of fish larvae in the sea to prey availability (Heath, 1992; Fortier et al., 1995). In the majority of these studies, there are indications that feeding was limited below some threshold density of prey. For example, the feeding ratio of larval Atlantic cod, *Gadus morhua*, was adequately described by an Ivlev equation, with feeding limited at nauplii concentrations <10/L (Ellertsen et al., 1989; Sundby and Fossum, 1990). The same model was used to describe stomach fullness and feeding incidence (proportion of predators with prey in the gut) in larvae of southern bluefin tuna, *Thunnus maccoyii*, as a function of zooplankton settled volume (Young and Davis, 1990; Heath, 1992). In this case, the feeding of larval tuna appeared limited at densities of approximately <0.5 prey/L (Heath, 1992). In ice-covered Hudson Bay, the feeding incidence and feeding ratio of Arctic cod, *Boreogadus saida*, and larvae of sand lance, *Ammodytes* sp. in relation to nauplii density were also adequately modeled by an Ivlev equation (Fortier et al., in press). Feeding was limited at densities <40,000 nauplii/m<sup>2</sup>, corresponding approximately to <1.6 nauplii/L. In large enclosures, the growth of larvae of capelin, *Mallotus villosus*, was related to prey biomass by a function resembling an Ivlev function (Frank and Leggett, 1982).

In the present study, there was no indication that predation on copepod nauplii and copepods by Atlantic mackerel larvae was dependent on the density of these prey in the environment. This may indicate that naupliar (261 to 4,134/m<sup>3</sup>) and copepod (1,170 to 7,190/m<sup>3</sup>) densities were at or above the level at which feeding Atlantic mackerel larvae saturated. However, the relationship between the incidence

of predation on fish and the density of fish larvae was adequately described by an Ivlev equation. Limitation began at prey densities <0.1 fish larva of suitable prey size per m<sup>3</sup>. This threshold was only slightly less than the mean density of fish larvae of suitable prey size (0.14 larva/m<sup>3</sup>), and predation on fish appeared limited in about 40% of our collections. Alternatively, Atlantic mackerel larvae preying on fish larvae appeared swamped by their prey in approximately 60% of the collections. Thus, the contracted production of large numbers of larvae in species such as yellowtail flounder and silver hake may reduce total cumulative predation by Atlantic mackerel larvae. Frank and Leggett (1982) suggested that the synchronized emergence of beach-spawned capelin larvae during onshore wind events in eastern Newfoundland resulted in the saturation of their predators and a reduction of percent predation mortality.

### Effect of alternative prey on cannibalism and piscivory by Atlantic mackerel larvae

Controlled studies have invariably reported that the presence of alternative prey provides fish larvae with some protection from larval, juvenile, or small-bodied adult fish predators. In the laboratory, the rate of cannibalism on larvae by juvenile Cape anchovy, *Engraulis capensis*, decreased in the presence of alternative copepod prey (Brownell, 1985). Bay anchovy juveniles preferred newly-hatched (2-d-old) sea bream, *Archosargus rhomboidalis*, but shifted to copepods when the density of the latter increased (Dowd, 1986). The presence of alternative copepod prey strongly protected larval Atlantic mackerel (Kean-Howie et al., 1988) and Atlantic cod (Gotceitas and Brown, 1993) from predation by the three-spine stickleback, *Gasterosteus aculeatus*. The addition of *Daphnia magna* reduced by five to tenfold the predation rate of juvenile bluegill, *Lepomis macrochirus*, on larval white perch, *Morone americana* (Margulies, 1990).

In the present study, we found some evidence that the presence of alternative prey reduced the predation by Atlantic mackerel larvae on fish larvae (Fig. 8). The daily predation rate on fish larvae of suitable prey size (assuming a digestion time of 24 h) declined with increasing density of copepod nauplii (the only other prey, along with fish larvae, selected for by Atlantic mackerel larvae), but not with an increasing density of copepods. The evidence for a reduction of predation was stronger when the actual consumption of alternative prey rather than their density was considered (Fig. 8). On average, the daily predation rate on fish larvae of suitable prey size was reduced from 47% to 12%/d when the average number of copepod prey in the gut of Atlantic mack-

erel larvae increased from 0 to >10 prey. Given that copepods were not selected for, it appears that the time spent manipulating them or the satiation resulting from their ingestion, rather than a switch in prey preference, interfered with the predation by Atlantic mackerel on newly hatched fish larvae.

### **The noncompensatory nature of cannibalism and piscivory by Atlantic mackerel larvae**

Cannibalism and interspecific predation have often been proposed as mechanisms for the density-dependent regulation of marine fish populations (Ricker, 1954; Rothschild, 1986). Because the probability of encounter between Atlantic mackerel larvae should increase with their density, Grave (1981) suggested that cannibalism could be a simple mechanism for the density-dependent (i.e. compensatory) regulation of year-class strength in this species. For compensatory mortality to occur, an increasing fraction of the prey population must be removed per unit of time as the abundance of prey increases. In the present study, the capacity of mackerel larvae 5–14 mm long to prey on conspecifics and other fish larvae increased initially (but at a decreasing rate) and then saturated quickly as prey density increased (Fig. 7). Our results suggest a type-II functional response (Holling, 1959) in which mortality is actually depensatory, a decreasing fraction of the prey population being removed per unit time as prey density increases. This would be the case when mackerel larvae prey on other species of fish larvae. In the case of cannibalism, percent mortality is expected to remain constant (i.e. density-independent) with increasing density of Atlantic mackerel larvae because both prey and predators increase in number.

