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ORIGINAL ARTICLE

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Small-scale patterns in distribution and feeding of Atlantic mackerel (*Scomber scombrus* L.) larvae in the Celtic Sea with special regard to intra-cohort cannibalism

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Abstract Short-term variability in vertical distribution and feeding of Atlantic mackerel (*Scomber scombrus* L.) larvae was investigated while tracking a larval patch over a 48-h period. The patch was repeatedly sampled and a total of 12,462 mackerel larvae were caught within the upper 100 m of the water column. Physical parameters were monitored at the same time. Larval length distribution showed a mode in the 3.0 mm standard length (SL) class (mean abundance of 3.0 mm larvae $\bar{x}$=75.34 per 100 m^3, s=34.37). Highest densities occurred at 20–40 m depth. Larvae <5.0 mm SL were highly aggregated above the thermocline, while larvae ≥5.0 mm SL were more dispersed and tended to migrate below the thermocline. Gut contents of 1,177 mackerel larvae (2.9–9.7 mm SL) were analyzed. Feeding incidence, mean number (numerical intensity) and mean dry weight (weight-based intensity) of prey items per larval gut were significantly dependent on larval size. However, while weight-based feeding intensities continued to increase with larval length, numerical intensity peaked at 4–4.9 mm SL, indicating a shift in the larval diet. While first-feeding larvae relied most heavily on copepod nauplii and eggs, larvae ≥5.0 mm SL initiated piscivorous feeding. All identifiable fish larvae were Atlantic mackerel. Thus, the piscivory was cannibalism. Larval feeding incidence and numerical feeding intensities peaked during daytime and were reduced at night. Daily ration estimates for first-feeding mackerel larvae <4.0 mm SL were extremely low $\bar{x}$=1.43% body dry weight, but increased dramatically at 5.0 mm SL, i.e., at the onset of cannibalism, reaching >50% body dry weight in larva ≥8.0 mm SL.

Keywords Mackerel larvae · Vertical distribution · Diet · Diel patterns · Cannibalism

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Introduction

In the eastern Atlantic, the highest densities of Atlantic mackerel (*Scomber scombrus*) larvae appear in the Celtic Sea and above the Celtic Shelf in May/June (O'Brien and Fives 1995), where the larvae hatch at the onset of the secondary productivity maximum (Colebrook 1986) into a stratified water column (Hillgruber et al 1997). The diet of mackerel larvae has been described in several papers; however, most studies investigated the western populations of the North Atlantic (Sette 1943; Lett 1980; Peterson and Ausubel 1984; Ware and Lambert 1985; Fortier and Villeneuve 1996), while little information exists about the eastern Atlantic populations, namely larvae from the North Sea (Lebour 1920; Last 1980; Grave 1981) and larvae from the European shelf edge – the western stock (Hillgruber et al. 1997; Conway et al. 1999). To date no consecutive sampling effort directed at Atlantic mackerel of the western stock as the primary target has been published.

Atlantic mackerel, like other scombrids, are characterized by high growth rates in the larval stage, reaching 0.8 mm day^{-1} in larvae 6.0–8.0 mm in length (Ware and Lambert 1985) or 1.2 mm day^{-1} for larvae of 10–20 days old (Kendall and Gordon 1981). While larvae might benefit from high growth rates by reducing the period of susceptibility to predation, they have to satisfy an increasing metabolic demand to sustain their growth. Hunter and Kimbrell (1980) estimated a daily ration of 87% body dry weight, or 165–538 rotifers day^{-1} for 3–4 day-old Pacific mackerel (*Scomber japonicus*). Instead of ingesting increasing numbers of small prey items, however, mackerel larvae appear to attempt to utilize a more efficient food source, namely fish larvae. All

but one study (Last 1980) targeting Atlantic mackerel larvae observed piscivorous and cannibalistic foraging behavior (Lebour 1920; Grave 1981; Peterson and Ausubel 1984; Ware and Lambert 1985; Fortier and Villeneuve 1996; Hillgruber et al. 1997; Conway et al. 1999). However, disagreement still exists as to the nature of this feeding mode, i.e., is it a density-dependent behavior (Fortier and Villeneuve 1996) or a feeding mode that the larvae are predisposed to by morphological adaptations (Tanaka et al. 1996; Conway et al 1999).

Feeding success in marine fish larvae is largely dependent on light (Paul 1983; Blaxter 1986) and larval feeding activity often follows a diel pattern as to quantity and composition of prey in the gut (Conway et al. 1998; MacKenzie et al. 1999; Hillgruber and Kloppmann 2000). While sufficient illumination is of primary importance, other factors have been suggested to affect larval feeding success, e.g., small-scale turbulence (Rothschild and Osborn 1988; Dower et al. 1997), temporal and spatial overlap between predator and prey (Lasker 1975; Cushing 1990), length-specific changes in predator prey capture success and preference, and prey visibility and escape capability (Buskey et al. 1993). The plethora of these factors suggests that large within-population variability in larval feeding success may be expected. Only a study that employs a small temporal and spatial resolution sampling strategy can detect these differences.

In this study we investigate small-scale variability in prey abundance and foraging patterns of Atlantic mackerel larvae by re-sampling a patch of larvae, while concurrently monitoring physical parameters over a period of 48 h. Particular focus is placed on light as a factor mediating vertical distribution and feeding patterns in mackerel larvae. In addition, the incidence of piscivorous feeding is investigated and discussed.

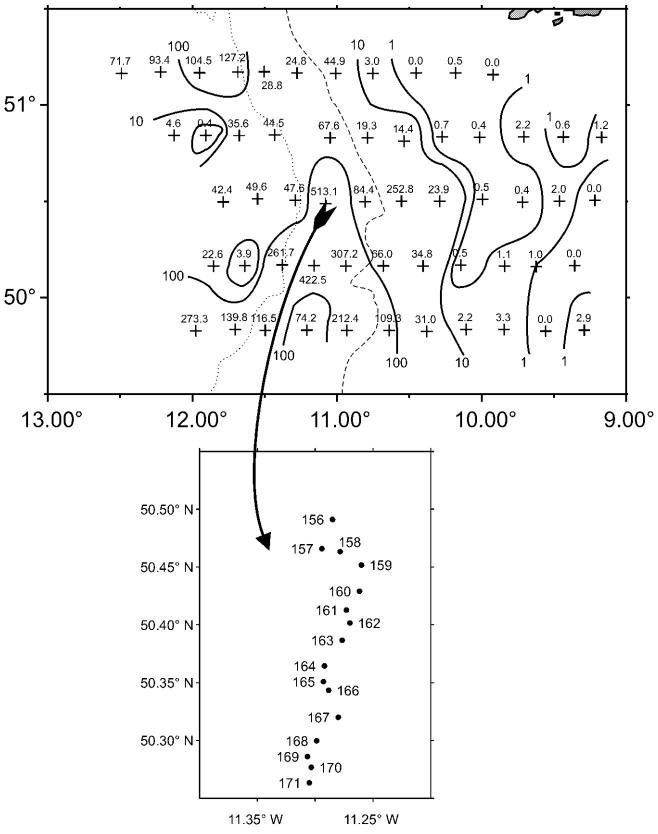

Fig. 1 Study area to the southwest of Ireland. *Numbers* indicate mackerel larvae abundance ($n \cdot m^{-2}$) per station. *Box* indicates location of the drift study. *Numbers* in the lower panel indicate path of the drifter during the 2-day drift study and location of sampling stations along the drift path

Methods

Study site and shipboard methods

General

Data for this study were collected off R.V. "Heincke" in June 1995 in an area of the Celtic Shelf, south-west of Ireland (Fig. 1). Exploratory sampling was conducted on a station grid in order to locate a high density of mackerel larvae. The highest concentration of mackerel larvae was marked with a drifter attached to a drogue at 30 m depth. The drogue consisted of four 2 m^2 (0.5×4.0 m) crosswise arranged rectangular Dacron sails (Kloppmann 1994). The position of the drifter was recorded hourly. During a 2-day drift study (9–11 June), sampling for mackerel larvae and associated plankton and environmental sampling were conducted every 3 h within the vicinity of the drifter, providing data on diurnal periodicity of the distribution and feeding of mackerel larvae.

Environmental sampling

True wind speed and direction were calculated from measurements of apparent wind speed and direction recorded every hour by a masthead anemometer and the ship's speed and direction.

At each station, physical data were recorded to a depth of 100 m using a CTD system. Light intensities in the water column were measured in terms of irradiance at the midpoint of each multiple opening-closing net (MCN) depth stratum (i.e., at 90, 70, 50, 30 and 10 m) using a LI-COR photometric sensor that was attached to the CTD system. Nothing is known about the feeding threshold irradiance value of Atlantic mackerel larvae. However, for other fish larvae threshold values have been estimated between 0.15 and 0.3 lux (Blaxter 1968; Paul 1983; Heath 1989) which, according to a conversion routine used by Fox et al. (1999) equals irradiance values between 0.003 and 0.005 µE m^{-2} s^{-1}. At these irradiance levels, measurements made with the submersible LI-COR system are unreliable due to noise inherent in the system (Jeffrey S. Briggs, LI-COR, personal communication). Therefore light measurements were only carried out during daytime hours.

