Journal of Plankton Research Vol.19 no.3 pp.287–301, 1997

Diet-shifts and food-dependent survival in *Engraulicypris sardella* (Cyprinidae) larvae from Lake Malawi, Africa

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Abstract. The diet of *Engraulicypris sardella* (Cyprinidae) larvae was determined from the open waters of Lake Malawi, Africa. The guts of first-feeding larvae of 2–3 mm total length (TL) usually contained many cells of 5–9 μm diameter tentatively identified as a non-colonial green alga (Chlorophyta). The number of these cells in the guts of larvae declined as larvae increased in size, and were not found in larvae greater than 9 mm TL. Other types of phytoplankton were rarely seen in the guts of larvae. Copepod nauplii were eaten by larvae greater than 4 mm TL, and copepodite copepods and cladoceans by larvae greater than 5 mm TL. The biomass of open water crustacean zooplankton and *E.sardella* larvae were determined over a 2-year sampling programme. The mortality rate of *E. sardella* was negatively correlated with zooplankton biomass, but was not significantly correlated with the amount of zooplankton food in the guts of larvae.

Introduction

Lake Malawi is meromictic, with a permanent barrier to mixing at ~230 m that forms the oxic-anoxic boundary layer. One or more thermoclines exists at 50–125 m, that are strongest during the hot wet season from January to April and weakest during the cool windy season when mixing occurs from May to September (Eccles, 1974; Patterson and Kachinjika, 1993). The peak period of primary production is reported to occur during the May–September mixing period (Degnbol and Mapila, 1982; Patterson and Kachinjika, 1995). Significant inter-annual variations in primary production are also suspected to occur (Patterson *et al.*, 1995).

The pelagic zone of Lake Malawi has only five common species of crustacean zooplankton, the cyclopoids *Mesocyclops aequatorialis aequatorialis* (Kiefer) and *Thermocyclops neglectus* (Sars), the calanoid *Tropodiaptomus cunningtoni* (Sars), and the cladocerans *Diaphanosoma excisum* Jenkin and *Bosmina longirostris* (O.F.Müller). The cladocerans tend to be more abundant in the southern part of the lake (Irvine, 1995a). The calanoid *Thermodiaptomus mixtus* Sars was not recorded north of 13°08′S, and was uncommon south of this latitude (Irvine, 1995a). Larvae of the lakefly *Chaoborus edulis* Edwards was also a common component of the pelagic zone (Irvine, 1995b).

The pelagic waters also support cyprinid, cichlid, mochokid and clariid fish species (Thompson *et al.*, 1996a, b). Perhaps the most exploited of these offshore species is the small endemic cyprinid *Engraulicypris sardella* (Günther 1868), which grows to a maximum total length of 130 mm and is an important human food resource for the riparian countries of Malawi, Mozambique and Tanzania (Lewis and Tweddle, 1990). *E.sardella* rarely live longer than one year (Thompson and Bulirani, 1993), and are the only species of fish in Lake Malawi known to have

pelagic larvae (Jackson *et al.*, 1963). Reports of *E.sardella* having pelagic eggs (Jackson *et al.*, 1963) are now believed to be in error (Thompson, 1996). The larvae are present in varying numbers throughout the year and mainly occupy the upper 100 m of the water column (Degnbol, 1982; Thompson, 1996). Turner (1982) suggests that spawning of *E.sardella*, or the survival of *E.sardella* larvae, is at a maximum from April to July, when the pelagic water column is undergoing vertical mixing. He proposed that the observed annual differences in *E.sardella* abundance was determined by annual fluctuations in food availability during the mixing period. Tweddle and Lewis (1990) also proposed that interactions between *E.sardella* larvae and primary productivity is important in determining adult abundance. There is, however, little or no data to support the above hypotheses.

This paper describes the diet of larval *E.sardella* from the first feeding stage at 2 mm total length (TL) to 11 mm TL over a 2-year sampling programme. The weight of food in the guts of larvae, and estimates of the mortality rates of *E.sardella* larvae (Thompson, 1996), are then related to the biomass of the crustacean zooplankton food resource (Irvine, 1995a). The results support the hypothesis that production is the main factor controlling the abundance of *E.sardella*.

Method

Diet studies

The diet of *E.sardella* larvae of 2–13 mm TL was analysed. A total of 65–156 individual larvae were selected randomly from 2–8 localities during each cruise, from the open waters of Lake Malawi between latitudes 13°00′S–14°00′S and from 08:00–16:00h (Table I). A maximum of 30 larvae were examined from each mm length class cruise^{-1}, although this number was seldom obtained in the small and large length classes. Larvae were measured to the nearest mm below, and the gut removed and placed in a drop of water for viewing under a coverslip. Food items in the gut were identified using a microscope at ×400 or ×1000 magnification. Phytoplankton were identified to class (or occasionally to genus) using data in Kachinjika and Patterson (1994). The majority of the zooplankton food items were assigned to four main groups: copepod nauplii (80–320 μm TL), cyclopoid copepodites comprising *Thermocyclops neglectus* and *M.a.aequatorialis* (270–990 μm TL), the calanoid copepodite *T.cunningtoni* (450–1200 μm TL), and the cladoceran *D.excisum* (540–1050 μm TL). Other species of zooplankton were rarely found in the guts of *E.sardella* larvae. The total length of zooplankton food items, excluding hairs, legs, antennae, or other projections, was determined from measurements of furcae length for copepodite copepods and maximum mandible dimension for *D.excisum* (Table II). Copepod nauplii were usually intact and their total length was measured directly. Normally it was possible to identify and measure food items through the gut wall. However, it was occasionally necessary to dissect items out of the gut so that they could be examined in more detail, especially for nauplii. Unidentified or unmeasured zooplankton food items were also recorded.