As predation on other fish larvae appears density-dependent and cannibalism seems density-independent, we conclude that piscivory by Atlantic mackerel larvae 3–14 mm long does not contribute to the density-dependent regulation of population size. In the laboratory, cannibalism by Pacific mackerel ceased when schooling developed at the time of metamorphosis (approximately 15.2 mm SL) (Hunter and Kimbrell, 1980). In St. Georges Bay, the longest Atlantic mackerel cannibal observed was 15.2 mm (Ware and Lambert, 1985), but Grave (1981) reported intense cannibalism in early juveniles 13–19 mm SL in the North Sea. Whether piscivory by Atlantic mackerel >14 mm SL is compensatory remains to be determined.

### **Potential impact of cannibalism and piscivory by Atlantic mackerel larvae on recruitment**

While predation on conspecifics and other species of fish larvae by Atlantic mackerel larvae <14 mm is

not compensatory, the resulting mortality may nevertheless have some important impact on year-class strength. The latitudinal and vertical distributions of Atlantic mackerel, yellowtail flounder, and silver hake larvae generally coincided on Sable Island Bank, and predation or cannibalism by mackerel larvae could be of significance during the early life of these species. As mentioned earlier, the actual mortality rate attributable to predation by Atlantic mackerel larvae cannot be determined without an estimate of the transit time of fish larvae in the gut. In the laboratory, half the gut content of Pacific mackerel larvae fed *Brachionus plicatilis* was evacuated in 2 h (Hunter and Kimbrell, 1980). In the North Sea, digestion time (from food intake to complete defecation of the last food remains) for Atlantic mackerel larvae 8–14 mm, feeding on copepods, cladocerans, and conspecifics was 8–10 h (Grave, 1981).

In the present study, there were several indications that the digestion of fish larvae by Atlantic mackerel larvae was a relatively slow process. First, a single fish larva was found in the gut of mackerel larvae in 97% of the cases. Second, the frequency of larval fish prey in the gut increased progressively during the day (Fig. 4), an unlikely result if digestion and evacuation were rapid. Third, the proportion of fish larvae in the fore- and midgut of mackerel larvae remained high during the day, suggesting a slow transit time due to the large size of the prey (Fig. 5). Finally, the high frequency of partly or well-digested fish larvae (>90%) in contrast to slightly digested material, also suggested that fish larvae remained for a long time in the gut. All our observations are consistent with a continuous search for fish larvae, saturation of the digestive tractus upon the capture of a larva, slow digestion completed during the night, and evacuation in the early morning. Thus, although the time between capture and complete assimilation of a fish larva could be faster than we estimate, our results suggest a digestion time of 24 h.

The impact of predation by Atlantic mackerel larvae was limited primarily to newly hatched fish larvae. Assuming a conservative 24 h for the time between capture and evacuation, the percent mortality rate of fish larvae of suitable prey size attributable to predation by Atlantic mackerel larvae ranged from 7% to 57%/d (average of 31%/d). A value of 8 h for digestion time (Grave, 1981) would triple these estimates. Recent studies have often reported high mortality rates for the period just before and after yolk resorption when the swimming abilities of the fish are still poorly developed: 80%/d in jack mackerel, *Trachurus symmetricus* (Hewitt et al., 1985), 56% and 60%/d in capelin (Fortier and Leggett, 1985; Taggart and Leggett, 1987). For Atlantic mackerel,

Kendall and Gordon (1981) calculated an average mortality rate of 35%/d (SD=20%/d) for larvae <13 mm, whereas Ware and Lambert (1985) reported a rate of 42%/d for larvae <8 mm. Thus, according to our conservative estimate of digestion time, predation by Atlantic mackerel larvae (average 31%/d) would represent a sizable fraction (>38%) of the total mortality typically experienced by newly hatched larvae in the sea. This is consistent with an estimate of 41% for the fraction of the total mortality of newly hatched bay anchovy that could be attributed to predation by medusae (Purcell et al., 1994). According to our highest estimate (average 93%/d), predation by Atlantic mackerel larvae could wipe out populations of newly hatched co-occurring species in a few days, and all the mortality of newly hatched Atlantic mackerel could be attributed to cannibalism.

Atlantic mackerel larvae can dominate the larval fish assemblage over large areas in spring and early summer. For example, the species represented from 62.2% to 76.9% of the ichthyoplankton in the neritic, transitional, and oceanic zones of the Celtic Sea in the spring of 1980 (Horstman and Fives, 1994). We conclude that, in these areas, predation by Atlantic mackerel larvae could represent a significant survival bottleneck for co-occurring species in the days after hatching.

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