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Feeding of larvae of mackerel (*Scomber scombrus*) to the west of the British Isles and the incidence of piscivory and coprophagy.

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ABSTRACT

The gut contents of mackerel larvae (2.1-9.2mm in length) were examined from samples taken in the spring and early summer over the shelf-edge to the south-west of the British Isles. Larvae <5.9mm in length fed mainly on unidentified phytoplankton material, copepod eggs and copepod nauplii. In larvae >6mm in length the proportion of copepodite stages of copepods increased, while the proportion of copepod nauplii remained relatively constant. A limited amount of coprophagous feeding on crustacean faecal pellets was observed in larvae >3mm in length (0.2-22.1% of gut contents by weight). Piscivorous feeding occurred in larvae in the length range 4-7.9mm and, although fish larvae were not numerous in the diet (0.3-4.6% numerically), they accounted for a significant proportion of the diet by weight (56.1-72.1%). Larvae developed teeth from 3.1mm in length; by 5mm in length all larvae had teeth, a feature possibly related to their piscivorous diet. There was a higher incidence of feeding larvae during daylight hours although at least 55% of larvae remained with food items in their guts at night.

INTRODUCTION

Several studies have examined the diet of larvae and early post-larvae of Atlantic mackerel (*Scomber scombrus*). Grave (1981) and Last (1980) based their studies on larvae from the North Sea, while Fortier and Villeneuve (1996), Peterson and Ausubel (1984) and Ware and Lambert (1985) examined specimens from the western North Atlantic. The study by Peterson and Ausubel (1984) was carried out between May and June during the onset of seasonal stratification and increasing production, the other studies later in the year, from July to September.

There is no published information on the diet of mackerel larvae from the spawning areas along the shelf-edge and adjacent areas to the west of the British Isles. The present study is based on sampling in these areas and describes the diet of mackerel larvae during establishment of thermal stratification, with particular reference to the incidence of piscivory and coprophagy. While coprophagic feeding is of relevance in the recycling of organic material, piscivory and, in particular cannibalism, has a potential effect on larval mortality and recruitment.

Piscivory has been recorded to varying extents in all of the above studies on *Scomber scombrus* larvae, except in that of Last (1980). It has been recorded for other scombriform larvae e.g. *Katsuwonus pelamis* (Nishikawa, 1975; Young and Davis, 1990), *S. japonicus* (Hunter and Kimbrell, 1980; Lipskaya, 1982), *Thunnus albacares* (Uotani *et al.*, 1981), *T. maccoyii* (Young

and Davis, 1990) and *Scomberomorus* spp. (Jenkins *et al.*, 1984; Finucane *et al.*, 1990). Piscivory is uncommon in non-scombriform fish larvae, although there are isolated records of fish prey being taken by larvae of various species e.g. *Micromesistius poutassou* (Conway, 1980), *Merluccius productus* (Sumida and Moser, 1980), *Pseudochaenichthys georgianus* (North and Ward, 1989) and by a range of neustonic and pseudoneustonic species (Tully and Ó Céidigh, 1989). Last (1980) noted no incidence of piscivory in any of the over 9000 larvae of the 20 fish species he examined from the North Sea. An isolated observation of a high percentage occurrence of fish larvae in the guts of particular length groups of non-scombriform larvae was recorded by Economou (1991), there being up to 35% in *Melanogrammus aeglefinus* and 6% in *Pollachius virens*.

There are few records of coprophagy in sea-caught fish larvae, but it has been reported in *Gadus morhua* (Ellertsen *et al.*, 1980; Fossum and Ellertsen, 1994), *Clupea harengus* (Bhattacharyya, 1957) and *Scomber japonicus* (Hunter and Kimbrell, 1980). In laboratory experiments, larvae of *Scophthalmus maximus* (Conway, unpublished) and *G. morhua* (Ellertsen *et al.*, 1979) occasionally fed on copepod faecal pellets.