Estimates of dry weight of zooplankton items in the gut were made using the relationships given in Table II. Weight loss through the digestive process was ignored. The dry weight of unmeasured food items was assumed to equal the

Table 1. Sampling details of lake-wide plankton hauls for abundance estimates of crustacean zooplankton and *E.sardella* larvae, and for the diet analysis of *E.sardella* examined for 'small' phytoplankton and crustacean zooplankton collected between latitudes 13°00'S–14°00'S.

Sampling periods		'Small' phytoplankton		Crustacean zooplankton	
	Number of samples lake-wide	Number of larvae (samples) examined	Mean size (and range) of larvae examined (mm)	Number of larvae (samples) examined	Mean size (and range) of larvae examined (mm)
27 February 1992–13 March 1992	53	–	–	–	–
7 May 1992–18 May 1992	52	–	–	78 (8)	5.8 (4–9)
16 July 1992–28 July 1992	45	48 (2)	4.2 (2–9)	95 (3)	6.4 (3–11)
30 September 1992–11 October 1992	52	47 (2)	4.7 (2–9)	140 (8)	6.7 (2–12)
2 December 1992–12 December 1992	47	47 (2)	4.8 (2–9)	80 (3)	7.1 (3–11)
24 February 1993–7 March 1993	56	–	–	65 (3)	6.7 (4–11)
21 April 1993–27 April 1993	33	50 (2)	4.4 (2–9)	92 (3)	6.3 (4–13)
13 July 1993–22 July 1993	40	48 (2)	4.9 (2–9)	156 (3)	7.3 (4–11)
15 September 1993–25 September 1993	35	50 (2)	4.2 (2–9)	97 (2)	7.1 (5–11)
24 November 1993–3 December 1993	41	–	–	–	–

– indicates no data. The 'small' phytoplankton are 5–9 μm in diameter and are believed to be Chlorophyta. Each sample was taken from a different location.

average weight of the measured food items in each mm length class of larvae. To allow for comparisons among cruises containing different mean sizes of larvae, a relative gut contents weight larva^{-1} (RW_g) was calculated by expressing the dry weight of food in the gut (W_g, g) as a proportion of the dry body weight (W_L, g). Hence,

$$RW_g = W_g / W_L \tag{1}$$

where W_L is calculated from total length (L, mm) by

$$W_L = 3.03 \times 10^{-7} L^{2.73} \tag{2}$$

(Thompson, 1996).

The importance and possible identity of the small spherical objects, common in the guts of small larvae, were elucidated towards the end of the study as probably being green algae belonging to the Chlorophyta. Additional samples of *E.sardella* larvae were therefore examined (Table I), and the tentatively identified objects were quantified, somewhat subjectively, as the proportion of the linear length occupied in the gut relative to the total length of the gut.

Estimates of E.sardella larvae abundance and mortality

Lake-wide sampling for fish larvae and crustaceans was undertaken at ~2-month intervals on 10 cruises between February/March 1992 and November/December

Table II. Equations for estimating the total length, excluding projections and hairs, and dry weight of food items in the guts of *E.sardella* larvae.

Species	Total length (TL) (μm)	Dry weight (W) (μg)
Copepod nauplii	Measured directly	$\ln W = -13.824 + 2.370 \ln TL$ $n = 6$; TL:140 – 290 μm (Irvine and Waya, 1995)
T.cunningtoni (Calanoid copepod)	$TL = -331 + 19.195FL$[a] $n = 49$; TL:450 – 1050 μm (Irvine, 1995a)	$\ln W = -17.56 + 2.732 \ln TL$ $n = 29$; TL:462 – 1178 μm (Irvine and Waya, 1995)[b]
T.neglectus (Cyclopoid copepod)	$TL = 49 + 10.058$FL $n = 78$; TL:272 – 985 μm (For *T.neglectus* and *M. a. aequatorialis* combined; Irvine, unpublished data)	$\ln W = -16.69 + 2.67 \ln TL$ $n = 12$; TL:285 – 532 μm (Irvine and Waya, 1995)[b]
M.a.aequatorialis (Cyclopoid copepod)		$\ln W = -8.07 + 1.31 \ln TL$ $n = 28$; TL:418 – 874 μm (Irvine and Waya, 1995)[b]
D.excisum (Cladocera)	$TL = 59.6 + 6.20ML$[c] $n = 34$; TL:540–1050 μm (Irvine, 1995)	$\ln W = -6.58 + 1.06 \ln TL$ $n = 8$; TL:690 – 1020 μm (Irvine and Waya, 1995)

[a]FL = furcae length (μm); [b]Copepods <0.5 mm TL and ≥0.5 mm TL were assumed to be *T.neglectus* and *M.a.aequatorialis*, respectively; [c]ML = mandible length (μm).