Biological sampling

The CTD was connected to a rosette sampler and physical data were recorded at every 0.5 dbar pressure increment on the downcast. Water was collected on the up-cast, at the midpoint of each MCN interval in 10-l Niskin bottles connected to the rosette sampler. The water was passed through a 45 µm sieve and the organisms retained were preserved in 4% buffered formalin–seawater solution. For convenience, we use the term microzooplankton to refer to the retained taxa. Because late stage and adult copepods have well-developed escape responses, they may have escaped capture with the water bottles and their densities are, thus, likely to be underestimated.

Ichthyoplankton was collected using an obliquely towed MCN (0.25 m^2 opening, 300 µm mesh), coupled with a continuous tem-

Table 1 Statistics of the amount of sea-water filtered (in m^3) per each net of the MCN during the 48-h drift study

	Mean	SD	Median	Maximum	Minimum	*n*
Net 1	53.46	13.80	57.38	71.18	34.13	17
Net 2	59.90	14.96	59.40	84.00	37.35	17
Net 3	45.74	9.75	46.18	60.71	27.17	17
Net 4	40.47	18.01	37.45	89.33	22.52	17
Net 5	61.99	12.68	60.38	94.43	41.48	17

perature, salinity and depth monitoring system. Larval abundance and length frequency data provided by the MCN have been proven similar to those acquired using a Bongo net (Kloppmann 1994). The MCN was lowered to a depth of 100 m and the first net was opened at depth. On the up-cast, the nets were opened consecutively, each sampling a 20 m depth interval, namely 100–80, 80–60, 60–40, 40–20 and 20–0 m. The mean amount of water filtered by each net is given in Table 1. Towing speed during up-cast was between 2.0 and 2.8 knots. Upon retrieval of the gear, each net was carefully hosed down, the samples rinsed into 300 µm sieves, then preserved in 4% buffered formalin–seawater solution.

For the analysis of dry weight, mackerel larvae were collected on brief oblique tows to 40 m depth using a 60 cm diameter Bongo net. Live larvae were immediately removed from the plankton sample, identified and measured to the nearest 0.1 mm standard length (SL) using a microscope fitted with an ocular micrometer. They were then placed into pre-weighed zinc-capsules and immediately frozen at –35°C for subsequent laboratory freeze-drying and measurement of dry weight. Time from recovery of the sampling gear to preservation of the larvae did not exceed 15 min.

Laboratory analyses

All fish larvae were subsequently sorted from the preserved MCN samples. Mackerel larvae were identified and counted and a subsample was measured to the nearest 0.1 mm SL as described above. No correction was made for larval shrinkage due to net-capture or fixation.

For dietary analyses, mackerel larvae were subsampled from 1.0 mm length categories, namely <4.0, 4–4.9, 5–5.9, 6–6.9, 7–7.9 and ≥8.0 mm SL. If sufficient numbers were available, a minimum of five feeding larvae per length category, depth and station were examined. Each larva was placed on a microscope slide, the whole alimentary canal dissected and the gut opened in a drop of glycerin. Each gut item was identified to the lowest possible taxon and measured to the nearest 0.01 mm. Dimensions measured were diameter for eggs, total length, carapace length and width for copepod nauplii, copepodite stages and adult copepods, standard length for fish larvae and width and length for all other items (Hillgruber et al. 1995). Prey volumes were calculated using those measurements and wet weights were estimated. Assuming an 87% water content for copepods (Hunter 1981; Lovegrove 1966 cited therein), wet weight was transformed to dry weight estimates. Dry weight of whole ingested mackerel larvae was estimated from regression equations obtained from our own dry weight measurements. If only pieces of fish prey were found, an average weight of 35.9 µg was assumed, which represents the average weight of all whole ingested mackerel larvae.

The whole microzooplankton sample was analyzed if it contained approximately 100 copepod nauplii. The whole sample was sieved through a 45 µm mesh, rinsed with fresh water to remove the formaldehyde and transferred into a graduated flask. The sample was stirred and an exact amount was extracted to provide approximately 100 copepod nauplii. When subsampling was necessary, we still counted the whole sample for copepod eggs, copepod nauplii, copepodite stages and adult copepods, while only the subsample was identified under the stereomicroscope to the lowest possible taxon and developmental stage and measured to the nearest 0.01 mm. Measurements taken were the same as those made for the gut contents.

Statistical analyses

Physical data

In order to obtain a measure of the wind-induced impact on feeding success, wind generated energy dissipation rate ε was estimated (MacKenzie and Leggett 1993):

$$\log_{10} \varepsilon = 2.688 \times \log_{10} W - 1.322 \times \log_{10} z - 4.812$$

where W is the wind speed in m s^{-1} and z the water depth in m. To compare the resulting values of ε in W m^{-3} with literature data given in cm^2 s^{-3}, ε was multiplied by a factor of $10^4/\rho$ (Kiørboe and Saiz 1995; see also Fox et al. 1999), ρ being the density of local seawater (1,027 kg m^{-3}).

Biological data

Density of mackerel larvae from the MCN samples was computed as number per 100 m^3. Regression analysis was carried out on length frequency distribution of mackerel larvae for possible length dependent instantaneous mortality rates.

Prior to statistical testing of numerical and weight-based feeding intensity, data were checked for violations of ANOVA. Normal probability plots were used to determine if data were normally distributed. Homoscedasticity was examined by plotting means against variances. Departures from the assumption of homoscedasticity were corrected by transforming data (Sokal and Rohlf 1981). Numerical feeding intensity variates were $\sqrt{(x+1)}$, weight-based feeding intensities were log(x*100) transformed.

Feeding patterns in regard to larval size were analyzed separately for 1 mm SL categories (<4.0, 4.0–4.9, 5–5.9, 6–6.9, 7–7.9 and ≥8.0 mm SL). Changes in the morphology of the feeding apparatus of fish larvae are an important prerequisite for dietary alterations (Hunt von Herbing et al. 1996). In mackerel larvae, the development of dentition at 5.0 mm SL has been suggested to support the transition in the larval diet from copepods to larval fish prey (Conway et al. 1999). Besides length-dependent feeding, all other dietary patterns in this study were analyzed for two larval length categories, namely larvae <5.0 mm and larvae ≥5.0 mm SL.

Feeding incidence was calculated as the proportion of larvae containing at least one food particle. Chi-square tests of independence were used to test the null hypothesis that larval feeding incidence was uniform with respect to time of day, depth and length category. The mean number of food items per larval gut (= numerical feeding intensity) and the mean weight of food items per larval gut (= weight-based feeding intensity) were calculated for each feeding fish larva, i.e. each larvae with at least one food item ingested. The null hypothesis that feeding intensities were uniform with time of day, depth and size class was tested with ANOVA. If significant differences were detected, Tukey's and Scheffé's multiple comparison procedures were used to test for pairwise relationships.

Feeding selectivity (L) was estimated using ln(L) of the Odds Ratio (O) as a measure of selectivity (Gabriel 1978; Hillgruber et al. 1995):

$$L = \ln(O) = \ln\left(\frac{p_1 * q_2}{p_2 * q_1}\right)$$

where p_1 is the proportion of diet comprised by a given prey taxon, p_2 is the proportion of food item in the environment comprised by a given taxon, q_1 is the proportion of diet comprised by all other taxa and q_2 is the proportion of food in the environment comprised by all other taxa. This selectivity index is symmetrically distributed around a mean of zero, ranging from zero to +∞ in case of positive selection, and from zero to –∞ in case of negative se-

lection. Since L has a log-normal distribution, the null hypothesis that an observed L is not significantly different from zero, and prey therefore were consumed non-selectively, can be tested (Gabriel 1978; Hillgruber et al. 1995).

Daily ration estimates are usually a function of gut passage times. However, few and disparate estimates exist as to the duration of gut passage in mackerel larvae. In a study on mackerel larvae from Long Island Sound, a digestion time of 1–2 h was proposed (Peterson and Ausubel 1984). However, since gut passage times are highly dependent on temperature and because sea-surface temperature during that study ranged from below 5°C to well above 15°C, it appears that the suggested gut passage time of 1–2 h cannot be generally applied. In comparison, Atlantic mackerel larvae in the North Sea completely evacuated their guts in 8–10 h at a water temperature of 15°C (Grave 1981). In the present study evacuation rates were estimated for two larval size classes, namely <5.0 and ≥ 5.0 mm SL by computing regressions between feeding incidence and time after ingestion (i.e., 2100 hours, time of sunset) using exponential models. The following equations were obtained for the estimated exponential evacuation rate (r) at a water temperature of 12.8–13.0°C:

larvae < 5.0 mm SL $r=0.6728*e^{-0.1952t}$; $r^2=0.68$, $n=9$, $P<0.0001$

larvae ≥ 5.0 mm SL $r=0.8261*e^{-0.119t}$; $r^2=0.50$, $n=11$, $P<0.0001$.