MATERIALS AND METHODS

Mackerel larvae were sampled for gut content analysis on 5 cruises in different years between April and June, at station positions in the spawning area south-west of the British Isles (Fig. 1, Table 1). Several different net systems were used for collection of the larvae. These included the Longhurst Hardy Plankton Recorder (LHPR - Williams *et al.*, 1983) which takes a series of samples at separate depths (typically ~10m depth intervals) on a single haul. Other sampling equipment consisted of a single (1m²), Rectangular Mid-water Trawl (RMT; Roe and Shale, 1979), a Lowestoft Tin Tow Net (TTN; Beverton and Tungate, 1967), a "Nackthai" sampler (Nellen and Hempel, 1969) and Bongo net (McGowan and Brown, 1966); hauls from all these latter samplers being integrated over the entire depth range sampled. The RMT and Bongo nets were towed at 2-3 knots, all other samplers at ~4 knots.

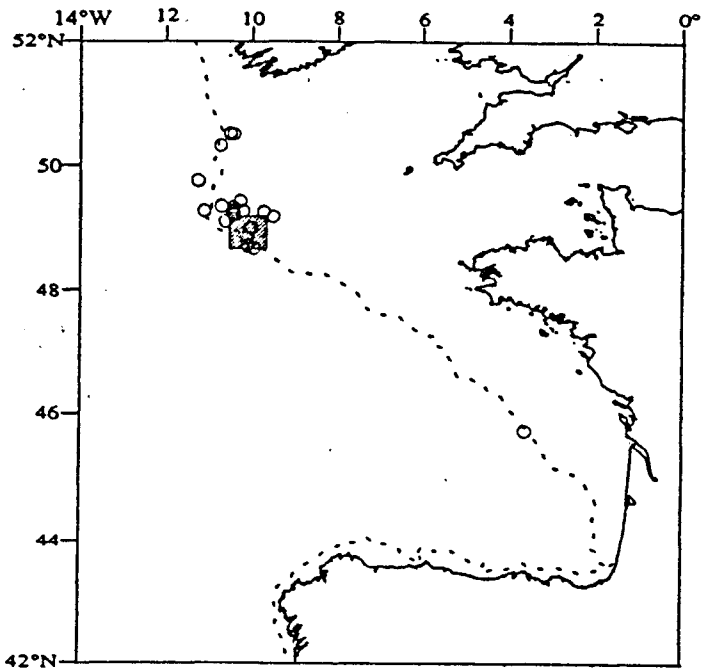

Fig. 1. Sample positions indicated by circles and, for the 1986 Anton Dohrn sample grid, as the shaded rectangle; the 200m depth contour is also indicated.

Table 1. Sampling information.

Ship	Month/year	Net/mesh aperture	No. of hauls	No. larvae examined
RV Cirolana	May 1980	LHPR (280μm)	6 (49 samples)	142
FRV Scotia	June 1980	LHPR (280μm)	3 (10 samples)	68
RRS Frederick Russell	May 1984	RMT/TTN (280μm)	13	109
FS Anton Dohrn	April 1986	Nackthai (280μm)	24	67
NO Thalassa	May 1987	Bongo (500μm)	10	70

Samples from all hauls were preserved in borax buffered 4% formaldehyde solution. A total of 456 larvae were measured (standard length after preservation and storage, no allowance being made for shrinkage), a note was made of gut colour and the the food items in their guts removed and identified. A selection of 692 food items were measured for information on the size range of food taken by different sizes of larvae. Conversion to dry weight (Table 2) was based on published information on copepod eggs, nauplii and copepodite stages (Fransz and Diel, 1985; Klein Bretler *et al.*, 1982; Ogilvie, 1953; Uye, 1981 and 1982), for tintinnids (Kawakami *et al.*, 1985) and faecal pellets (Bathmann, 1988); where required, a conversion from carbon to dry weight was based on a body content of 50% carbon. The dry weight values for ingested fish larvae was derived from data given by Grave (1981), Peterson and Ausubel (1984) and Hunter and Kimbrell (1980). Mean number of individual food items per feeding larvae was calculated for each length class together with the percentage composition in the diet and incidence of occurrence for each item. The upper jaw length of a sub-set of larvae was also measured as a guide to jaw gape (Shirota, 1978).

High Performance Liquid Chromatography (HPLC) analysis was carried out on mackerel larvae for information on phytoplankton pigments of the gut contents. 44 larvae (2-8mm in length) were preserved at -20°C on GFC filter papers from sampling in 1986. Pigments were subsequently extracted in 90% acetone for reverse-phase HPLC using a modified method of Mantoura and Llewellyn (1983).

