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POPULATION STRUCTURE, FEEDING BEHAVIOUR AND FECUNDITY OF THE LOBATE CTENOPHORE, BOLINOPSIS INFUNDIBULUM

by

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Abstract

The lobate ctenophore Bolinopsis infundibulum (O.F. Müller) is a dominant predator in a Scottish sea loch between April and mid July each year. The maximum density recorded over a three year period was 28 m^{-3}. It feeds on a wide unselected range of herbivorous zooplankton at a constant rate over the natural range of prey densities. Although Bolinopsis are capable of producing eggs throughout their growing season, field evidence suggests that, in 1977 two generations were produced, one in April/May and the other in June/July out of which a very few individuals will overwinter.

Introduction

The tentaculate ctenophores are important pelagic predators whose numerical abundance has frequently resulted in an observed inverse relationship between their density and that of their herbivore prey (Kamshilov, 1960; Fraser, 1962; Burrell & van Engel, 1976). Recently specific work has been done on the predation ecology of Pleurobrachia spp. (Hirota, 1974; Greve, 1971, 1972) and on the lobate genus Mnemiopsis (Baker & Reeve, 1974; Walter, 1976; Kremer, 1976a). This paper summarises observations made on a population of Bolinopsis infundibulum occurring in a small sea loch, L. Thurnaig, on the west coast of Scotland.

Population Structure

Bolinopsis is one of the most delicate macroplankters. It cannot withstand any handling in air, it is broken up by conventional plankton nets and it disintegrates on contact with preservatives such as formaldehyde. Consequently two special methods were adopted to survey the population. Firstly "in-situ" counts were made using diving gear and secondly a new net was devised for collection of live, intact, individuals. The diving sampling was carried out at a single site and consisted of horizontal traverses at four depths, 0-2 m, 9-11 m, 19-21 m and 29-30 m (bottom). Ctenophores which passed through a 50 cm x 50 cm square frame pushed along each traverse were counted.

The Bolinopsis population, like Mnemiopsis leidyi in Narragansett Bay (Kremer & Nixon, 1976) is pulsed; ie it blooms for a short period each year (Fig. 1b). During this period numbers rise to a maximum in June only to crash dramatically in July. Diving observations were continued throughout the winter of 1975-76 during which occasional sightings were made of single individuals in the 40 m^3 sampled. Bolinopsis showed a distinct avoidance of the surface waters and a preference for midwater (Fig. 1a). Dense concentrations at the surface were only seen at times of high abundance, eg mid-June 1976, or when the sea state was exceptionally calm or into July when isolated lobes or senile, decaying individuals became very common. No diurnal vertical migration was noted during a 24 hour observation period in June 1977 while a vertical "drop-dive" survey throughout the loch revealed a horizontally uniform population with a density maximum between 10-15 m.

A net survey of the 1977 population pulse was carried out with a 1 m diameter 950 µ net fitted with a 25 l detachable cod-end bucket. This net, when towed very slowly (0.2 m sec^{-1}) collected the Bolinopsis in sufficiently intact condition for measurement along the oral-aboral (gut) axis. Duplicate vertical hauls were made at four stations, three within L. Thurnaig and one at the entrance, in L. Ewe, at two week intervals from mid March until the end of July. As with the "drop-diving" survey the population was seen to be uniformly spread throughout the loch.

The growth of the population is shown in Fig. 2 which represents the sum of the collection of individuals from all stations. The abundance curve (Fig. 2a) follows much the same form as the 1977 diving observation: a gradual increase until late June/early July followed by a rapid decline before the end of July. Over 200 Bolinopsis were collected on July 8 but only one on July 27. The absolute abundance values have not been fitted to Fig. 2a since the net filtration efficiency is still being determined (the slow speed of towing necessary to collect intact Bolinopsis is at the limit of T.S.K. current meter accuracy).