1993 (Table I). From 33 to 56 samples cruise^{-1} were collected during daylight with a high speed plankton sampler (Brander *et al.*, 1993) using a two net system throughout the open waters of the lake >3 km offshore. Samples were assigned to one of six lake areas delimited by lines of latitude, with the southern boundaries of each of the six areas (Areas 0, 1, 2, 3, 4 and 5) being 14°20′S, 13°45′S, 13°08′S, 12°14′S, 11°19′S, and 10°27′S, respectively, which gave an average of 7.5 (range 3–14) zooplankton samples area^{-1} cruise^{-1}. The sampler was towed at 1.5–2.0 m s^{-1} from the surface to 150 m depth (initial five cruises), or from the surface to 200 m depth (remaining cruises), in double oblique hauls. Mesh sizes were 80 μm (initial four cruises) or 56 μm (remaining cruises) aperture for crustacean zooplankton, and 280 μm (initial two cruises) or 140 μm (remaining cruises) aperture for *E.sardella* and *C.edulis* larvae. Changes in mesh sizes and sampling depth were undertaken to ensure improved estimates of the younger stages of copepods and *C.edulis*. Correction factors were used when estimating areal standing biomass values from the larger mesh sizes used earlier in the study (Irvine, 1995a,b). *E.sardella* larvae of 2–3 mm TL were found to be under-represented in the 280 μm mesh net relative to the 140 μm mesh net, with catches of larger larvae showing no significant differences. *E.sardella* larvae were found to be rare below 150 m depth, hence sampling from the surface to 150 m or 200 m would not affect areal abundance estimates (Thompson, 1996). The net was calibrated with a flow meter to measure the volume of water sampled.

Samples were preserved in 4% buffered formalin and numbers, size and species of zooplankton caught were determined in the laboratory. Counts were converted to areal biomass m^{-2} for zooplankton (Irvine, 1995a) and numbers or biomass m^{-2} for *E.sardella* larvae (Thompson, 1996).

The average instantaneous mortality rate of *E.sardella* larvae of 5–9 mm TL was calculated for nine cruises from May 1992 to November/December 1993 for each of the six lake areas. Samples were pooled by area and cruise. No estimates of mortality rate were obtained in February/March 1992 owing to very low densities of fish larvae. A least-squares linear regression was fitted to log-transformed numbers of larvae in each mm size class regressed against total length. The slope of the regression line gives the instantaneous mortality rate mm^{-1}. The advantage of using growth rate units of mm^{-1} rather than day^{-1}, is that no assumption is made about growth rate. Each data point in the regression plot was assumed to be independent, since sampling at a single point in time implies that larvae in the different length classes are derived from different spawning periods. This method assumes that there has been a constant hatching rate, growth rate, and mortality rate over the previous month (the approximate age of a 9 mm larva, Thompson, 1996).

Results

The diet of first-feeding E.sardella larvae

The first food taken by *E.sardella* larvae consisted of small spherical algal cells, with a diameter of 5–9 µm. The cells seen in the gut did not appear to be colonial and a mucilage sheath was not observed. Transmission electron micrographs show that these cells have a distinct cell wall, a conspicuous pyrenoid, a nucleus, and membrane bound vesicles in the cytoplasm, and were tentatively identified as Chlorophyta. Degnbol (1982) records similar algal cells from the guts of *E.sardella* larvae which he tentatively identifies as *Botryococcus braunii* Kützig (Chlorophyta). Mucilage strands and the matrix in which *B.braunii* cells are imbedded, were not observed by Degnbol (1982), nor in the present study, and this identification may be in error.

An estimate of the abundance of the algal cells in the guts of 290 *E.sardella* larvae of 2–9 mm TL from six cruises (Table I) was determined. These cells occurred in 27 of 33 larvae of 2 mm TL examined and, on average, occupied 30% of the gut length. The abundance in the gut was inversely related to the size of the larvae. By 4 mm TL the cells occupied, on average, 10% of the gut length, and by 8–9 mm TL their occurrence in the gut was negligible (Figure 1). No other types of phytoplankton were observed in larvae of 4 mm TL or smaller.

The diet of larger E.sardella larvae

Crustaceans were the main zooplankton food items eaten by larger *E.sardella* larvae (Figure 1). The smallest larva with zooplankton in the gut, which contained the remains of a single copepod nauplii, was 3 mm TL. However, the presence of zooplankton in the gut of 3 mm larvae was atypical. Nauplii were regularly found in the guts of larvae from 4 mm TL up to the largest size examined of 11 mm TL, although their contribution to the diet was <10% by weight in larvae >8 mm TL. Copepodite cyclopoid and calanoid copepods, and the cladoceran *D.excisum*, appeared in the diet of larvae >5 mm TL. Most of the cyclopoids eaten were small and probably *T.neglectus*, which grows to a maximum length of 540 µm.

