DIET OF MACKEREL (SCOMBER SCOMBRUS) LARVAE AT THE SHELF-EDGE TO THE SOUTH-WEST OF THE BRITISH ISLES AND THE INCIDENCE OF PISCIVORY AND COPROPHAGY

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SCOMBER SCOMBRUS
LARVAE
FEEDING
PISCIVORY
COPROPHAGY

ABSTRACT. – The gut contents of mackerel larvae (2.1-9.2 mm 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 < 5.9 mm in length fed mainly on unidentified phytoplankton material, copepod eggs and copepod nauplii. In the diet of larvae > 6 mm 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 > 3 mm in length (0.2-22.1 % of gut contents by weight). Piscivorous feeding occurred in larvae in the length range 4-7.9 mm 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 3.1 mm in length; by 5 mm all larvae had teeth, a feature which may facilitate their piscivorous feeding. There was a higher incidence of feeding during daylight hours, although at least 55 % of larvae sampled at night still had food items in their gut contents.

SCOMBER SCOMBRUS
LARVES
RÉGIME ALIMENTAIRE
RÉGIME PISCIVORE
COPROPHAGIE

RÉSUMÉ. – Le contenu du tube digestif de larves de Maquereaux (1,2 à 9,2 mm de longueur) a été examiné à partir d'échantillons prélevés au printemps et au début de l'été sur le talus continental du sud-ouest des Iles Britanniques. Les Larves < 5,9 mm de longueur se nourrissent principalement de phytoplancton non identifié, d'œufs de Copépodes et de nauplii de Copépodes. Dans le régime des larves de plus de 6 mm de longueur, la proportion de stades copépodites de Copépodes augmente tandis que celle des nauplii est relativement constante. Un nombre limité de pelotes fécales de Crustacés a été observé chez les larves de plus de 3 mm de longueur (0,2 à 22,1 % du contenu du tube digestif en poids). Un régime piscivore a été observé chez les larves comprises entre 4 et 7,9 mm de longueur et, bien que les larves de Poissons ne soient pas nombreuses (0,3 à 4,6 % numériquement), elles représentent une proportion significative du régime en poids (56,1 à 72,1 %). A partir de 3,1 mm de longueur les larves développent des dents ; à partir de 5 mm toutes les larves ont des dents, une caractéristique qui peut faciliter leur alimentation piscivore. La prise de nourriture montre une plus forte fréquence pendant la journée, bien que au moins 55 % des larves échantillonnées durant la nuit présentent également de la nourriture dans le tube digestif.

INTRODUCTION

The diet of larvae and early post-larvae of Atlantic mackerel (*Scomber scombrus*) has been studied by Fortier & Villeneuve (1996), Peterson & Ausubel (1984) and Ware & Lambert (1985) who examined specimens from the western North Atlantic, by Grave (1981) and Last (1980) based on larvae from the North Sea and by Hillgruber

et al. 1997 who worked on larvae from the shelf-edge west of the British Isles. The present study is also based on sampling from the mackerel spawning areas along the shelf-edge and adjacent areas to the south-west of the British Isles. A broad description is given of the diet of mackerel larvae over the period of 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, could significantly affect larval mortality rates and ultimately recruitment.

Piscivory has been recorded to varying extents in all of the above studies on mackerel larvae, except in that of Last (1980). It has been recorded for other scombriform larvae e.g. *Katsuwonus pelamis* (Nishikawa 1975, Young & Davis 1990), *S. japonicus* (Hunter & Kimbrell 1980, Lipskaya 1982), *Thunnus albacares* (Uotani *et al.* 1981), *T. maccoyii* (Young & Davis 1990) and *Scomberomorus* spp. (Jenkins *et al.* 1984, Finucane *et al.* 1990). Piscivory is uncommon in non-scombriform fish larvae, although there are a few records of insignificant numbers of fish prey being taken by larvae of various species e.g. *Micromesistius poutassou* (Conway 1980), *Merluccius productus* (Sumida & Moser 1980), *Pseudochaenichthys georgianus* (North & Ward 1989) and by neustonic and pseudo-neustonic species (Tully & Ó Céidigh 1989). Last (1980) noted no incidence of piscivory in any of over 9000 larvae of the 20 fish species he examined from the North Sea. However, an isolated observation of a high percentage occurrence of fish larvae in the gut contents 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 for *Gadus morhua* (Ellertsen *et al.* 1980, Fossum & Ellertsen 1994), *Clupea harengus* (Bhattacharyya 1957) and *Scomber japonicus* (Hunter & Kimbrell 1980). In laboratory experiments, larvae of *Scophthalmus maximus* occasionally fed on copepod faecal pellets (Conway unpubl.).