The different estimates for the two larval size classes appear justified, because mackerel larvae switch at 5.0 mm SL to piscine prey (Hillgruber et al. 1997), which are likely to need more time for digestion. Based on these digestion times, daily ration estimates were calculated using the Elliott and Persson (1978) model:

$$C_{\Delta t} = \frac{(\overline{W_t} - \overline{W_{t-1}} * e^{-rt}) * rt}{1 - e^{-rt}}$$

where $C_{\Delta t}$ is the food consumption between sampling periods t and t–1, and W is the average larval gut weight estimated as percentage bodyweight at sampling period t and t–1, while r is the above mentioned estimated exponential evacuation rate. Daily ration was estimated for the complete potential feeding period from sunrise (0600 hours) to sunset (2100 hours).

Results

Hydrography and meteorology

During the 2 days of the drift study (9–11 June 1995), strong northerly winds, force 5 – 7, prevailed. Wind speeds varied between 9.5 and 16.7 ms^{-1} (Fig. 2a). Wind generated turbulent energy dissipation at the depth of maximum mackerel larvae density was always $\varepsilon > 10^{-3}$ cm^2 s^{-3}, values that proved to be suboptimal for larval blue whiting feeding (Hillgruber and Kloppmann 2000; Fig. 2b).

Over the entire period of the drift study, the drifter was transported southwards (Fig. 1). Displacement, however, was not dependent on wind stress (Hillgruber et al. 1997), but appeared to follow a generally southward directed drift in that area (Mohn 2000; Bartsch and Coombs 1997).

At the time of the drift experiment, sea surface temperature in the sampling area was between 12.8 and 13.1°C. Analyses of vertical temperature distribution revealed a thermocline of about 2°C between 40 and 60 m depth. The depth of the thermocline showed a tidal response (Hillgruber et al. 1997; Fig. 3).

Light measurements during the drift study indicated an average daytime period of 17 h. During daytime, light intensity ranged from 0.08 $\mu E \cdot m^{-2} \cdot s^{-1}$ to 711 $\mu E \cdot m^{-2} \cdot s^{-1}$ in the upper 100 m of the water column (Fig. 4). At depth of maximum mackerel larvae density (20 – 40 m, see below) daytime light intensities varied between 1.44 and 79.46 $\mu E \cdot m^{-2}$ s^{-1} with maximum values occurring around noon. Light intensities were distinctly lower on the second day of the drift study, due to a mostly overcast sky.

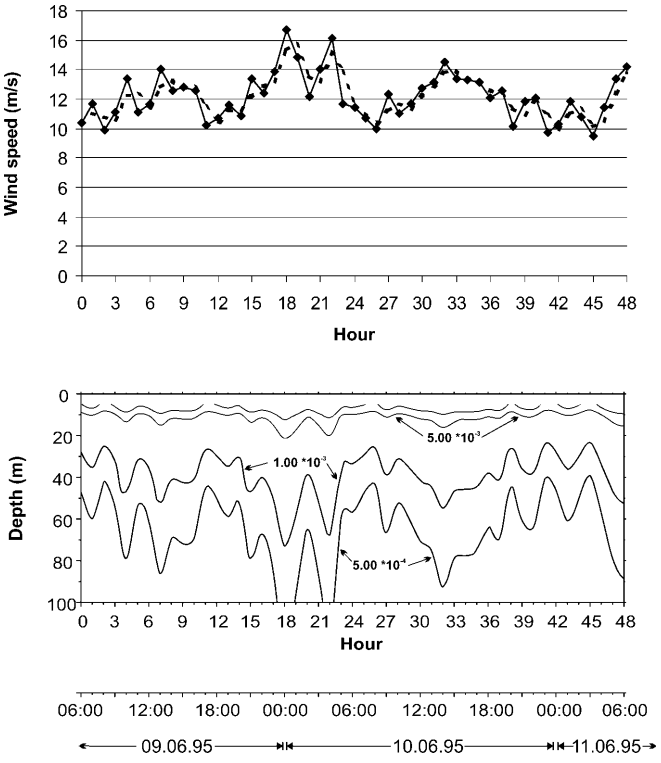

Fig. 2 **a** Observed wind speed (ms^{-1}) during the 2-day drift study, 9–11 June 1995. *Hatched line* indicates the 2-hourly mean wind speed. **b** Estimated turbulent energy dissipation (ε) profile (cm^2 s^{-3}) during the 2-day drift study, 9–11 June 1995

Larval distribution

A total of 12,462 mackerel larvae were caught within the upper 100 m of the water column, resulting in a mean density of 337.0 mackerel larvae per 100 m^3 averaged over the sampled 100 m depth (s=102.0; median = 309.5; range: 212.6–638.9). Most larvae were found in the upper 60 m of the water column with highest larval densities between 20 and 40 m depth. The majority of mackerel larvae <5 mm SL occurred in the 20 – 40 m depth stratum (Fig. 5). At depth of maximum abundance (20 – 40 m) mean density was 1,096.8 larvae per 100 m^3 (SD=412.5; median = 978.2; range: 646.6–2,256.5). Measured length of larvae ranged from 2.0 to 8.5 mm SL and showed a mode in the 3.0 mm length class. Mean abundance of these 3.0 mm larvae was 75.34 per 100 m^3 (s=34.37; median = 70.97; range: 27.16–151.44).

There was an exponential decline in larval density from the 3.0 mm length class onwards (Fig. 6; Table 2).

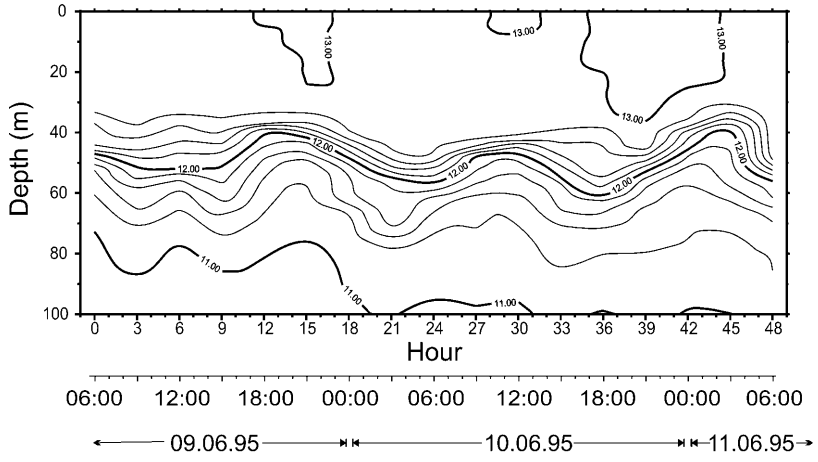

Fig. 3 Vertical temperature profile throughout the drift study, 9–11 June 1995

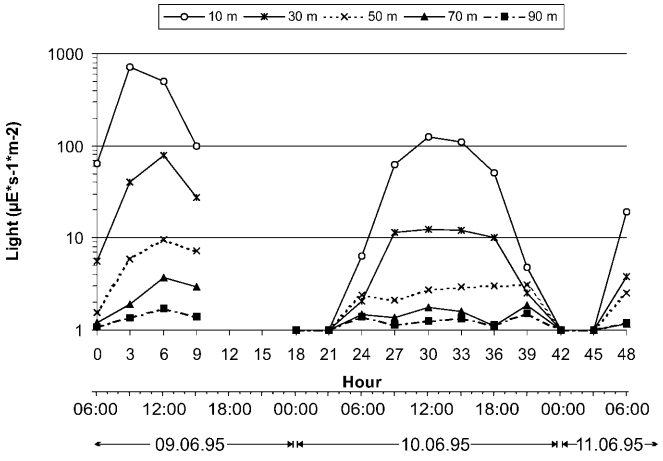

Fig. 4 Vertical profile of light intensity (µE $m^{-2}s^{-1}$) during the 2-day drift study, 9–11 June 1995

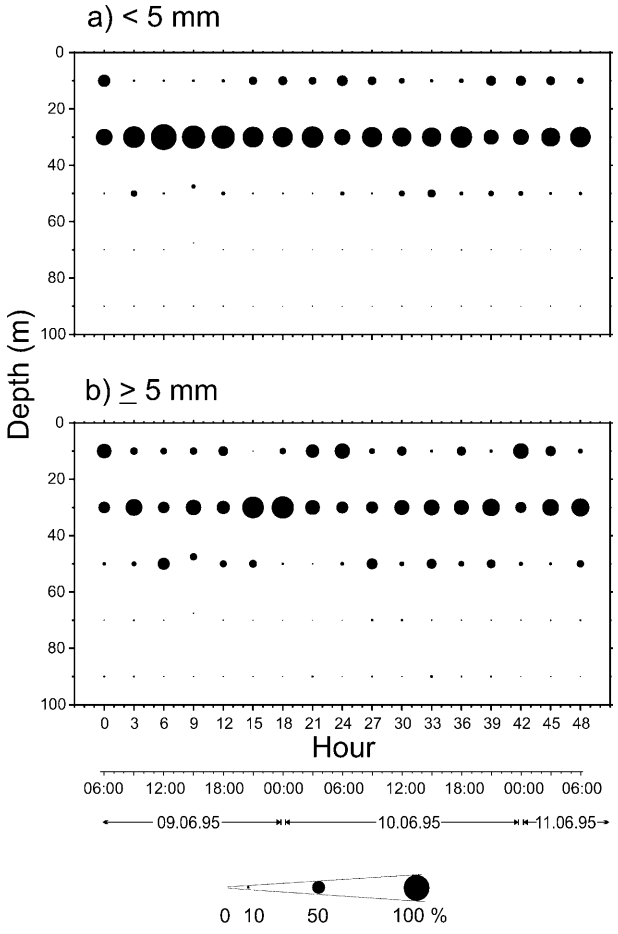

Fig. 5 Relative vertical distribution of mackerel larvae <5.0 (**a**) and ≥5.0 mm SL (**b**) during the drift study, 9–11 June 1995. Size of each bubble is proportional to the relative abundance of larvae per each depth stratum