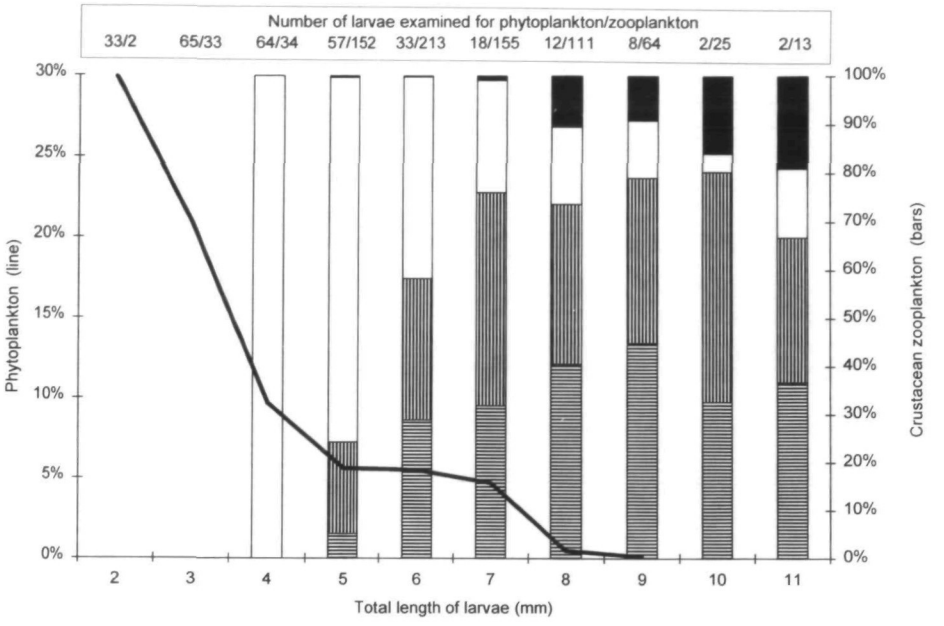


Fig. 1. The occurrence of the 'small' algal cells as a percentage of the linear length of the gut occupied (line, left-hand axis) and of crustacean zooplankton as a percentage of the dry weight in the gut (bars, right-hand axis), from the open waters of Lake Malawi. Key to bars: copepod nauplii (open), *T.cunningtoni* (calanoid copepod, solid), *T.neglectus* and *M.a.aequatorilis* (cyclopoid copepods, horizontal barring), and *D.excisum* (cladoceran, vertical barring).

M.a.aequatorialis, the larger cyclopoid in Lake Malawi, grows to a total length of almost 1000 μm, but individuals approaching this size were apparently not eaten by larvae. The calanoid *T.cunningtoni* has a maximum length of 1200 μm, and contributed significantly to the diet of larvae exceeding 9 mm TL. The only other zooplankton species recorded in the guts of *E.sardella* were single occurrences of the cladoceran *Bosmina longirostris* and the rotifer *Brachyonus* sp.; two species that were rare in the open water plankton of Lake Malawi.

There is a degree of selectivity in the size range of the crustaceans eaten, when compared to the size range present in the aquatic environment (Figure 2). Only nauplii with a size of <200 μm were found in the guts of 4 mm larvae, whose gape size is ~0.27 mm. (Gape (mm) = 0.077TL (mm) – 0.070; Thompson, unpublished.) It appears that larger prey are unable to be swallowed, whereas, copepods and cladocerans up to 1000 μm were found in the guts of larvae of 10 mm TL, whose gape size is ~0.7 mm. However, smaller prey items were under-represented in the guts when compared to the size range observed in the pelagic environment. This indicates a degree of feeding-selectivity with a preference towards larger prey items.

Phytoplankton, other than the small spherical algal cells seen commonly in the small larvae, were rare in the guts of *E.sardella* larvae of 5–11 mm TL and occurred in only 44 of 803 larvae examined. Most were concentric diatoms with diameters of 12–72 μm, and resembled *Stephanodiscus* in appearance. A few

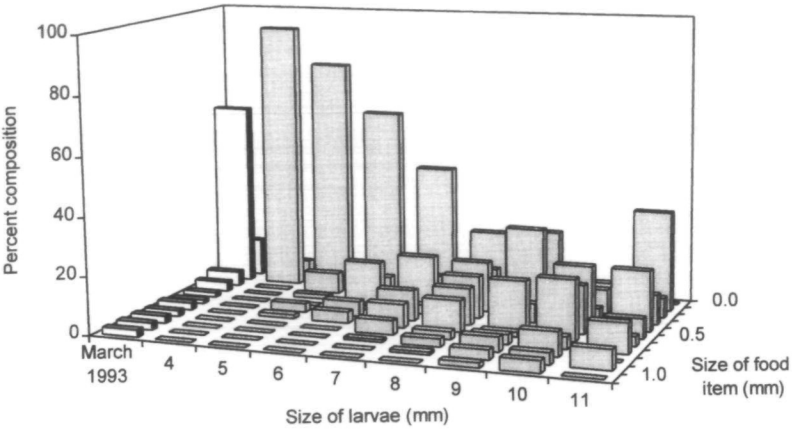


Fig. 2. The percent composition by number of the size range of crustacean zooplankton food items found in the guts of *E.sardella* larvae of 4–11 mm total length from Area 1 in Lake Malawi in 1992–1993 (stippled bars) compared with the size range of crustacean zooplankton found in the natural environment in March 1993 (open bars).

other types of algae were recorded and identified on their overall shape as *Surirella*, *Staurastrum*, *Oocystis*, *Eudorina*, and some colonial Cyanophyta. The number of individual phytoplankton cells, other than of the small spherical cells, was usually only one or two larvae^{-1}, but occasionally up to 10 were recorded.