METHODS

Gut contents of mackerel larvae were analysed from plankton samples taken on 5 cruises between April and June spanning different years, south-west of the British Isles (Fig. 1, Table I). Five different net systems were used for collection of the larvae. These included the Longhurst Hardy Plankton Recorder (LHPR – Williams *et al.* 1983), a single (1 m^2), Rectangular Mid-water Trawl (RMT; Roe & Shale 1979), a Lowestoft Tin Tow Net (TTN; Beverton & Tungate 1967), a "Nackthai" sampler (Nellen & Hempel 1969) and a Bongo net (McGowan & Brown 1966). The RMT and Bongo nets were towed at 2-3 knots, all other samplers at ~ 4 knots. All sampling times are given in UTC.

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 food items in their guts removed and identified. A selection of 692 food items were measured for information on

Table I. – Sampling information.

Ship	Month/year	Net/mesh aperture	Number of hauls	Number of 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

Table II. – Dry weight (µg) conversion values used for the food of different mackerel larval length categories.

Length category (mm)	Tintinnid	Copepod egg	Nauplii	Copepodite	Faecal pellet	Fish larva
2-3.99	0.03	0.35	0.13	0.15	0.16	-
4-5.99	0.03	0.48	0.37	0.34	0.16	27.0
6-9.20	0.03	0.42	0.38	1.06	0.16	27.0

the size range of food taken by different sizes of larvae. Conversion to dry weight (Table II) was based on published information on copepod eggs, nauplii and copepodite stages (Klein Bretler *et al.* 1982, Uye 1982, Fransz & Diel 1985), for tintinnids (Kawakami *et al.* 1985) and faecal pellets (Bathmann 1988). The dry weight values for ingested fish larvae were derived from data given by Grave (1981), Peterson & Ausubel (1984) and Hunter & Kimbrell (1980). The upper jaw length of a sub-set of larvae was also measured as an index of 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 (2-8 mm 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 & Llewellyn (1983).
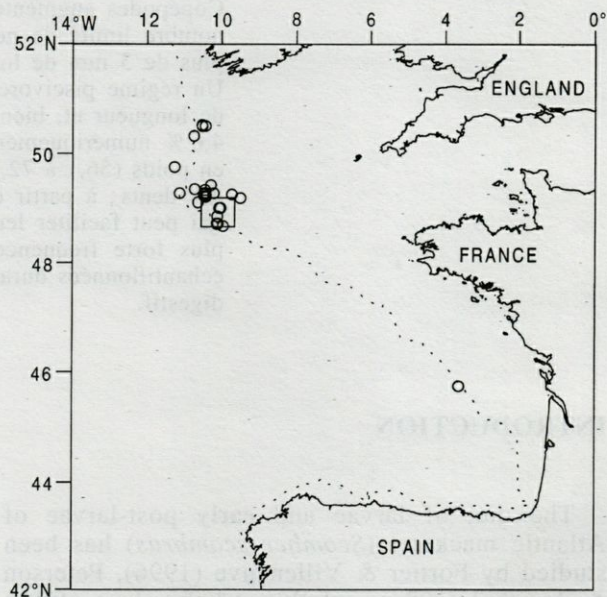