The population size structure changes (Fig. 2b) suggest that a single generation of ctenophores, presumably produced from overwintering individuals developed from April until early June after which a second influx of small individuals became apparent. The uniform abundance (Fig. 2a) from May until mid-June together with the steady increase in the average population size is also evidence for a single generation of ctenophores growing steadily during the period. However, despite the late June influx of small individuals the entire population disappears in mid-July except for the few, very sparsely distributed, overwintering individuals.

Feeding Behaviour

Bolinopsis infundibulum like other tentaculate ctenophores is a voracious predator on herbivorous zooplankton. The feeding response curves of three different sizes of Bolinopsis are illustrated in Fig. 3, together with the calculated filtering rates. 8 hour feeding experiments were carried out at 9-11°C in constant darkness, for the two larger size groups, in 5 l beakers containing 4.75 l of 68 µ filtered sea water. The smallest group were contained in 1 l of water in proportionately smaller vessels. Each point represents the mean of five independent observations. The food material was 250 µ mesh retained organisms consisting primarily of the copepods Temora longicornis Acartia clausi and Pseudocalanus elongatus. Cladocerans were excluded because of their tendency to stick to the water surface. Feeding rate, as emphasized in Fig. 3a, is linearly related to prey density; a slope of unity best describes the log: log relationship. This is corroborated by the filtration rates which are more or less constant over the range of fish densities measured. The only suggestion of any non-linearity is at the highest food concentration used, 160 copepods l^{-1} (Fig. 3b), but in this situation it is felt that the ctenophore will still filter at the same rate, although the gut itself cannot cope. At these high concentrations boluses of live copepods enmeshed in ctenophore mucus are frequently produced. This behaviour furthermore occurs at concentrations in excess of natural levels.

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STRUCTURE DEMOGRAPHIQUE, COMPORTEMENT ALIMENTAIRE ET FECONDITE DU LOBATE CTENOPHORE, BOLINOPSIS INFUNDIBULUM

par

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Précis

Le lobate ctenophore *Bolinopsis infundibulum* (O.F. Müller) est un prédateur dominant dans un bras de mer écossais, chaque année, entre avril et la mi-juillet. La densité maximale enregistrée au cours d'une période de trois ans était de 28 m^{-3}. Il se nourrit d'une grande variété, non sélectionnée, de zooplancton herbivore à un rythme constant sur la plage naturelle de densité des proies. Bien que les *Bolinopsis* soient capables de produire des oeufs pendant toute leur saison de croissance, les études effectuées sur place laissent penser qu'en 1977 deux générations ont été produites, une en avril-mai et l'autre en juin-juillet et que, sur la quantité, très peu d'entre eux survivront à l'hiver.

Prey capture by Bolinopsis depends largely on the stimulation of the sensitive inner surface of the extended lobes which causes their rapid contraction to trap the prey in a pouch around the mouth and buccal tentacles. It would seem therefore that the rate of intake is a function of lobe area which, considering the average gut lengths of the size groups measured (7.3, 16 1 and 32.1 mm) should mean that their respective feeding rates will increase by a factor of 4. It can be seen however in Fig. 3a that only the two smaller groups have this relationship (mean ratio 1:4.37) while ratio of intermediate largest size group is only 1:1.64. Since there was a proportional increase in experimental vessel size between the two smaller size groups only, this result could be an effect of too small a vessel inhibiting the feeding of the 32.1 mm size group. Perhaps measurement of their feeding rate in 20 l vessels, instead of 5 l, is required.

Observations have also been made on the gut contents of freshly caught individuals in order, primarily, to see whether the ctenophores show any signs of food selectivity. These data have yet to be fully evaluated but an initial assessment suggests that there was no obvious selection. Specific laboratory tests with the two species of copepod Acartia and Temora and with 68 µ Vs. 250 µ mesh zooplankton showed no distinct choice (Table 1). This result is in accord with the observations on natural gut content and indicates the catholic choice of Bolinopsis. All the common neritic plankters were recorded in the gut including fish larvae. Experiments with the latter showed the usual density dependent feeding on 4.5 mm haddock larvae, that 7.00 mm plaice larvae were taken by 12 mm gut length Bolinopsis but that 11.5 mm herring larvae were too strong and evaded capture by Bolinopsis up to 35 mm in length. Interestingly plaice eggs were ingested but ejected undigested from the gut after some hours.