Seasonal patterns in diet

There were significant differences among the six cruises in the average amount of the small spherical algae in first-feeding larvae (F = 3.0; d.f. = 5,213; $P < 0.05$, Figure 3a). These differences in the small algal component of the diet were due to more algae being present in the guts during samples taken in July 1992 and September 1993. Since the identification of this algae is tentative, it is not possible to relate this to changes in the natural population in Lake Malawi.

The relative weight of zooplankton in the gut of *E.sardella* larvae, expressed as a percentage of the body weight, showed significant differences for samples from eight cruises collected from Area 1 (F = 10.7; d.f. = 7,686; $P < 0.01$, Figure 3b). The relative weight of zooplankton in the guts of *E.sardella* larvae was low during May 1992 and March 1993, and increased towards December 1992 and September 1993. However, the relative weight of zooplankton in the guts of larvae was not significantly correlated with the total zooplankton biomass in Lake Malawi (r = 0.22; n = 8; $P > 0.05$), or with mortality rates of larval *E.sardella* (r = 0.48; n = 8; $P > 0.05$).

Relationships with mortality rate

The average of 54 instantaneous mortality rates of *E.sardella* of 5–9 mm TL was 0.39 mm^{-1} and ranged from a maximum of 1.10 mm^{-1} to a minimum of –0.26

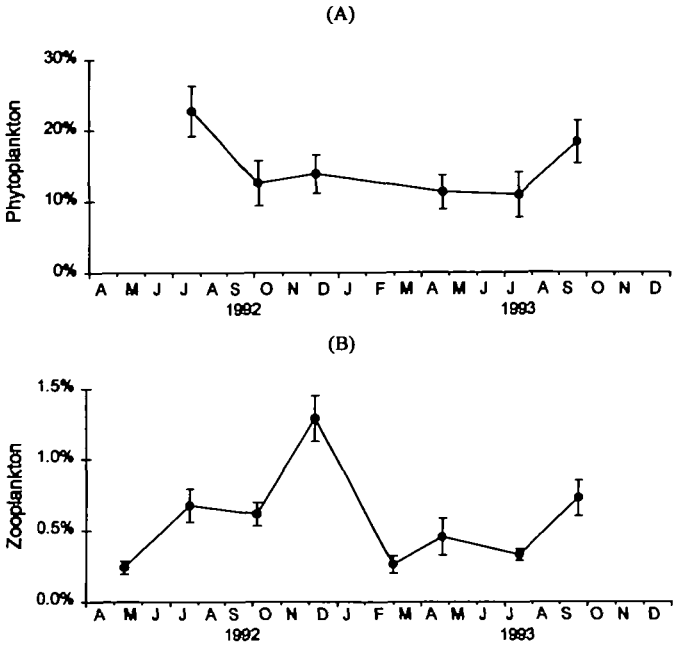


Fig. 3. Seasonal patterns in the (A) percent length of gut occupied by the 'small' algal phytoplankton in *E.sardella* of 2–5 mm total length, and (B) crustacean zooplankton as a proportion of body weight in *E.sardella* of 5–9 mm total length. Error bars are ±1 SEM.

mm^{-1}, for the six lake areas and nine cruises. Two rates were negative, indicating that the assumption of constant hatching does not always hold. Significant negative correlations between mortality rate and total crustacean zooplankton areal biomass were observed in Areas 0 and 1 ($P < 0.05$, Figure 4). The overall correlation for all six areas combined was also highly significant ($r = -0.42$; $n = 54$; $P < 0.001$).

There was no significant correlation between overall instantaneous mortality rate for larvae of 5–9 mm TL and relative weight of food in the guts from all six length classes of larvae ($r = -0.31, -0.52, -0.50, -0.58$ and -0.62 for the 5, 6, 7, 8 and 9 mm length classes, respectively, $r_{P=0.05;n=8} = 0.63$).

Seasonal patterns in biomass and mortality

Total crustacean zooplankton standing biomass fluctuated seasonally with maximum values of over 2.5 mg dry weight m^{-2} around July in 1992 and 1993, and minimum values of approximately 1 mg dry weight m^{-2} in April–May, giving a range of ~2.5 times (Figure 5a). In Area 1, the average percent compositions of the total crustacean zooplankton standing biomass were: *T.cunningtoni* (62.4%), *M.a.aequatorialis* (13.6%), nauplii (11.5%), *T.neglectus* (8.3%), *D.excisum* (3.6%), and *B.longirostris* (0.7%). The biomasses of the above six groups were correlated with total crustacean zooplankton biomass (r = 0.92, 0.82, 0.45, 0.48,