Fig. 1. – Sample positions indicated by circles and, for the 1986 Anton Dohrn sample grid, as a rectangle; the 200 m depth contour is also marked.
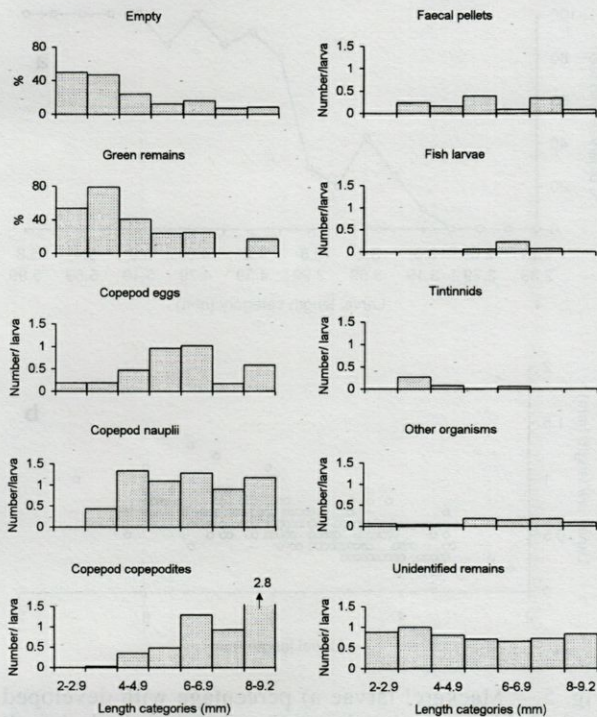
Fig. 2. – Percentage incidence by lengths of larvae with empty guts and those with green contents. Also, the mean number of the main food organisms per feeding larva (unidentified remains counting as one item).

RESULTS

Comparison of the diet

In most larvae the yolk-sac was absorbed by 4.0 mm in length, although the majority of 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 < 4.9 mm in length contained unidentifiable green material; a lower percentage of larger larvae had green gut contents.

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 2-9.2 mm in length. Eggs were taken in increasing numbers up to a larval length of 6.9 mm. The eggs observed in the gut contents were the free-spawned eggs of a range of species, mainly *Acartia* spp. (~80 μm diameter) or of *Calanus* spp. (~180 μm diameter). Larger larvae contained detached egg sacs originating

from direct feeding on egg-bearing copepods such as *Oithona* spp. or *Oncaea* spp., but these eggs were not counted. Copepod nauplii were the most common food item in larvae > 4 mm 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 10.7 % of the gut contents items in larvae at 3-3.9 mm in length and up to 50.0 % in larvae 8-9.2 mm in length.

Brown/green faecal pellets were taken in relatively low numbers (0.1-0.4/larvae) by larvae > 3 mm in length, without clear preference for them by any particular size category of larvae. Numerically they formed between 1.9-10.7 % of the diet. Pellet length was from 60-600 μm (mean ~ 150 μm) and width from 20-100 μm (mean ~ 40 μm).

Fish larvae comprised numerically between 0.3 % and 4.6 % of the diet of the larger larvae 4-7.9 mm in length (Fig. 2). The prevalence of piscivory was most developed in larvae 6-6.9 mm in length, in which fish remains 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 accurate measurements; the few positively identifiable larvae were yolk-sac stages of mackerel larvae.