The mean density of piscivorous or cannibalistic (see below) larvae ≥5.0 mm SL was only 75.66 per 100 m^3. Mean density of non-piscivorous larvae <5.0 mm SL was 261.33 larvae per 100 m^3. Their density at depth of maximum abundance (20–40 m) ranged between 590.4 to 1,971 larvae per 100 m^3 (mean = 975.2; SD=362.0; median = 824.4). There was a conspicuous decline in larval abundance from 7.5 mm SL onwards, suggesting that these larvae had better capabilities to avoid the sampler. At this length – regarding shrinkage due to preservation – flexion of the urostyle is almost completed (Russell 1976) and should enable the larva to obtain higher burst swimming speeds. A comparison of length frequency distributions for both sampling days showed that the densities of larger larvae in particular were lower on the second day (Table 2). The differences, however, were not significant (Kolmogorov-Smirnov test, $P>0.1$). Thus, assuming a quantitative catch efficiency of the MCN for mackerel larvae between 3 and 7 mm preserved SL, the regression corresponding to the length frequency distribution pooled over both days

$$D=421.171*e^{-0.568l},\ r^2=0.9555,\ p<<0.0001$$

with D = density and l = standard length in mm, suggests an instantaneous mortality rate of about 43.3% per each 1 mm increment SL.

Table 2 Mean abundance (larvae per 100 m^3) of each 0.5 mm standard length class mackerel larva for each day of the drift study

Length class (mm)	Day 1					Day 2				
	Mean	SD	Median	Min	Max	Mean	SD	Median	Min	Max
2.0	5.6	10.2	1.9	0.0	29.9	5.3	5.2	3.8	0.0	15.1
2.5	27.0	35.3	16.5	0.6	110.6	36.3	9.9	38.9	15.4	49.0
3.0	77.7	40.8	74.8	27.2	151.4	73.0	29.2	66.1	37.1	123.7
3.5	82.9	41.8	76.4	43.6	168.6	60.6	20.5	61.6	27.3	84.1
4.0	52.4	19.2	45.3	30.2	91.7	39.5	18.6	34.0	17.6	74.6
4.5	36.7	13.4	41.4	15.9	56.2	25.7	11.7	22.4	9.5	44.2
5.0	28.3	20.4	25.7	5.9	64.4	15.5	11.2	11.9	6.2	40.1
5.5	19.8	7.9	19.3	9.5	29.8	7.9	5.9	6.5	2.0	17.9
6.0	18.2	9.9	15.7	6.6	38.9	7.6	6.1	6.0	0.7	18.3
6.5	17.2	9.9	13.9	5.6	30.5	4.5	4.1	3.4	0.0	11.5
7.0	10.2	8.6	10.0	0.8	23.6	10.2	10.4	6.0	0.7	24.5
7.5	5.1	4.9	3.3	0.6	13.5	0.7	0.9	0.3	0.0	2.4
8.0	1.6	2.4	0.3	0.0	6.7	2.0	4.4	0.3	0.0	12.8
8.5	0.7	0.7	0.8	0.0	1.8	1.1	2.8	0.0	0.0	8.1
9.0	0.0	0.0	0.0	0.0	0.0	0.9	2.1	0.0	0.0	6.1
9.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

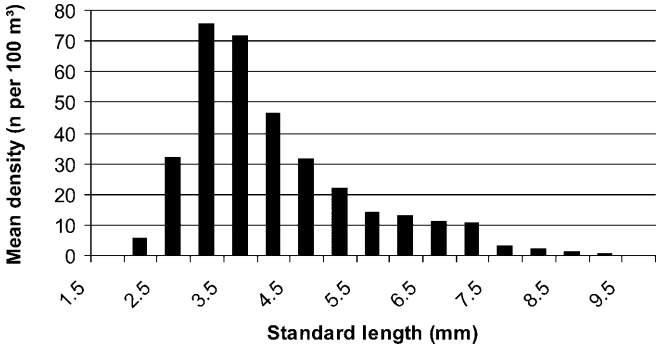

Fig. 6 Mean abundance per each 0.5 mm standard length class of mackerel larvae during 2-day drift study, 9–11 June 1995

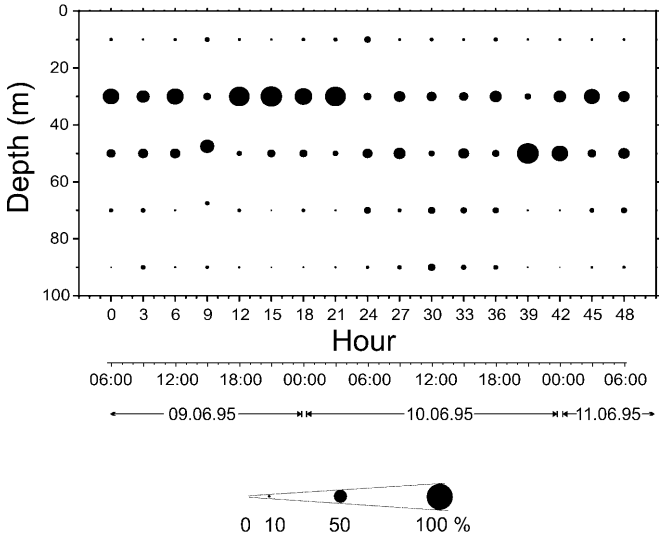

Fig. 7 Relative vertical distribution of other fish larvae during the drift study, 9–11 June 1995. Size of each bubble is proportional to the relative abundance of larvae per each depth stratum

At night an indication of a migration towards the surface near stratum could be detected. No larvae <5 mm SL descended below the thermocline. While larvae ≥5.0 mm SL were more dispersed, they were also most abundant at 20–40 m depth. However, the larvae were not completely restricted by the thermocline and frequently occurred at depth >60 m. There was also a slight indication of a diurnal vertical migration with larvae being found nearer the surface at night.

Other fish larvae

Mackerel larvae were by far the most abundant species sampled. However, a considerable amount (about 32%, mean 159.4 larvae per 100 m^3; SD=55.6; range: 72.8–264.2 larvae per 100 m^3) of the total ichthyoplankton belonged to other species, predominantly larvae of the mesopelagic *Maurolicus muelleri* and *Benthosema glaciale*. In contrast to the mackerel larvae, vertical distribution of these larvae was more dispersed and generally slightly deeper in the water column (Fig. 7). At 20–40 m depth their density was significantly lower than that of the smaller mackerel larvae (*t*-test, t=5.9650, $P<<0.0001$) and reached a mean value of only 355.3 larvae per 100 m^3 (SD=227.7; median = 282.1; range: 83.0–802.7).

Prey environment

Copepod nauplii dominated the microzooplankton. Distribution of microzooplankton taxa was dependent of sampling depth, with highest numbers occurring above the thermocline. Differences in density between sampling depth were highly significant for copepod eggs (F=16.986, $P\leq0.001$), copepod nauplii (F=71.562, $P\leq0.001$) and copepodite stages and adult copepods (F=60.101, $P\leq0.001$). A pairwise comparison revealed

Table 3 Density of microzooplanktonic prey taxa (number per liter) in the water column. Averages are given for taxa above the thermocline (depth strata 10 and 30 m), and below the thermocline (depth strata 50, 70, 90 m). Standard errors of the means are given in parentheses

	Copepod eggs	Copepod nauplii	Copepodite stages and adults
Above thermocline	16.35 (1.30)	70.96 (2.98)	28.17 (1.21)
Below thermocline	1.62 (1.27)	20.20 (2.92)	2.50 (1.18)