Table 2. Unit dry weight (μg) conversion values.

Size Category	Tintinnid	Copepod egg	Nauplii	Copepodite	Faecal pellet	Fish larva
2-3.99 mm	0.03	0.35	0.13	0.15	0.16	-
4-5.99 mm	0.03	0.48	0.37	0.34	0.16	27.0
6-7.99 mm	0.03	0.42	0.38	1.06	0.16	27.0

RESULTS

Comparison of the diet

The yolk-sac was mostly absorbed in larvae by 4.0 mm in length, although most larvae with some remains of the yolk-sac already had food in their guts. Between 7% and 50% of larvae had no food in the gut with a steady reduction in the occurrence of empty guts with increase in length of the larvae (Fig. 2). A significant percentage (41-79%) of larvae <4.9mm in length contained unidentifiable green material; larger larvae had a lower percentage of green guts.

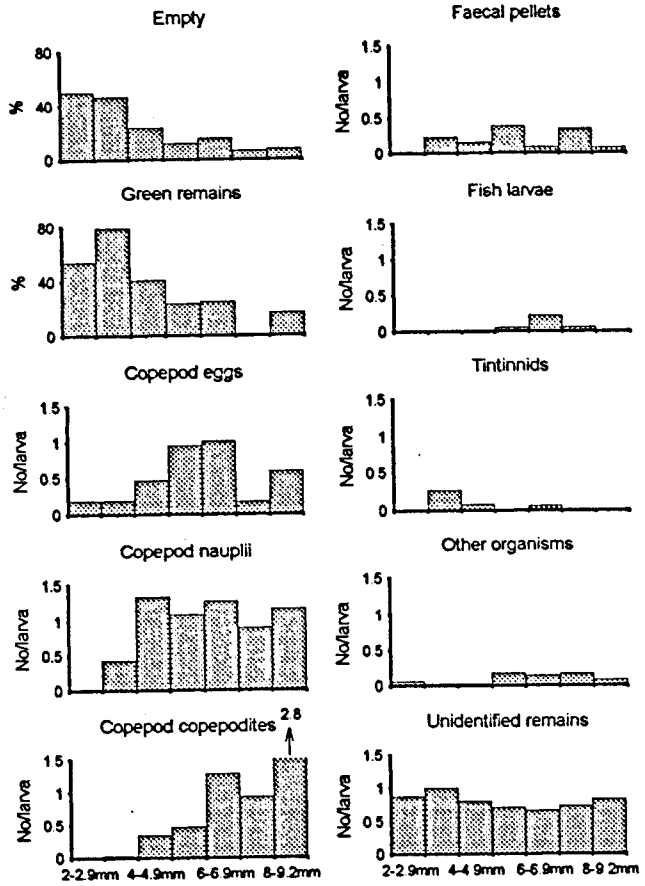

Fig. 2. Percentage incidence by lengths of larvae with empty guts and those with green contents, together with the mean number of the main food organisms per feeding larva (unidentified remains counting as one item).

The main dietary items were the eggs, nauplii and copepodite stages of copepods each of which was typically present at average numbers of 0.5-1.5/larva (Fig. 2). Copepod eggs were relatively common in the gut contents, numerically representing between 8.6% and 24.8% of items in the diet of larvae 2-9.2mm in length. They were taken in increasing numbers until a length of 6.9mm and then with a second peak in larvae 8-9.2mm in length. This bimodal distribution was related to the smaller larvae feeding on free-spawned eggs of *Acartia* spp. (~80µm dia.) or of *Calanus* spp. (~180µm dia.) while many of the eggs taken by the larger larvae originated from feeding directly on egg-bearing copepods such as *Oithona* spp. or *Oncaea* spp. Copepod nauplii were the most common food item in larvae >4mm in length (0.9-1.3/larva), numerically representing between 21.2% and 41.3% of the diet of these length groups. Copepodite stages of copepods were taken in increasing numbers with increase in larval length; numerically they represented from 10.7% of the gut contents items in larvae at 3-3.9mm in length to 50.0% in larvae 8-9.2mm in length.