Fecundity

A routine monthly experiment was carried out to measure the egg production by Bolinopsis. Individuals, after being equilibrated overnight, were isolated in 5 l beakers containing 100 copepods. They were then left for 12 hours in darkness. The results, in Fig. 4a, show a well marked direct relationship between size and egg production, that animals down to 8 mm long can produce eggs nd that there were no overt differences between monthly samples. The maximum rate measured represented a daily production of 5000 eggs.

The effect of food consumption on egg production is illustrated in Fig. 4b. In this experiment approximately equal sized individuals were kept for a week in 5 l beakers containing different concentrations of 250 µ copepods. Water was exchanged daily and fresh prey added at the original concentration. The details, listed in Table 2, show that daily egg production was maintained or even increased at the higher food concentrations while it declined at the lower levels. However it appears that there is a latent period of about 4 days before the dietary regime takes effect.

Discussion

Unlike the pulsed Narragansett Bay population of Mnemiopsis leidyi described by Kremer and Nixon (1976), the Bolinopsis infundibulum population pulse does not decline at the end of the autumn when the temperature is dropping and seasonal changes occur. Instead the population abruptly crashed in mid-July on three consecutive years. This raises one intriguing question. A second is why is there apparently only one generation of Bolinopsis during the bloom period?

The egg laying experiments (Fig. 4a) indicate the great reproductive capability of these animals throughout their season, yet the population analyses (Fig. 2b) show large numbers of small individuals only in early May and late June/early July. In this respect the fecundity measurements could be misleading since they may essentially show an induced response to handling and enclosure under experimental conditions. They are more likely to be a measure of reproductive potential rather than reproductive actuality. It was very noticeable during routine monthly gut contents analyses that on June 15th 10% of the potentiall fecund *Bolinopsis* were laying or carrying eggs while on July 12th 57% were in this condition. Clearly the suggestion is that, as with some other ctenophores (Pianka, 1974), there is some synchronisation of the spawning behaviour of *Bolinopsis*.

The other question as to what causes the decline of the population is less easy to understand. Zooplankton collections suggest that, in 1977 particularly when the ctenophores did not reach a high density, there were adequate populations of food organisms. Certainly during this period the predatory scyphomedusan *Cyanea capillata* was present in the Loch, but its density was too low to have such a rapid impact. Routine monthly observations however have suggested that the *Bolinopsis* become senile. The observed natural egg production has already been mentioned, the gut contents in July were less than in previous months (although this has to be corrected for prey density) and the larger individuals performed much less well in a routine monthly feeding experiment. Furthermore increased parasitism (both endo and the ecto-parasitic hyperiids) and a large proportion of deformed, eroding individuals were evident in July. Kremer (1976b) similarly found it difficult to explain the demise of the *Mnemiopsis* population and one might suggest that a natural senescence of the population takes place.

Ctenophores are mostly simultaneous hermaphodites (Pianka, 1974) which implies that there will be very little cross fertilization. Speculatively this might result in the simultaneous decline and ageing of different sized individuals, with the few that survived, the overwintering forms, being the results of rare cross-fertilization.

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TABLE 1 SUMMARY OF CHOICE EXPERIMENTS

Choice	<u>Acartia</u>	us.	<u>Temora</u>	68 /u	us.	250 /u
Total Offered	550		550	700		700
Total Eaten	255		290	436		441
No observations		14			14	

TABLE 2 EGG PRODUCTION AT DIFFERENT FEEDING REGIMES

Regime (Copepods day^{-1})	25	50	100	200	400	800
Total Copepods consumed after 7 days	157	308	515	802	1370	1303
Total Eggs Produced after 7 days	667	591	769	840	2140	1048
Size (Gut length) mm	20.8	18.1	19.0	20.5	22.3	20.8