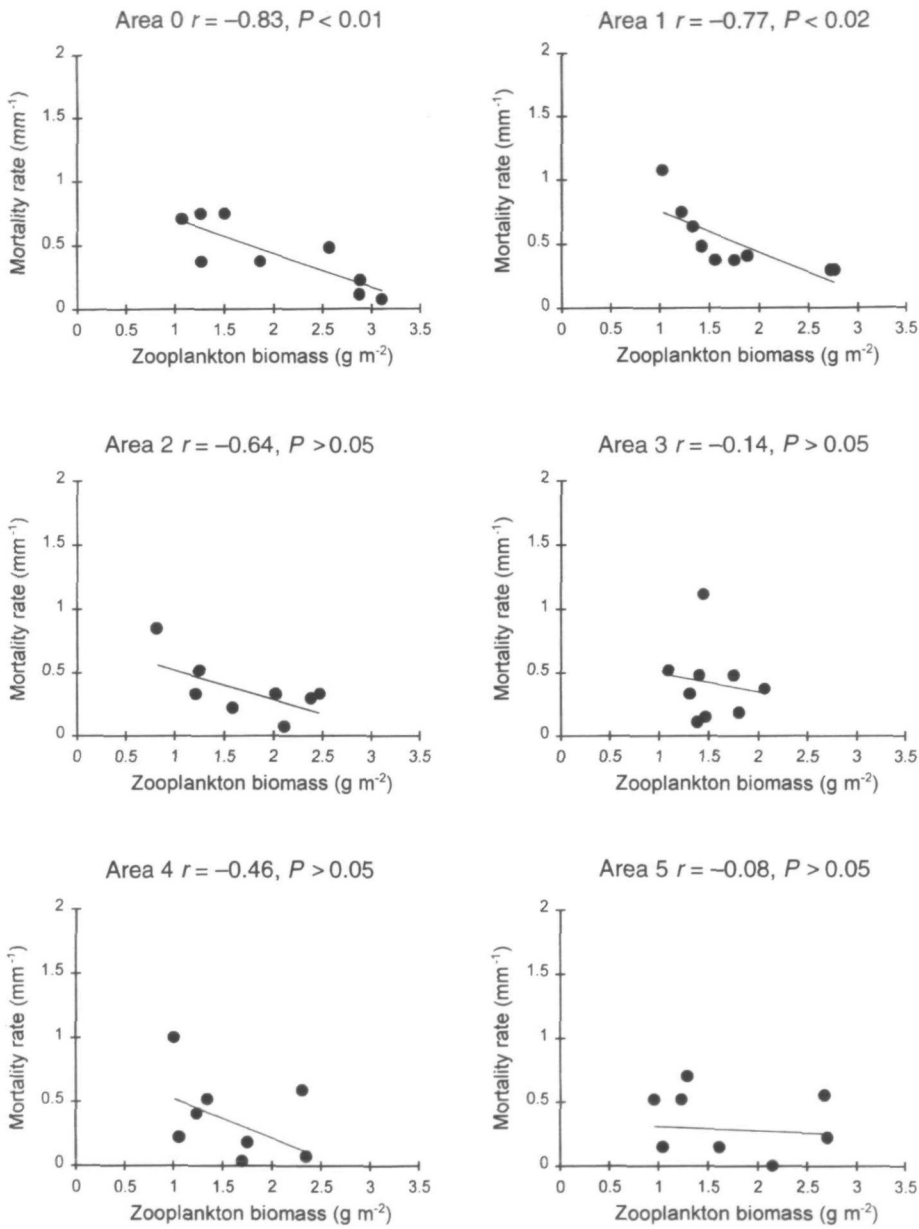
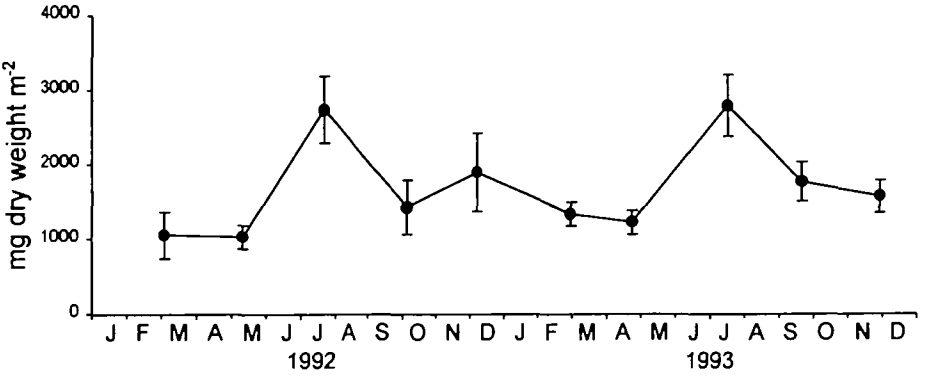
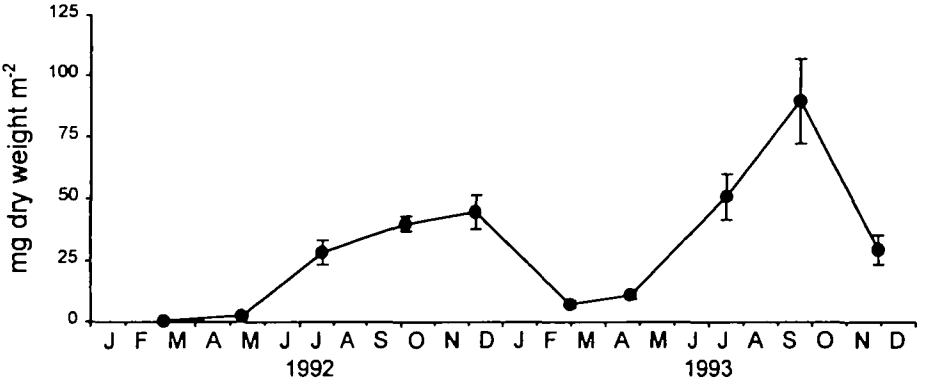


Fig. 4. Correlations between the instantaneous mortality rate (mm^{-1}) of *E.sardella* larvae and total crustacean zooplankton biomass (g dry weight m^{-2}) from nine cruises between May 1992 and November/December 1993 for six areas in Lake Malawi. The overall correlation for all six areas combined is $r = -0.42$; $n = 54$; $P < 0.001$.