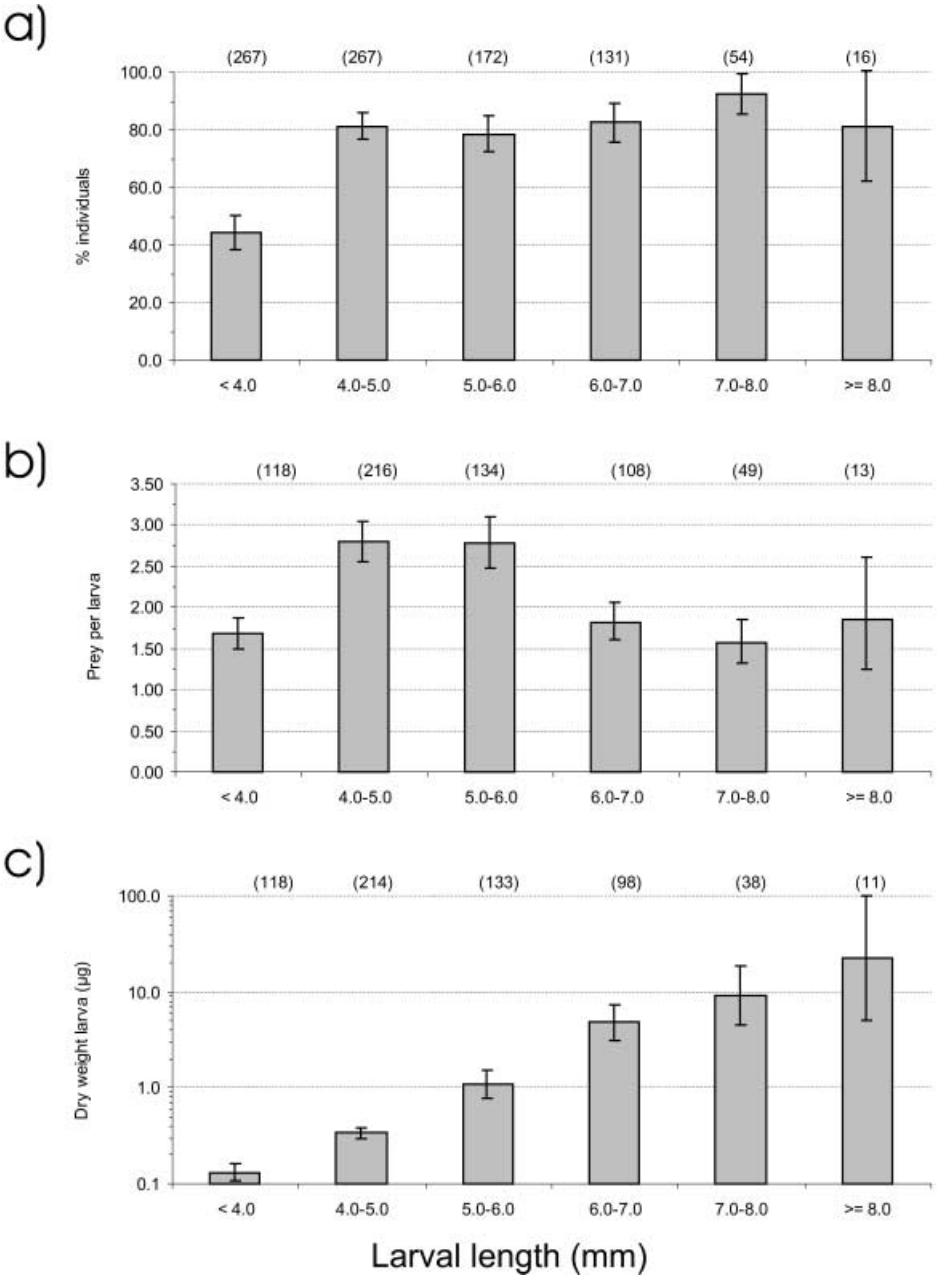

Fig. 8a–c Larval mackerel feeding success by length; values in parentheses indicate sampling size per larval length class. **a** Mean feeding incidence (%); **b** mean numerical feeding intensity (number of prey items per larva); means and 95% confidence intervals were calculated from log (x+1) transformed variates; **c** mean dry weight of larval gut contents (µg prey weight per larva); means and 95% confidence intervals were calculated from log (x*100) transformed variates

that the two upper strata contained significantly more prey items than the three deeper strata (i.e., 50, 70 and 90 m depth; Table 3). No significant differences were observed in the density of copepod eggs, nauplii and copepodite stages and adult copepods between the two days of the drift study.

Larval feeding

Gut contents of 1,177 mackerel larvae, ranging from 2.9 to 9.7 mm SL were analyzed to determine dietary patterns. Averaged over all sizes and stations, 65% of the larvae were observed to have food in their guts (Fig. 8a). Proportion of larvae observed with food in their guts

Table 4 Diet of *Scomber scombrus* larvae by larval length class as the percentage number (*%N*) and percentage dry weight (*%W*) of each prey item

%N	<4.0	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	≥8.0	Total
Copepod eggs	32.6	14.2	21.3	12.2	1.2	1.1	17.4
Copepod nauplii	65.4	82.0	55.9	24.3	15.9	10.0	57.1
Copepodites and adults	0.8	2.2	8.6	15.0	9.1	0.0	6.0
Fish larvae	0.0	0.0	13.3	47.0	64.3	72.4	17.2
Others	1.2	1.6	1.0	1.5	9.5	16.5	2.3
%W	<4.0	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	≥8.0	Total
Copepod eggs	34.6	17.9	24.7	12.2	0.3	0.9	19.9
Copepod nauplii	63.6	78.4	48.0	19.0	16.8	7.6	53.3
Copepodites and adults	0.8	1.9	9.4	13.8	8.5	0.0	5.8
Fish larvae	0.0	0.0	18.0	54.4	72.3	83.2	19.9
Others	1.0	1.8	0.0	0.6	2.1	8.3	1.2

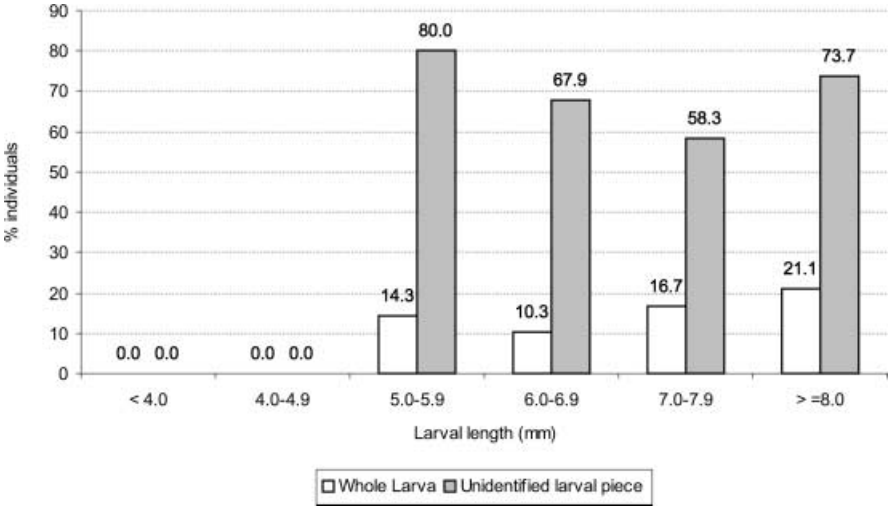

Fig. 9 Proportion of larval fish prey occurring whole or in parts in larval guts by larval length

during daytime was significantly related to larval length (χ^2=146.89, P≤0.001). The proportion of larvae with food in their gut was especially low in first-feeding larvae <4.0 mm SL.

The mean number of food items in the gut of larvae of all sizes was 2.33 per larva. Considering daytime feeding, only, numerical feeding intensities were significantly dependent on larval size (ANOVA; F=14.17, P≤0.001). Feeding intensities increased to the 4.0–4.9 mm category but decreased thereafter (Fig. 8b). The maximum number of food items found in a larval gut was 15 items for a 5.5 mm mackerel larva.

Weight-based feeding intensity was also significantly dependent on larval size (Fig. 8c). During daytime, mean dry weight of gut contents increased steadily with increasing larval length (ANOVA; F=119.447, P≤0.001). Significant differences were observed in weights of gut contents among larvae of all size classes, except for the two largest, the latter primarily due to a high degree of variation and a small sample size.

A shift in the diet of mackerel larvae was indicated by an increase in mean weight of gut contents accompanied by a decrease in numerical feeding intensity (Table 4). First-feeding larvae relied most heavily on copepod nauplii and eggs. Numerical and weight-based percentage of copepod nauplii peaked in the 4.0–4.9 mm length class and declined thereafter. At the same time, copepodite stages and adult copepods increased in importance for the mackerel diet. Mackerel larvae in the 5.0–5.9 mm SL class were the first to initiate piscivorous feeding. The smallest mackerel larva that had ingested fish prey was 5.0 mm SL. The numerical and weight-based importance of piscivorous feeding increased with increasing larval length. In terms of weight, larval fish prey exceeded 80% in the diet of mackerel larvae ≥8.0 mm SL.

In general, fish prey in the larval mackerel guts were partly or well digested. This made it particularly difficult to identify larval fish prey to species. However, of 192 cases of piscivory observed in Atlantic mackerel, a total of 38 (19.8%) were still identifiable. All 38 fish larvae were Atlantic mackerel. Therefore, piscivorous feeding of Atlantic mackerel larvae appeared to be exclusively cannibalism.