Brown/green faecal pellets were taken in relatively low numbers (0.1-0.4/larvae) by larvae >3mm in length without any clear preference for them by any size category of larvae. Numerically they formed between 1.9-10.7% of the diet. Pellet length was from 60-600μm, with a mean of ~150μm, and a width from 20-100μm with a mean of ~40μm. There was no trend in the size of pellet selected by different sizes of larvae.

Fish larvae were not prominent in the gut contents, numerically comprising between 0.3% and 4.6% of the diet of the larger larvae of 4-7.9mm in length. The prevalence of piscivory was most developed in larvae 6-6.9mm in length (Fig. 2), but in which fish remains still only represented numerically 4.6% of the gut contents. Specimens were invariably digested to the extent that it was difficult to make an identification to species or to take useful measurements; the few identifiable larvae were predominantly yolk-sac stages of mackerel larvae.

Other less common items in the diet included tintinnids which were taken by the smallest larvae (3-3.9mm in length). Low numbers of the diatom *Coscinodiscus* sp., larvaceans, echinoderm larvae, cladocera and the thecosome *Limacina retroversa* were present sporadically in the gut contents; all these occasional items have been grouped together in the category "Other organisms" (Fig. 2). Unidentifiable remains were also present in all sizes of larvae.

Dietary value by weight

Conversion of the number of food items to dry weight biomass results in significant changes to the contribution made by the different components. Tintinnids remain a small proportion of the diet (a maximum of 4.7% in larvae 3-3.9mm in length), due to their small body mass, and faecal pellets make only a slightly greater contribution by weight (0.2-22.1% in larvae >3mm in length). Although copepod eggs are not particularly numerous in the smallest larvae (2-2.9mm in length; Fig. 2) they comprise 93.8% of the gut contents by weight at this size; for other sizes of larvae the proportion of eggs by weight varies between 2.2% and 38.6% of the diet. Copepod nauplii comprise a significant proportion of the diet of a wide size range of larvae (5.9-42.6% in larvae >3mm in length). However, the largest part of the diet is derived from fish larval prey in the intermediate size categories of larvae (56.1-72.1% in larvae 5-7.9mm in length) and by copepodites in the larger larvae (16.6-80.5% in larvae 6-9.2mm in length).

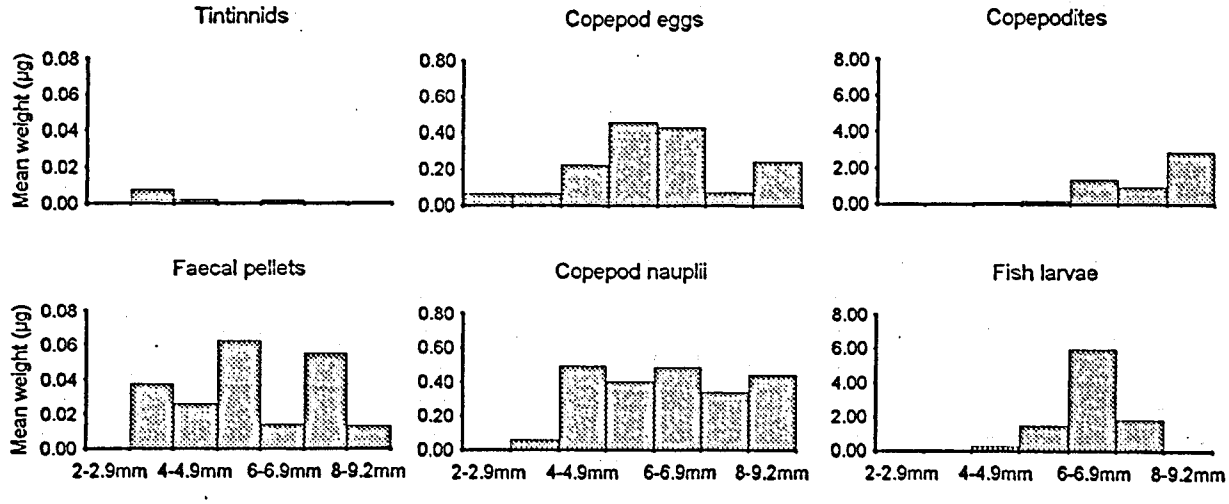

Fig. 3. The mean dry weight per larva of the main food items in the guts of feeding larvae; note the logarithmic change in scale between different components.