(B)



(C)

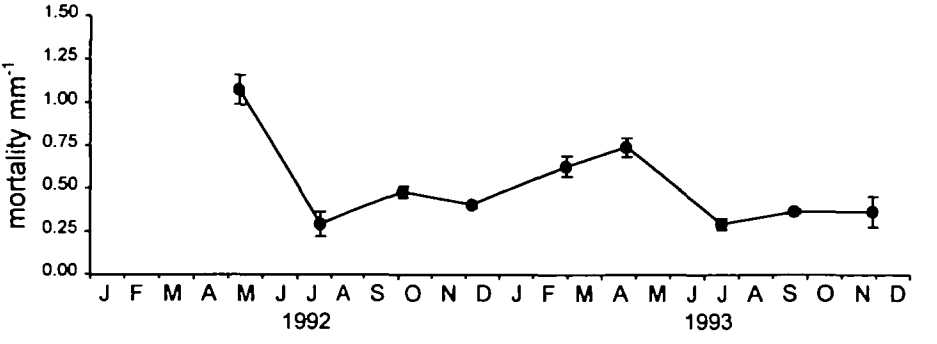


Fig. 5. Average seasonal standing biomass values for (A) crustacean zooplankton, (B) *E.sardella* larvae, and (C) mortality rates mm^{-1} of *E.sardella* larvae, for Area 1. Error bars are ± 1 SEM.

0.45, 0.87, respectively, $r_{P=0.05;n=10} = 0.58$) over the ten sampling periods, showing that the biomasses of these groups tended to fluctuate in synchrony.

The biomass of *E.sardella* larvae from Area 1 also fluctuated seasonally and approximately, but not significantly, in phase with total zooplankton biomass

($r = 0.51$; $n = 10$; $P > 0.05$), although this correlation was highly significant when all six areas were combined ($r = 0.49$; $n = 60$; $P < 0.001$). The magnitude of the fluctuations in larvae biomass was ~30 times, ranging from 2.7 to 89.4 mg dry weight m^{-2} in Area 1 (Figure 5b).

The instantaneous mortality rate of *E.sardella* larvae of 5–9 mm TL also showed seasonal variations. Mortality rates were high in May 1992 and April 1993 at 1.10 and 0.74 mm^{-1}, respectively, with lower rates of 0.29–0.63 mm^{-1} at the other sampling periods (Figure 5c).

Discussion

Variation in the biomass (Hecky and Kling, 1987; Bootsma, 1993a; Patterson and Kachinjika, 1993; Patterson *et al.*, 1995) and production (Degnbol and Mapila, 1982; Bootsma, 1993b) of phytoplankton occurs in Lake Malawi over time scales from a few days to regular seasonal patterns which repeat annually. These variations are primarily caused by changes in meteorological conditions, which result in surface cooling and mixing. Both these processes lead to the entrainment of deep, nutrient-rich waters into the mixed surface layers, especially at the southern end of the lake (Eccles, 1974; Bootsma, 1993b; Patterson and Kachinjika, 1995). This is reflected in changes in the biomass of the crustacean zooplankton and *E.sardella* larvae. These populations all fluctuate approximately in phase, showing maxima around July to September and minima from January to April (Allison *et al.*, 1995). Cichlids comprise 88% of the open water adult fish biomass, and their populations show little seasonal (and probably little annual) variation in abundance (Thompson *et al.*, 1996a). This is to be expected for *k*-selected fish species that live for many years and are typically adapted to a more constant environment (Pitcher and Hart, 1982; Lowe-McConnell, 1987). The cyprinid *E.sardella*, however, shows large fluctuations in abundance within and between years (Turner, 1982; Thompson *et al.*, 1996b). This species is short lived with high adult numbers resulting from good survival in the larvae stage (Tweddle and Lewis, 1990; Thompson, 1996; Thompson *et al.*, 1996b). *E.sardella* appears to be the only fish species whose population size is able to respond quickly enough to exploit the seasonal variation in Lake Malawi, owing to its *r*-selected life-history strategy.