Piscine prey occurred in two distinctly different states in the larval guts (Fig. 9). Firstly, some larvae were obviously ingested whole and occurred in varying stages of digestion in the larval guts, and secondly, a high proportion of larval fish were present only as part bodies, suggesting that they had been mechanically disrupted before ingestion. Mainly fish trunks were observed with missing heads, but in a few cases (n=4) heads were found with the trunks missing. With increasing size of mackerel larvae, the proportion of larval prey ingested whole increased, reaching 21.1% in mackerel ≥8.0 mm.

Table 5 Results of the Odds Ratio selectivity analyses for mackerel larvae by larval length class during daytime, given if comparative data are available

Taxa	<4.0	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	≥8.0
Copepod eggs	1.57**	0.50**	0.97**	0.33	–2.08*	–1.90
Copepod nauplii	–0.37**	0.56**	–0.79**	–2.15**	–2.50**	–2.95**
Copepodites and adults	–3.15**	–2.16**	–0.74**	–0.11	–0.60	–
Fish larvae	–	–	7.49**	9.25**	10.19**	11.13**

* Significant at $\alpha<0.05$, ** significant at $\alpha<0.01$

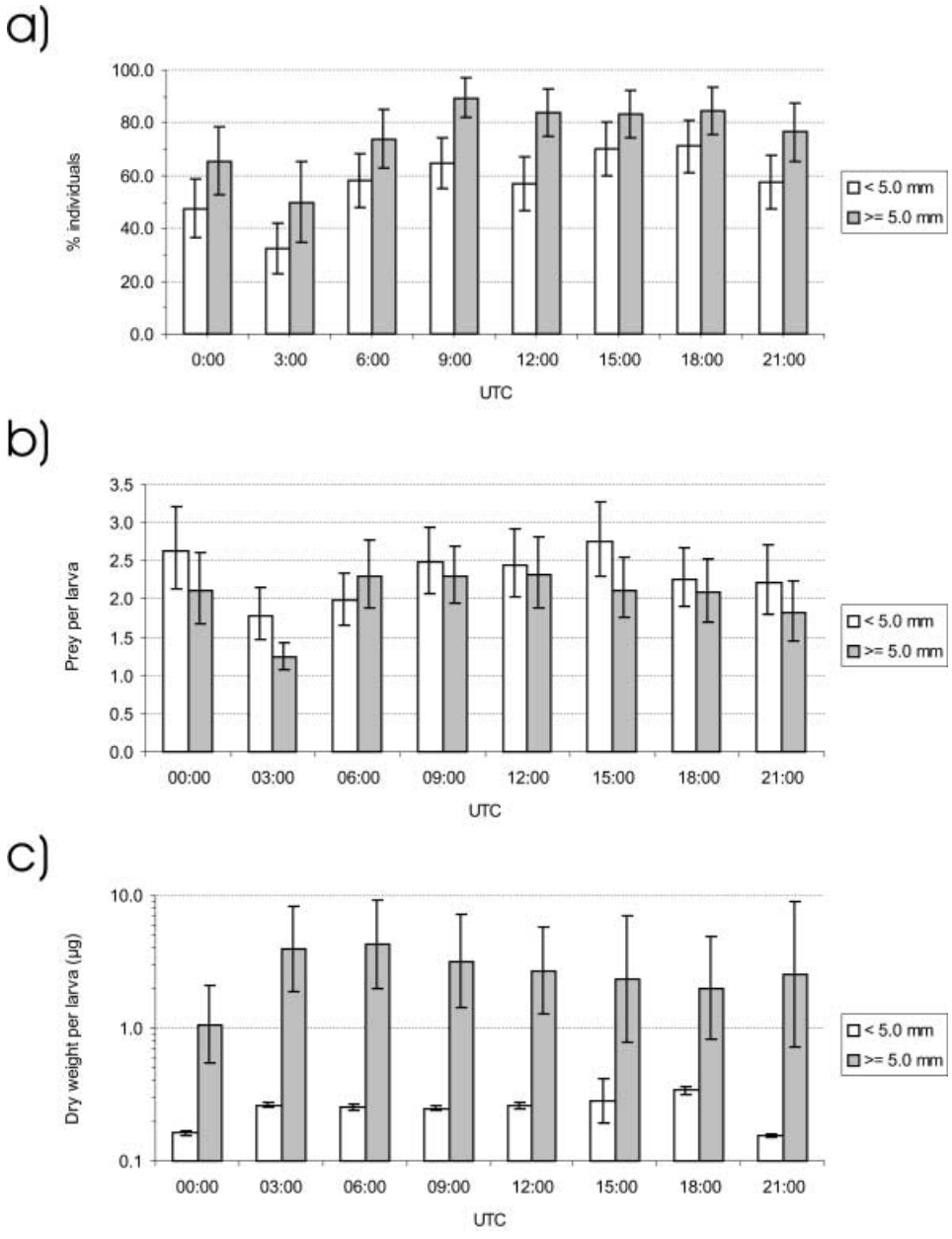

Fig. 10a–c Larval feeding success at different times of the day (UTC). **a** Mean feeding incidence (%); *error bars* indicate 95% confidence interval around the mean. **b** Mean numerical feeding intensity (prey items per larva); means and 95% confidence intervals were calculated from log (x+1) transformed variates. **c** Mean weight-based feeding intensity (µg prey weight per larva); means and 95% confidence intervals were calculated from log (x*100) transformed variates

First-feeding mackerel larvae <4.0 mm significantly selected for copepod eggs and against copepodite stages and adult copepods (Table 5). Since no fish prey was encountered in larvae <5.0 mm SL, this prey item was excluded from selectivity analyses for the two smallest size classes. With increasing larval length, prey selection patterns changed to increasingly larger and more mobile prey items. At the 5.0–5.9 mm class larvae began to select for piscine prey. At the same time, all developmental stages of copepods, with the exception of copepod eggs, were selected against.

Larval feeding was significantly influenced by the time of day, for both larvae <5.0 mm (χ^2=41.282, $P\leq0.001$) and ≥5.0 mm (χ^2=32.933, $P\leq0.001$). The per-

Table 6 Daily ration estimates for mackerel larvae by larval length, during the drift study, 9–11 June 1995, recorded as mean dry weight (µg per day) and mean percentage body weight (% per day)

Daily ration	<4.0	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	≥8.0
Sampling size	144	257	158	116	48	13
Dry weight (µg)	1.50	10.04	61.93	207.21	321.15	603.56
% Body weight	1.43	4.82	19.70	44.60	48.46	58.37

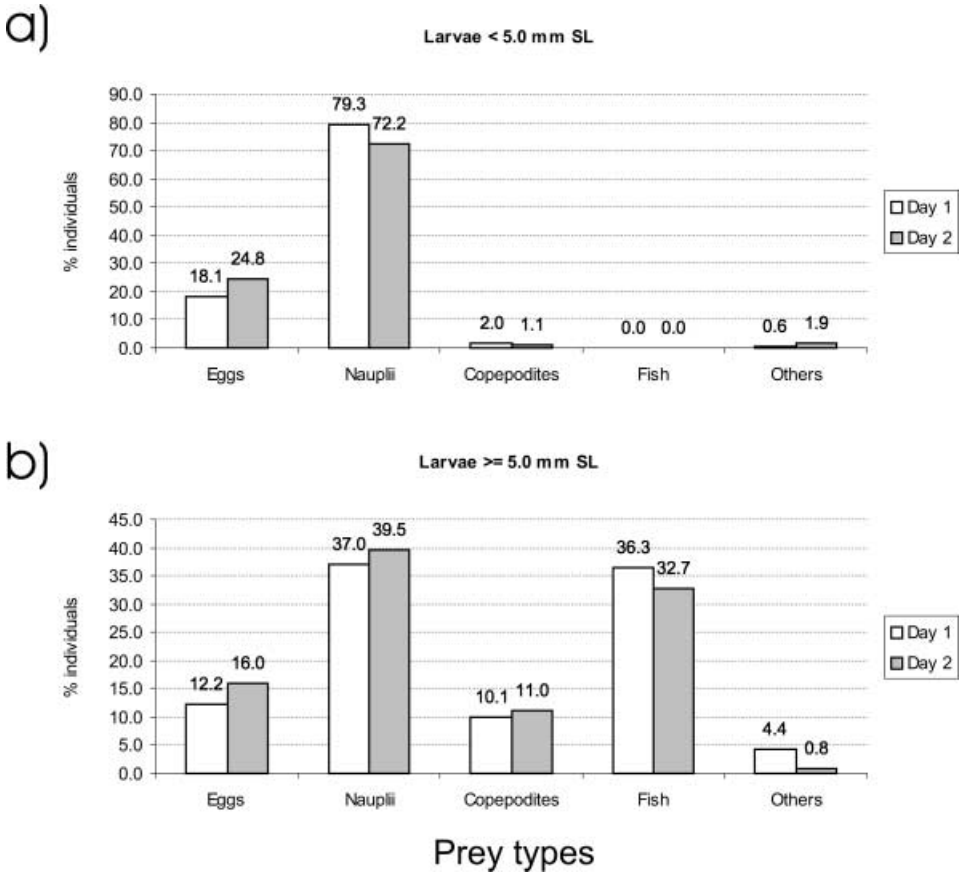

Fig. 11 Numerical composition of prey items found in guts of larvae <5.0 mm SL (**a**) and ≥5.0 mm SL (**b**) with respect to day of sampling

centage of feeding larvae was lowest at 0300 hours UTC (Coordinated Universal Time) and increased towards 0900 hours UTC in both larval length categories (Fig. 10a). Numerical feeding intensity was also dependent on time of day, with noticeably reduced numbers of prey items per larval gut around 0300 hours UTC (Fig. 10b). However, the pattern was not repeated for weight-based feeding intensities, where a reduction in larval gut weights was only apparent for larvae collected at midnight (Fig. 10c).