Other less common items in the diet included tintinnids, which were taken mainly by larvae 3-3.9 mm in length. Low numbers of the diatom *Coscinodiscus* spp., larvaceans, echinoderm larvae, cladocera and the thecosome *Limacina retroversa* were occasionally present in the gut contents; 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 resulted in significant changes in the dietary contribution made by the different components (Fig. 3). Tintinnids remained a small proportion of the diet (a maximum of 4.7 % in larvae 3-3.9 mm in length), due to their low body mass, and faecal pellets made only a slightly greater contribution by weight (0.2-22.1 % in larvae > 3 mm in length). Although copepod eggs were not particularly numerous in the smallest larvae (2-2.9 mm in length; Fig. 2) they comprised 93.8 % of the gut contents by weight for this larval length category; for other lengths of larvae the proportion of eggs by weight varied between 2.2 % and 38.6 % of the diet. Copepod nauplii
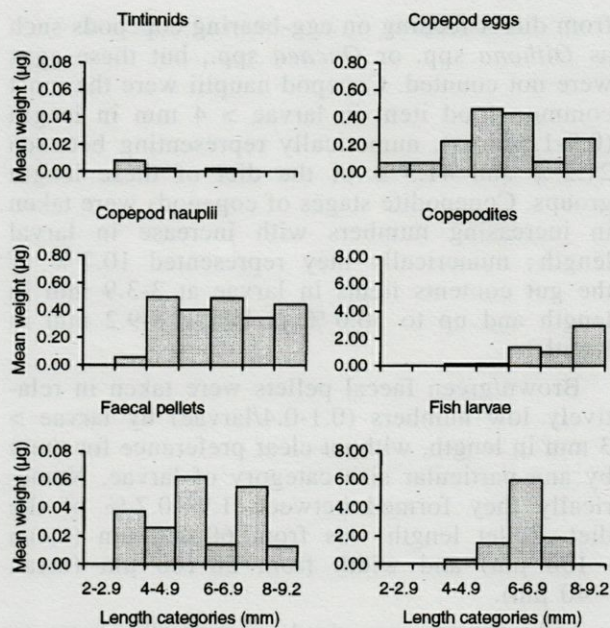
Fig. 3. – The mean dry weight per larva of the main food items in the gut contents of feeding larvae of different length categories; note the logarithmic change in scale between different components.
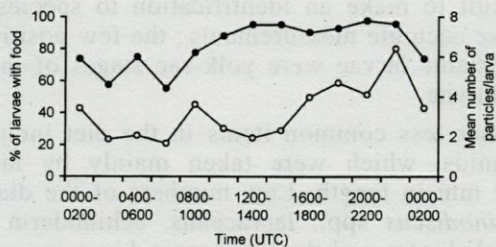

Fig. 4. – Diel changes in the percentage of mackerel larvae of all lengths with food in the gut (closed circles) and in the mean number of food particles per feeding larva (open circles). Range of sunrise was 0436-0537 h and range of sunset 1941-2037 h.

comprised a significant proportion of the diet of a wide length range of larvae (5.9-42.6 % in larvae > 3 mm in length). However, the highest proportion of the diet was derived from fish larval prey in the intermediate length categories of larvae (56.1-72.1 % in larvae 5-7.9 mm in length) and by copepodites in the larger larvae (16.6-80.5 % in larvae 6-9.2 mm in length).

Diel changes in feeding incidence

Overall, 81 % of larvae had food in their gut contents. Samples were grouped into 2 hourly periods over 24 hours to examine changes in the percentage of larvae containing food. There was
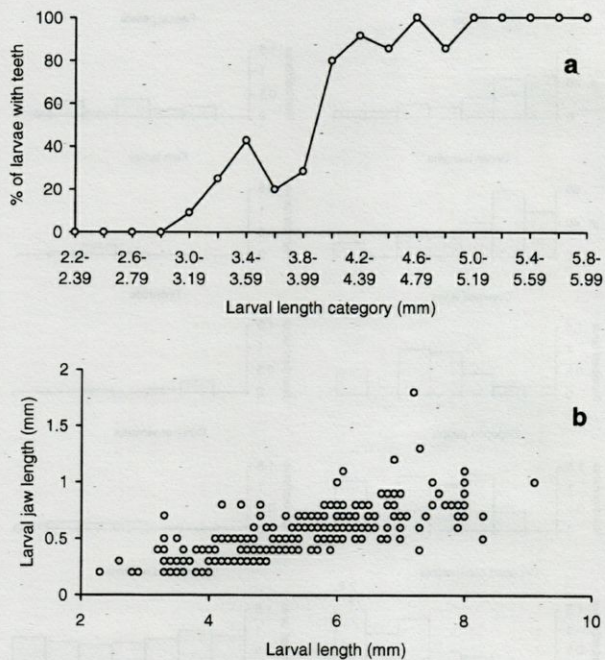
Fig. 5. – Mackerel larvae a) percentage with developed teeth and b) upper jaw length in relation to body length (n = 257).