Diel changes in feeding incidence

Samples were grouped into 2 hourly periods over 24 hours to examine the diel feeding pattern of larvae. There was relatively little variation, the lowest percentages of larvae with food in their guts being found during the later hours of night and early morning (0000-0800h; Fig. 4), although there was never less than 55% of larvae which contained some food remains. From 0800h the percentage of larvae with food increased and remained at between 78-98% until 2400h.

The day/night variation in feeding intensity was also compared using the mean number of food particles per larva (Fig. 5). There was some similarity with the pattern for gut fullness (Fig. 4), there being a period of relatively low numbers of food particles per larva from 0200-0800h, but also with a second period of low feeding incidence from 1000-1600h.

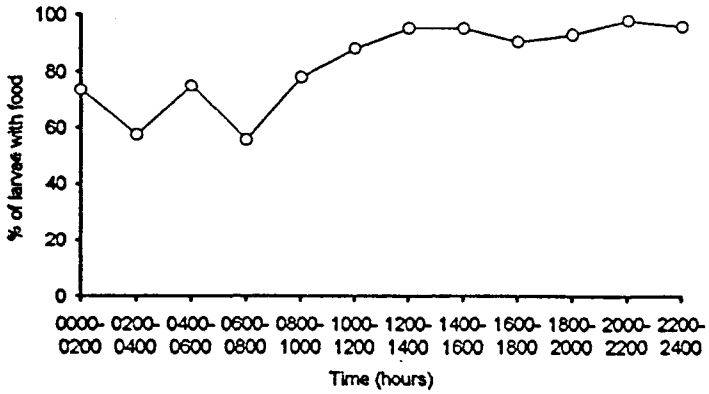

Fig. 4. Diel changes in the percentage of mackerel larvae of all lengths with food in the gut.

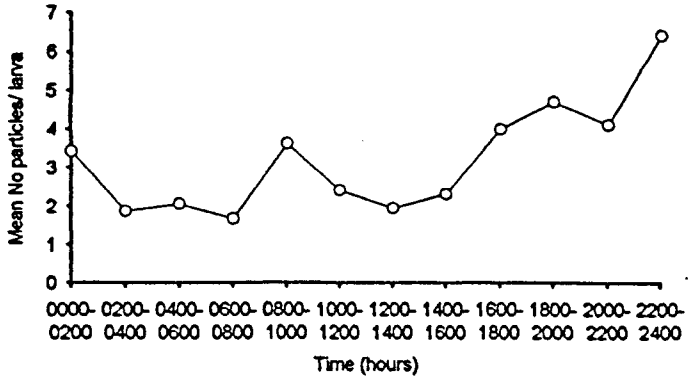

Fig. 5. Diel changes in the mean number of food particles per feeding larva; data included for all lengths of larvae.

Teeth formation and mouth gape

Teeth of mackerel larvae were developing in larvae from a length of 3.1mm and by 5.0mm all larvae had teeth (Fig. 6).

Upper jaw lengths of larvae are plotted in Fig. 7 as an indication of mouth gape. Shirota (1978) gives the mouth gape as $\sqrt{2}L$, where L=upper jaw length. The results suggest that by 6mm, larvae would be able to ingest e.g. a copepod with a cephalothorax width of around 1mm. The largest copepod taken, was by a larva of 6mm and had a cephalothorax width of 0.34mm and length of 0.7mm, well within the theoretical capability of the larva.

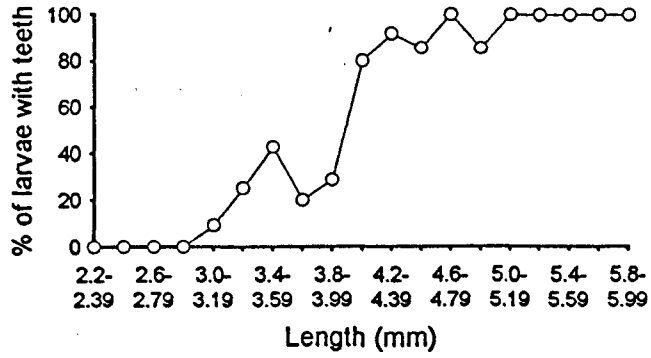

Fig. 6. Percentage of mackerel larvae with developed teeth.