The diet of *E.sardella* shows ontogenic shifts. The size at first-feeding can not be accurately defined, as the spawning sites are unknown and eggs and yolk-sac larvae are found extremely rarely in the plankton (Thompson, 1996). However, it is clear that small algal cells of 5–9 μm diameter are the first food of the larvae. The guts of 2–3 mm TL larvae almost always contained many of these cells that, on average, occupied 20–30% of the length of the gut. It is unlikely that such small items could be actively selected by a visual predator, and it seems likely that these food items are ingested by filter-feeding. Filter-feeding in fish larvae has been recorded in *Gadus morhua* and *Engraulis capensis*, and has been noted as a mechanism that allows successful feeding during day and night periods (James and Findlay, 1989; van der Meeren, 1991). The zooplankton diet of the *E.sardella* larvae of 4–11 mm TL was typical of that observed in most cyprinids (Mark *et al.*, 1987). Larvae of 4 mm TL ate the smallest zooplankton, nauplii in this case, with the larger prey items,

such as copepodite copepods and cladocerans, being eaten by larger larvae. There were no other food items of a suitable size available for *E.sardella* to eat in the open water pelagic zone of Lake Malawi. It is worth mentioning that *E.sardella* hatches at approximately 2 mm TL. This is small for a cyprinid, with more typical sizes at hatching being 4–7 mm TL (Williamson, 1964; Bracken and Kennedy, 1967; Kennedy, 1969). The smallest size of larvae regularly containing nauplii in their guts were 4 mm TL, and so the availability of phytoplankton to 2–3 mm TL larvae would be vital to the survival of post yolk-sac larvae.

Apart from the small algal cells, phytoplankton were rare in the diet of offshore *E.sardella* larvae. This contrasts with Degnbol's (1982) study on the diet of *E.sardella* larvae collected off Nkhata Bay (11°36'S 34°18'E) on 7–8 June 1979, when phytoplankton were recorded commonly in the diet. Another difference was that Degnbol did not record nauplii in the diet of *E.sardella* larvae, whereas they were a common and essential part of the diet of larvae of 4–5 mm TL in the present study. The reason for these differences is unknown, although it is possible that the availability of food items in the one day study by Degnbol was atypical.

A number of studies have attempted to relate zooplankton abundance to the quantity of food in the gut of fish larvae, with some recording improved growth rates at higher zooplankton densities (Øiestad and Moksness, 1981; Karjalainen, 1991; Canino *et al.*, 1991; Fortier *et al.*, 1995). However, the relationship between zooplankton abundance and the amount of food in the gut may not be a simple one, owing to changes in evacuation rates with food intake rates (Govoni *et al.*, 1986). In the present study, the gut contents of *E. sardella* larvae, expressed as a percentage of body weight, was not correlated with total crustacean zooplankton biomass, nor with larval *E.sardella* mortality rates. However, differences in gut contents weight were observed among sampling dates, and the correlations above were in the direction expected.

How does the seasonality in the food supply affect the survival of *E.sardella* larvae? Before answering this question it is worth noting that the units of mortality used in this paper are mm^{-1} and not day^{-1} as is more usual. This is because growth rates of *E.sardella* larvae throughout the year are unknown. The few available estimates show that growth rate is variable: 0.43 mm day^{-1} (calculated from Figure 2.2 in van Lissa, 1982), and 0.22 and 0.31 mm day^{-1} (Thompson, 1996). Hence, the observed differences in mortality rate mm^{-1} could arise from changes in daily growth rates and/or from changes in daily mortality rates. It is also likely that these two processes are not independent, as slow growing larvae may be less capable of escaping from predators.

Allison *et al.* (1996) found that *E.sardella* larvae up to 15 mm TL suffered high predation mortality from the cichlids *Rhamphochromis longiceps* (Günther) and *Diplotaxodon limnothrissa* G.F. Turner, but that predation mortality on *E.sardella* larger than 15 mm TL was much reduced. Therefore, there is a vulnerable size-range through which *E.sardella* must grow. This is likened to the concept of 'susceptible windows of predation' developed by Ricker and Foerster (1948) and Cushing (1976), and also mentioned by Cushing and Horwood (1994) when considering overall mortality through the larval phase. Overall mortality is therefore directly proportional to the time spent in this 'window'. If the daily predation

mortality rate is assumed to be constant and the main source of mortality, then the observed variations in mortality rates of *E.sardella* larvae mm^{-1} throughout the study could be accounted for by a 3.6-fold range in daily growth rate. This is a little outside the observed range in growth rates of 0.22–0.43 mm day^{-1}. Larvae can grow quickly when food is abundant and hence suffer a lower overall mortality and *vice versa*. However, the processes operating on the mortality of *E.sardella* larvae are known to be more complex than this. Allison *et al.* (1996) has shown that *E.sardella* larvae were a significant component of the diet of *D.limnothrissa* sampled in the south of the lake in August and November 1992, but were virtually absent from the diet in February 1993. Comparisons with Figure 5b show that *E.sardella* larvae were abundant in the plankton during the initial two sampling periods, but almost absent on the last sampling period. *R.longiceps* feed consistently on *E.sardella* during the above three sampling dates, but feed on larvae during August and November 1992, and shifted towards feeding on larger *E.sardella* of 30–70 mm TL during February 1993, although some larvae were still eaten. Therefore, there may be a degree of density-dependent mortality according to *E.sardella* larvae abundance, although this appears not to be compensatory enough to ameliorate the effects of a rapid growth rate.

Acknowledgements

ABT is very grateful for laboratory facilities provided by Prof. Barry Roberts, Trinity College, University of Dublin, and to Dr Ro Lowe-McConnell for much assistance and helpful advise. KI wishes to thank several algologists for examining TEM photographs of the small algal cells in the guts of *E.sardella* larvae. We are both grateful for comments made by two anonymous referees.

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Received on April 2, 1996; accepted on September 30, 1996