relatively little diel variation, the lowest percentages being found during the later hours of the night and early morning (0000-0800 h; Fig. 4), although there was never less than 55 % of larvae which contained some food remains. From 0800 h the percentage of larvae with food increased and remained at between 78-98 % until 24.00 h.

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

Teeth formation and mouth gape

Teeth were developing in some mackerel larvae from a length of 3.1 mm and by 5.0 mm all larvae had teeth (Fig. 5a). Upper jaw lengths of larvae are plotted in Fig. 5b as an indication of mouth gape. Shirota (1978) gives the mouth gape as 2L, where L = upper jaw length. The results suggest that by 6 mm, larvae would be able to ingest e.g. a copepod with a cephalothorax width of around 1 mm. The largest copepod taken, was by a larva of 6 mm in length and had a cephalothorax width of 0.34 mm and length of 0.7 mm, well within the suggested theoretical capability of the larva.
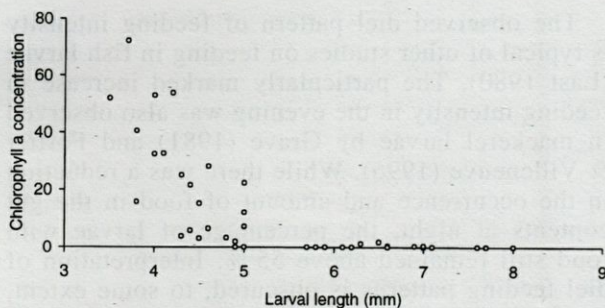
Fig. 6. – Chlorophyll *a* concentration (ng/µg larval tissue) in individual mackerel larvae from HPLC analysis.

HPLC analysis

HPLC analysis of the phytoplankton pigment content of mackerel larvae showed a decrease in chlorophyll *a* content with increasing larval length (Fig. 6) and negligible amounts in larvae > 5 mm in length. Pheophorbides and pheophytins, breakdown products of chlorophyll *a*, also declined in parallel with the decrease in chlorophyll*a*.

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 & Ausubel 1984, Ware & Lambert 1985, Fortier & Villeneuve 1996, Hillgruber *et al.* 1997) and for fish larvae in general (e.g. Last 1980). Larvae commenced feeding before the yolk-sac was fully absorbed, which appears to be the case in many fish larvae (Last 1980) apart, possibly, from clupeoids (e.g. Arthur 1976). A high proportion of the smaller larvae had phytoplankton remains in their gut contents. HPLC results corresponded to visual observations made on the colour of gut contents, the levels of chlorophyll *a* being consistent with the smaller larvae having been feeding directly on phytoplankton. While copepod eggs were common in the diet of early larvae, it is known that they can resist digestion (Conway *et al.* 1994), so may contribute little nutritionally. There was a progressive change in the diet with increase in larval length, as larvae were able to take larger and potentially more motile prey. Empty guts became progressively less common with increase in larval length, possibly reflecting both improved foraging ability and mortality of any under-nourished larvae.

While faecal pellets have been noted in the gut contents of fish larvae in several studies (Bhattacharyya 1957, Ellertsen *et al.* 1980, Hunter &

Kimbrell 1980, Fossum & Ellertsen 1994) the pellets were present in consistently low numbers. Shelbourne (1953) noted faecal pellets in the gut contents of post-larval plaice, typically contained within indigestible vesicles. However, these were identified as remains from digested appendicularians. In the present study, between 4 % and 14 % of feeding larvae, depending on length, contained faecal pellets, which are believed 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 & Herndl 1992), they may not be readily digestible unless the membrane is breached, so may have little food value (Conway *et al.* 1993).