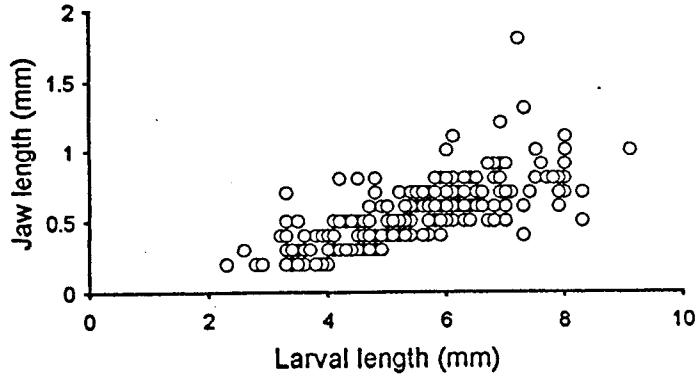

Fig. 7. Upper jaw length of mackerel larvae against body depth (n=257).

HPLC analysis

HPLC analysis of the phytoplankton pigment content of mackerel larvae showed a decrease in chlorophyll *a* content with increasing larval length (Fig. 8) and negligible amounts in larvae >5mm in length. Phaeophorbides and phaeophytins, breakdown products of chlorophyll *a*, also declined in parallel with the decrease in chlorophyll *a*. Examples of these changes are given in Fig. 9 where the absorbancy and fluorescence peaks are compared for individual larvae at 3.5mm and 7.7mm in length.

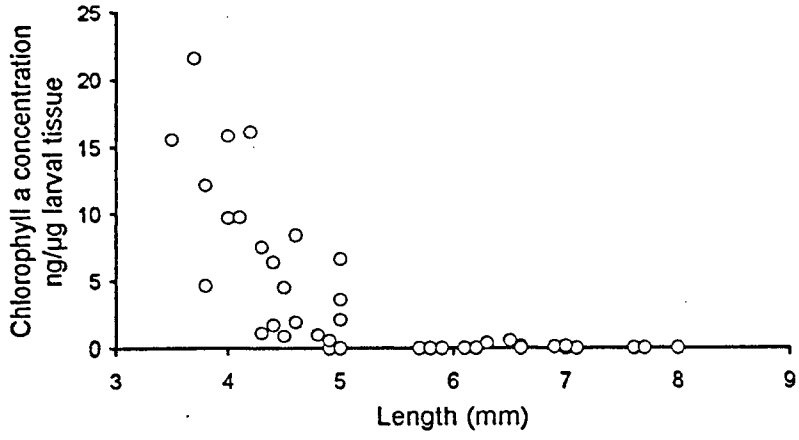

Fig. 8. Chlorophyll *a* concentration in individual mackerel larvae from HPLC analysis.