The two days of our drift study were distinctly different in illumination levels (Fig. 4). However, no significant differences were observed in numerical or weight-based feeding intensity with respect to day of sampling. While feeding intensities did not change significantly, there was, however, an indication of a change in the composition of the diet (Fig. 11). Larvae <5.0 mm ingested proportionately more copepod nauplii and copepodite stages on day 1, while they relied more heavily on copepod eggs on day 2 of the drift study. The same tendency was noticeable for larvae ≥5.0 mm, namely a shift towards more mobile and larger prey, i.e., mackerel larvae, on the first day of the drift study, and developmental stages of copepods on day 2.

Daily ration estimates for mackerel larvae increased conspicuously with larval length class (Table 6). Estimates for first-feeding larvae <4.0 mm were extremely low, with a mean ration of 1.43% body dry weight per day (1.5 µg). This increased by more than fourfold in larvae 5–5.9 mm, i.e., at the onset of piscivory. For larvae ≥8.0 mm a daily ration of 58.37% body dry weight (603.56 µg) was estimated.

Discussion

Vertical distribution of Atlantic mackerel larvae

One of the most striking results of this study was the differential vertical distribution of the two larval mackerel

length classes (<5.0 and ≥ 5.0 mm). Youngest fish larvae are often less aggregated and occur at greater depths than larger fish larvae, particularly under high turbulent energy dissipation rates. With improving swimming ability during growth, larger larvae become more able to compensate for turbulent dispersion and tend to be more aggregated (Heath et al. 1988; Heath 1992; Hillgruber and Kloppmann 2000). The results of our study were the opposite of the aforementioned scenario, i.e., mackerel larvae <5.0 mm were highly aggregated near the thermocline and showed distinct diel vertical migration patterns, while mackerel larvae ≥5.0 mm were more dispersed with only slight diurnal movement patterns discernible. Despite the unusual pattern in aggregation, the distribution pattern of mackerel larvae <5.0 mm may be related to the high density of potential food near the thermocline. To satiate the high energy demands relative to body size of the youngest larvae (Laurence 1977), patches of high food density are required (Lasker 1975), and therefore the co-occurrence of mackerel larvae with their prospective prey is not surprising. As visual feeders (Hunter 1981), fish larvae need sufficient light levels to feed, thus, migration to the near-surface layers at dusk or dawn can be expected. However, the dispersion of the larger mackerel larvae, even to layers below the thermocline, cannot be explained in relation to light or food densities alone.

As has been shown in this and other studies (e.g., Lebour 1920; Grave 1981; Peterson and Ausubel 1984; Ware and Lambert 1985; Fortier and Villeneuve 1996; Hillgruber et al. 1997; Conway et al. 1999), mackerel initiate cannibalistic piscivory around 5 mm, a behavior which becomes increasingly frequent with increasing size. Thus, to be less aggregated in the water column might be a strategy to avoid being eaten by conspecifics. Predation avoidance, by selecting depth strata of low predator abundance, has been discussed as motivation for vertical migration (Ohman et al. 1983; Gliwicz 1986; Ohman 1990) and has been reported for fish larvae with respect to invertebrate predators (e.g., Yamashita et al. 1985; Fortier and Harris 1989). However, nothing is known about predator avoidance with respect to conspecifics.

Furthermore, because mackerel larvae ≥5.0 mm switch to larger, energy-rich prey, they no longer are forced to stay in depth layers with high food densities and may, thus, choose strata that have other important benefits to growth and survival. Undoubtedly at the higher temperatures above the thermocline growth rates should be higher than in the cooler environment below. However, these maximized growth rates are achieved at the cost of higher metabolic rates (Brett 1979) and possibly higher mortality rates (Pepin 1991; Steinarsson and Björnsson 1999). In addition, the best conversion efficiency of ingested food into growth is achieved at submaximal rations and lower temperatures (Brett 1979). Thus, in descending below the thermocline after filling their stomachs, larger mackerel larvae might not only benefit from reduced predation pressure by conspecifics but also by gaining bioenergetic advantages for better survival. However, in a review study on the motivation of vertical migration behavior, Neilson and Perry (1990) discussed the possibilities of a bioenergetic advantage in migrating to cooler water layers. They conclude that even though there exists some evidence for bioenergetic advantages, these advantages do not control vertical migration rather than being a consequence of it.

Daily ration estimates for Atlantic mackerel larvae

Larval feeding success was dependent on larval size. Daily ration estimates increased with larval mackerel length, starting with 1.5 µg dry weight per day for first feeding larvae <4.0 mm. These estimated values were extremely low and may be inaccurate as they are probably inadequate to support larval growth (Hunter and Kimbrell 1980) and survival. Since daily ration estimates were derived from gut content analyses, it is possible that a proportion of first-feeding mackerel larvae partially (low numerical feeding intensity) or completely (low feeding intensity) regurgitated their gut contents. However, while the relatively high feeding incidence in the present study makes it unlikely that mackerel larvae should have completely evacuated their gut contents, a partial defecation of the hind-gut due to net-capture or fixation cannot be completely ruled out. Since the differentiation of the digestive system progresses rapidly in mackerel larvae (Tanaka et al. 1996), regurgitation as a source of bias should quickly decrease with consecutive size classes. This was supported by the correspondence in daily ration estimates in the present study for progressively larger larvae (e.g., 61.9 µg for size class 5.0–5.9 mm, and 207.2 µg for size class 6.0–6.9 mm, see Table 5) with estimates for western Atlantic mackerel larvae (Peterson and Ausubel 1984), which were back-calculated from growth estimates, reaching mean daily dry weights of 42.3 or 69.9 µg for a 5.0–5.5 mm larva. Another explanation could be that a high proportion of first-feeding mackerel larvae fed at suboptimal levels. Due to the high metabolic demand of scombrids (Hunter and Kimbrell 1980), suboptimal feeding might result quickly in mortality. This might be supported by the observation that first-feeding mackerel larvae in the Gulf of St Lawrence consistently experienced slightly higher mortality rates than later larval stages (Ware and Lambert 1985). Also, a high proportion of suboptimally fed larvae, which might be more susceptible to predation, might increase the chance for larger mackerel larvae to successfully capture and ingest conspecifics. The vertical migratory behavior of the cannibalistic mackerel larvae suggests that, instead of constantly feeding on copepods to support their energy demands, they rely on infrequent vertical predatory excursions into the depth of highest mackerel larval abundance. Thus, older mackerel larvae still take advantage of the high secondary production above the thermocline by utilizing the next higher trophic level – their younger conspecifics (Nellen 1986).

In the present study, daily ration estimates reached values exceeding 600.0 µg (50% body dry weight) for larvae ≥8.0 mm. These results were considerably higher than those reported in a preliminary paper on feeding of mackerel larvae (Hillgruber et al. 1997). However, daily ration in 1997 was based on a very preliminary set of data, with only 42 mackerel larvae ≥5.0 mm SL and, thus, at a length where cannibalism occurs. In comparison, in the present study 335 mackerel larvae ≥5.0 mm SL up to ≥8.0 mm SL were investigated. In these larger length classes larval fish are the most important prey type, contributing substantially more to the larval gut weight and, thus, to an increased estimate for the daily ration. In addition, daily ration estimates were obtained using a variation of Bajkov's model (Bajkov 1935; Canino et al. 1991). In the present study we used Elliott and Persson's (1978) model, as in a comparison of different models used to estimate daily ration, they concluded that Bajkov's model, even though widely used, cannot be recommended since it grossly underestimates daily food consumption.

Cannibalistic feeding in Atlantic mackerel larvae

Both daily ration estimates and larval growth rates increase considerably at a length when piscivory is first observed in mackerel larvae (Kendall and Gordon 1981). Piscivorous and cannibalistic feeding has been noted in all studies analyzing mackerel larval feeding habits (Lebour 1920; Grave 1981; Peterson and Ausubel 1984; Ware and Lambert 1985; Fortier and Villeneuve 1996; Hillgruber et al. 1997; Conway et al. 1999), with the exception of Last (1980), who found no piscivory. However, he observed a high proportion of appendicularia in the larval guts, occurring first in 5–5.9 mm larvae. While a few instances of appendicularia in the larval gut contents have been mentioned in other studies (Fortier and Villeneuve 1996; Conway et al 1999), their occurrence was always occasional and low in numbers. Since piscivory is extremely uncommon in marine larvae (Conway et al. 1999) and since appendicularia were first noted by Last (1980) in larvae of 5.0–5.9 mm (i.e., the length at which piscivorous feeding is first initiated) it appears conceivable that the apparent occurrence of appendicularia in the mackerel larval guts may be a result of a misidentification of the larval fish prey.