Piscivory by *Scomber scombrus* larvae has been documented by Peterson and Ausubel (1984), Ware & Lambert (1985), Grave (1981), Fortier & Villeneuve (1996) and Hillgruber *et al.* (1997). Piscivory was recorded consistently in the present study, and thus appears to be a feature over most of the distributional range of the species. Fish remains were particularly prominent in the diet of larvae in the length group 6-6.9 mm (4.6 % numerically but 72.1 % by dry weight) and were not found in larvae > 7.9 mm in length. Hillgruber *et al.* (1997) noted that piscivory (cannibalism) started at a length of 5 mm. Fortier & Villeneuve (1996) showed the incidence of piscivory increasing from 12 % in larvae < 5 mm to 69 % in larvae 9 mm, while Grave (1981) found piscivorous feeding restricted to mackerel larvae > 10 mm, with the greatest incidence in larvae 13-19 mm in length. This variation between studies may be related to the relative availability of mackerel larval prey and of other prey items (Fortier & Villeneuve 1996). The study by Grave (1981), which recorded piscivory in larger larvae, was based on observations in August/September, when other prey items may be less readily available than in the present study, which took place closer to the spring plankton bloom. Additionally, the more restricted vertical distribution of mackerel larvae later in the season (Coombs *et al.* in press) may give higher larval concentrations, a greater overlap of the different sizes of larvae and hence increased potential for intra-specific predation. This is supported by results from laboratory studies and aquaculture experience, where larvae are concentrated in unnaturally high densities and cannibalism can occur in species which are not recorded as being cannibalistic in the wild (e.g. Hecht & Pienaar 1993). The only study on *Scomber scombrus* larvae which examined the larval fish concentrations at which piscivory occurred, was by Fortier & Villeneuve (1996). In that study piscivory was limited when the density of fish larval prey of a suitable size was < 0.1 larva/m^2

and rapidly reached a plateau when the concentrations of these larvae increased.

The concentration of most fish larvae in the sea is generally quite low, but those which occur in high natural concentrations generally show little or no predisposition to piscivory (e.g. *Micromesistius poutassou*; Conway 1980), so mackerel larvae appear to have adopted this mode of feeding due to other factors. Scombrid larvae are unusual in that they develop prominent teeth at a relatively early stage, in this study in larvae between 3 mm and 5 mm in length. At a length of 5 mm all larvae had developed teeth, which was also the length at which piscivory was first noted. Scombrid larvae have teeth which are particularly sharp and spinous compared with the more usual peg-like teeth of most other fish larvae and they also have a wide mouth gape, both features which may particularly adapt them 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 during development (Hunter & 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 have been shown to occur at the length at which the larvae begin to feed piscivorously (Kendall & Gordon 1981).

Weight of food items is not necessarily an indication of nutritional quality, but it 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 in the diet (25.3-72.1 %), they were not abundant numerically (0.34-4.6 %). Since it was mainly the smaller larvae which were taken as prey, the larger more motile larvae being less susceptible to capture (Fortier & Villeneuve 1996), and as these early developmental stages experience the highest mortality, piscivory may have little impact on overall mortality. Limited positive identification of the larvae in the gut contents indicated that mackerel larvae were the prey, although feeding on larvae of other species could not be excluded. Thus, the piscivorous habit of mackerel larvae is predominantly one of cannibalism, as noted by Hillgruber *et al.* (1997); as such it may form, to some extent, a density-dependent regulation method for the species, possibly of significance when food resources are scarce.

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 & Villeneuve (1996). While there was a reduction in the occurrence and amount of food in the gut contents at night, the percentage of larvae with food still remained above 55 %. 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 & Bailey 1995). In order to satisfy metabolic requirements, gut passage time in mackerel larvae has been estimated at 1-2 hours (Peterson & Ausubel 1984), although from an analysis of gut contents at different times of day, Fortier & 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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