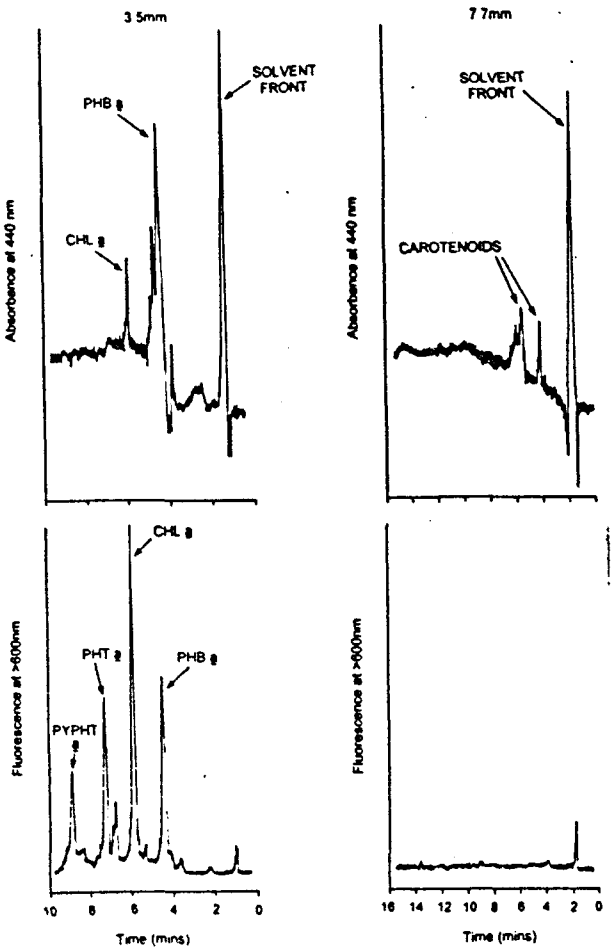

Fig. 9. HPLC absorbance and fluorescence traces for individual larvae.

DISCUSSION

Numerically, the diet of mackerel larvae, was composed mainly of the developmental stages of copepods which is similar to observations from other studies on mackerel larvae (Grave, 1981; Peterson and Ausubel, 1984; Ware and Lambert, 1985; Fortier and Villeneuve, 1996) and for fish larvae in general (e.g. Last, 1980). Larvae commenced feeding before the yolk-sac was fully absorbed and a high proportion of the smaller larvae had phytoplankton remains in their guts. HPLC results corresponded to visual observations made on gut colour, the levels of chlorophyll *a* being consistent with the smaller larvae having been feeding directly on phytoplankton. The presence of phytoplankton material may be under-represented in some studies based on visual observations because it loses colour in preservatives and may be noted as unidentifiable remains.

There was a progressive change in the diet with size of larvae as they were able to take more active and larger prey. Empty guts became progressively less common with increase in length of larvae, possibly reflecting both experience in feeding and mortality of under-nourished larvae. It is not known to what extent there is food loss from the guts due to defecation during sampling. This has been observed particularly in straight-gutted *Clupea harengus* larvae (Blaxter 1965) and is considered a problem in all species with this type of gut (Dekhnik, 1974). This may be less of a consideration for mackerel larvae which have a coiled gut, however, defecation problems have also been observed in the coil-gutted *Theragra chalcogramma* (Canino and Bailey, 1995). Larvae, even of species which eventually have a coiled gut, tend to have a simple straight gut during the early developmental stages, so that small larvae of all species may be prone to defecation of the gut contents following capture and preservation.

While faecal pellets have been noted in the gut contents of larvae in several studies (Bhattacharyya, 1957; Ellertsen *et al.*, 1980; Hunter and Kimbrell, 1980; Fossum and Ellertsen, 1994) the pellets were consistently present in low numbers. Shelbourne (1953) noted faecal pellets in the guts of post-larval plaice, typically contained within indigestible vesicles. However, these were identified as remains from appendicularia following digestion of the body. In the present study between 4% and 14% of feeding larvae, depending on length, contained faecal pellets, appearing visually to be of copepod origin. Faecal pellets were generally a relatively minor component of the diet, both numerically (1.9-10.7%) and by weight (0.2-22.1%). Additionally, because copepod faecal pellets are sometimes tightly encased in a peritrophic membrane, probably largely composed of chitin (Bochdansky and Herndl, 1992), they may not be readily digestible unless the membrane is breached. A proportion of the pellets may thus pass through the larval digestive tract without contributing to nutrition (Conway *et al.*, 1993).

Piscivory by *Scomber scombrus* larvae has been documented by Peterson and Ausubel (1984), Ware and Lambert (1985), Grave (1981) and Fortier and Villeneuve (1996). Piscivory was recorded consistently in the present study, and thus appears to be normal behaviour over the distributional range of the species. In the present study, fish remains were particularly prominent in the diet of larvae in the length group 6-6.9mm (4.6% numerically but 72.1% by dry weight) and were not found in larvae >7.9mm in length. Fortier and Villeneuve (1996) showed the incidence of piscivory increasing from 12% in larvae <5mm to 69% in larvae ≥9mm while Grave (1981) found piscivorous feeding restricted to mackerel larvae >10mm, with greatest incidence in larvae 13-19mm in length. This variation may be related to availability of other prey items, the above studies which recorded piscivory in larger larvae being based on observations after the main spring bloom when other prey items may be less readily available; the present study being based on sampling nearer to the time of the bloom. Additionally, the more restricted vertical distribution of mackerel larvae later in the season (Coombs *et al.*, 1996) gives higher concentrations and more distributional overlap of the different sizes of larvae and hence the potential for intra-specific predation.