While only a small proportion of the fish prey could be identified due to the often advanced state of digestion, all identifiable larvae were still mackerel. Therefore, the piscivory that we observed in Atlantic mackerel larvae was at least predominantly if not exclusively cannibalism. Even though mackerel were the dominant ichthyoplankton species, it is surprising that no other larval fish species were ingested. However, similar results were obtained by Grave (1981), Peterson and Ausubel (1984) and Conway et al. (1999), i.e., all identifiable incidences of piscivory, when the prey could be identified, was cannibalism. Only larvae from the northern component of the Northwest Atlantic stock of Atlantic mackerel ingested larvae of other species in addition to conspecifics (Ware and Lambert 1985; Fortier and Villeneuve 1996). However, larval mackerel densities in both these studies were relatively low (<20 per 100 m^3 and 11±23 per 100 m^3) compared with 261.33 per 100 m^3 for larvae <5.0 mm in the present study. This large difference in larval fish density may account for the higher proportion of cannibalism found in this study. In addition, vulnerability to predation has been suggested to be partially dependent on the spatial and temporal overlap between predator and prey (Bailey and Houde 1989). In the present study, mackerel larvae occurred conspicuously higher in the water column than the majority of other ichthyoplankton, and larvae <5.0 mm SL were quite concentrated at 20–40 m depth, resulting in a mean density of 975.2 per 100 m^3 in that depth stratum, which might be a further explanation for the preference for conspecifics in the larval diet that we observed.

Piscivory and its special form, cannibalism, is an uncommon foraging mode for marine fish larvae and is primarily found among members of the scombridae (Lipskaya 1982; Jenkins et al. 1984; Shojii et al. 1997; Young and Davis 1990; Sakakura and Tsukamoto 1996) and larvae of freshwater species (for review see Hecht and Pienaar 1993). Folkvord (1997) ascribed the higher occurrence of larval (coeval) cannibalism in freshwater species, to the fact that those are generally more developed at hatching than marine larvae. Mackerel larvae, like the larvae of many freshwater species, have a variety of morphological features that might particularly adapt them for piscivorous and cannibalistic foraging, i.e., cannibalistic morphs. At the onset of piscivory, mackerel larvae are characterized by a well-developed, streamlined body, a relatively large mouth gape (Shirota 1978), a set of prominent teeth (Conway et al. 1999) and a precocious digestive system (Tanaka et al. 1996).

While the large mouth gape appears to equip larval mackerel particularly well to piscine prey, it should, however, pose a problem when attempting to ingest siblings with similarly large gapes and equally proportioned heads. Yellowtail (*Seriola quinqueradiata*) larvae in culture have been observed to suffocate because of their inability to swallow larvae of similar size (Sakakura and Tsukamoto 1996). In sharptooth catfish (*Clarias gariepinus*) two distinctly different types of cannibalistic strategies, largely a function of head and mouth width, became evident (Hecht and Appelbaum 1988). In type I cannibalism the prey was caught tail-first and swallowed up to the head, which was bitten off and discarded. The relationship between predator mouth width and prey head width showed that the predator's gape was not sufficient to swallow siblings whole. Type II cannibalism (i.e., the prey being swallowed head-first and whole) replaced type I cannibalistic behavior after a period of differential growth among the larval population. Type I cannibalism has also been observed for vundu catfish (*Heterobranchus longifilis*; Baras 1999) and walleye (*Stizostedion vitreum*) larvae (Li and Mathias 1982). In

the present study, a high incidence of fish trunks minus the heads, suggests that a type I feeding strategy might be applicable to mackerel larvae, thus, enabling the larvae to feed on siblings closer to their own size. The observation that piscivorous feeding is initiated simultaneously with the development of prominent teeth (Conway et al. 1999) might support this hypothesis, in that it might enable the larvae to better handle and mechanically manipulate fish prey. Because of the larva's apparent ability to swallow siblings similar to its own size, it can be concluded that size variations within a larval population could be both the cause and the effect of cannibalism (Hecht and Appelbaum 1988).

Only one other study, which analyzed the foraging patterns of Atlantic mackerel larvae, actually measured the density of potential food organisms, developmental stages of copepods (Fortier and Villeneuve 1996). In spite of the fact that their sampling was carried out in July, observed densities of copepod eggs and nauplii were extremely low with a mean of <2.0 per liter. Fortier and Villeneuve (1996) attributed these low densities to the fact that sampling was conducted over the upper 75 m of the water column and concentrations of developmental stages of copepods were depth averaged. However, while in the present study densities of developmental stages of copepods were significantly reduced below the thermocline, densities averaged over the whole upper 100 m of the water column were considerably higher (45.1 per liter) than in the study by Fortier and Villeneuve (1996). Daily predation rates of western Atlantic mackerel on fish larvae declined with increasing naupliar density to a maximum naupliar density of $<3.0\ l^{-1}$ (Fortier and Villeneuve 1996), which is dramatically lower than any naupliar count in the present study. In comparison to the aforementioned study, however, a considerably higher proportion of mackerel larvae in the present study were observed to feed on fish larvae, thus, making it unlikely that the incidence of piscivory was dependent on density of alternative prey. For a species such as the Atlantic mackerel, which is on the one hand particularly well equipped for piscivory and on the other hand pressured by high energy requirements, fish larvae appear to be the most profitable energy source.

Variations in Atlantic mackerel larvae feeding due to light

Mackerel feeding followed a diel pattern, as has been observed in other studies (Last 1980; Conway et al. 1999). However, while other studies reported a marked increase in feeding intensity at the onset of nightfall (Grave 1981; Fortier and Villeneuve 1996; Conway et al. 1999), no such pattern could be established in the present study. During the night, a reduced proportion of mackerel larvae were observed with food in their guts, and this was particularly noticeable for larvae <5.0 mm SL, possibly indicating a higher digestion rate for copepod prey. The diel pattern was somewhat obscured in the weight-based feeding intensities for larvae ≥5.0 mm SL, which was probably due to a lower digestion rate for fish prey. Differences in diel feeding intensity patterns between larvae <5.0 mm and ≥5.0 mm SL, which could purely be a result of differences in digestion rates, stress the importance of acquiring more information on gut passage times in mackerel larvae, particularly with regard to the effect of different prey types and sizes.

The two days of the drift study varied markedly in illumination levels, but not in turbulence or densities of potential prey items. While no significant differences in larval feeding intensities were observed, there was, however, an indication of a shift in the composition of the larval diet. This was demonstrated by a preference for smaller prey on the day of lower light intensities (day 2), with larvae <5.0 mm ingesting proportionately more copepodites and nauplii on day 1 and more copepod eggs on day 2, and larvae ≥5.0 mm ingesting more fish prey on day 1 and more developmental stages of copepods on day 2. Fiksen et al. (1998) performed a modeling study and observed that both turbulence and light could have a strong impact on larval ingestion rates. While turbulence in the present study was at a level that proved not to be beneficial for larval blue whiting foraging success (Hillgruber and Kloppmann 2000), it did not change over time, so that changes in the composition of the diet should be solely due to light. However, mackerel larvae of both size classes ingested proportionately more smaller prey at lower light levels. Light has an effect on the visual range of fish larvae, particularly at low irradiance levels. Aksnes and Utne (1997) showed that while there was a pronounced increase of visual range up to 10 $\mu E\ m^{-2}\ s^{-1}$ it did not increase considerably above that value. On the first day of our study, irradiance values at the depth of maximum mackerel larvae density were much higher than the threshold value. In contrast, on second day the minimum irradiance we observed was slightly above 10 $\mu E\ m^{-2}\ s^{-1}$. Since measurements were taken at mid-depth of each depth stratum, it is possible that the bulk of mackerel larvae had encountered suboptimal light levels on the second day of the drift study. However, reactive distance of fish larvae to their potential prey is also positively correlated to prey size (Aksnes and Utne 1997; Utne 1997) and mobility (Utne-Palm 1999). Therefore one might expect a higher proportion of larger and more mobile prey in the larval stomachs on the second day of our study. The opposite was the case. Our study was carried out under highly turbulent conditions, the benefits of which fish larvae would have mostly only been able to utilize under the adequate illumination levels of the first day (see Fiksen et al. 1998). At the low light conditions of the second day, large and highly mobile but comparatively rare prey items like copepodites and fish larvae, might at high turbulent conditions be more likely to escape out of the visual range of mackerel larvae. Therefore, a higher proportion of less mobile or immobile and more abundant prey items, namely copepod eggs and nauplii, might be expected in the diet of mackerel larvae.

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