The concentration of most fish larvae in the sea is generally quite low, thus piscivory is more likely to occur where spawning is concentrated and where there is a broad co-occurring size range of larvae. This is supported by results from laboratory studies and aquaculture experience, where larvae are concentrated in unnaturally high densities and cannibalism occurs in species which are not recorded as being cannibalistic in the wild (e.g. Brownell, 1985, Fujiya, 1976). The only study on *Scomber scombrus* larvae which examined the concentrations at which piscivory occurred was by Fortier and Villeneuve (1996). In that study piscivory was limited when the density of larval prey of a suitable size was <0.1 larva/m^3 and rapidly reached a plateau when the concentrations of suitable prey larvae increased.

Because of the variation in size of the different components of the diet, a comparison by weight can give a more useful indication of the relative importance in the diet of the different food types than numerical abundance. Although weight of food items is not necessarily an indication of nutritional content, presentation of the gut contents by weight highlights the potentially greater feeding efficiency obtained in moving from high numbers of small items such as copepod eggs and nauplii to lesser numbers of larger organisms such as copepodites and larval fish; fish larvae are likely to be an efficient food source since they may contain a greater digestible proportion than crustacean prey. Although fish larvae make a significant contribution by weight (25.3-72.1%) they were not abundant numerically (0.34-4.6/larva) and thus the relatively few consumed are less likely to impact significantly on mortality. Equally, since it was mainly the smaller larvae which were taken as prey, the larger more motile larvae being less susceptible to capture (Fortier and

Villeneuve, 1996), and these early developmental stages habitually experience the highest mortality, the piscivorous habit may have little impact on overall mortality. The limited positive identifications of the larvae in the gut contents indicates that mackerel larvae were the prey, although a diet on larvae of other species could not be excluded. Thus the piscivorous habit of mackerel larvae is predominantly one of cannibalism; as such it may form, to some extent, a density-dependent regulation method for the species, possibly of significance when food resources are scarce.

Scombrid larvae are unusual in developing prominent teeth at a relatively early stage of development, in this study in larvae between 3mm and 5mm in length. The length at which all larvae had developed teeth (5mm in length) was also the length of onset of piscivory. Scombrid teeth are particularly sharp and spinous compared with the more usual peg-like teeth of most other fish larvae; mackerel larvae also have a wide mouth gape that may be particularly adapted to piscivory. The piscivorous habit may also be related to the developmental pattern of the digestive system in scombrids. *Scomberomorus niphonius* have a highly developed digestive system and prey on fish larvae from first feeding (Tanaka *et al.*, 1996). Scombrids typically have a high metabolism, a rapid growth rate and therefore an increasingly high food requirement (Hunter and Kimbrell, 1980). While *Scomber scombrus* may not be morphologically as well adapted to the piscivorous habit as some of the tropical scombrids, increased growth rates are obtained at the length when larvae begin to feed piscivorously (Kendall and Gordon, 1981).

The observed diel pattern of feeding intensity is typical of other studies on feeding in fish larvae (Last, 1980). The particularly marked increase in feeding intensity in the evening was also observed in mackerel larvae by Grave (1981) and Fortier and Villeneuve (1996). While there was a reduction in the occurrence and intensity of feeding at night, the percentage of larvae with food remained above 55%. This suggests a reduction in feeding at night, although not to the extent of gut clearance at night as found in studies of larvae of mackerel in the North Sea (Grave, 1981). Interpretation of diel feeding patterns is obscured, to some extent by gut passage rates having been shown to be slower and more variable, when feeding stops (Canino and Bailey, 1995). In order to satisfy metabolic requirements, gut passage time in mackerel larvae has been estimated at 1-2 hours Peterson and Ausubel, (1984), although from an analysis of gut contents at different times of day, Fortier and Villeneuve (1996) considered that 24 hours was required for digestion of fish larvae. These observations may be reconciled, in part, by reports of gut passage rate varying with size of food particle in *Scophthalmus maximus* (Conway *et al.*, 1993). For precise information direct observations of gut passage time are required.

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