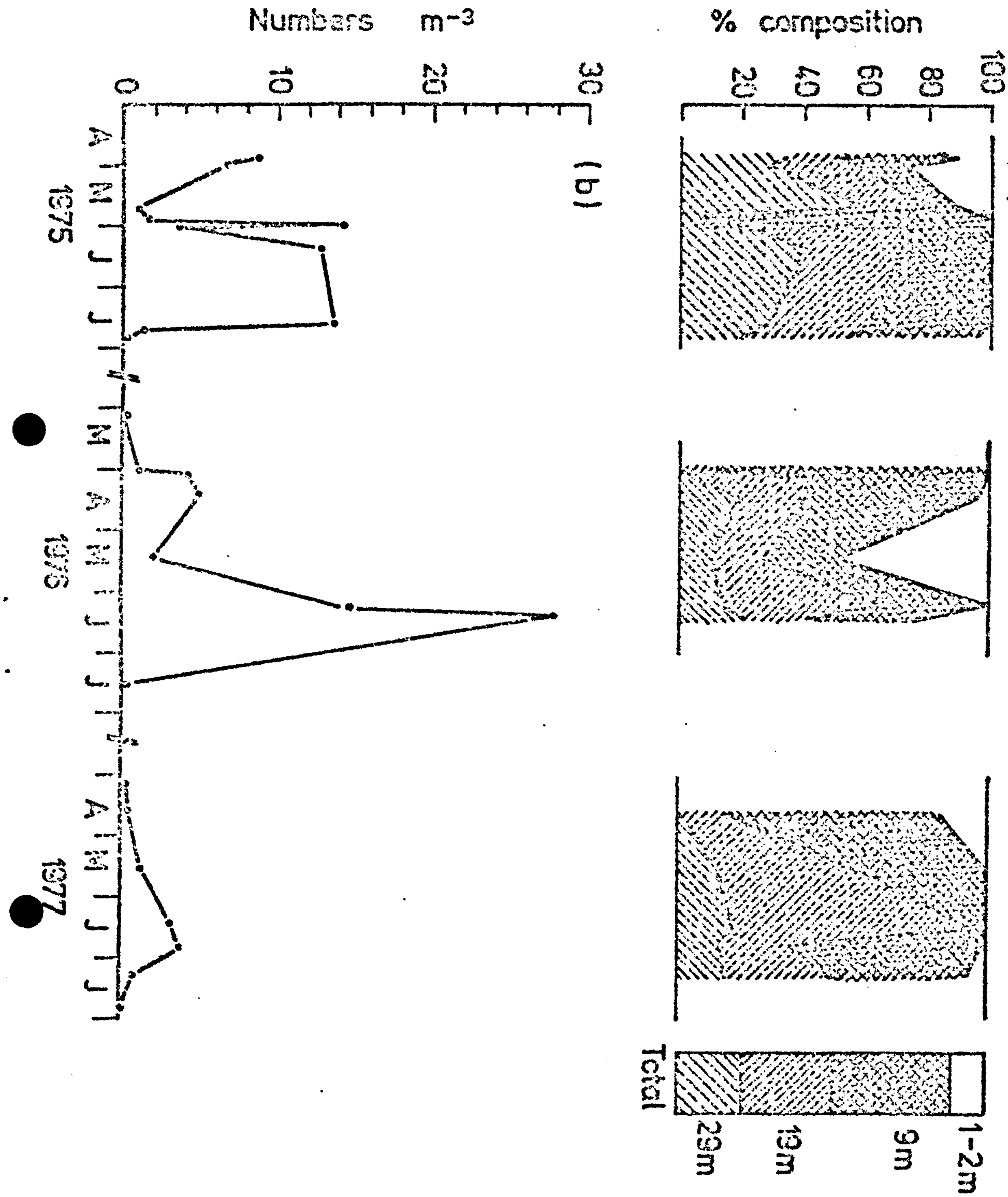

Fig. 1 'In situ' counts of Bolinopsis made along fixed horizontal traverses. (a) Vertical distribution (b) Abundance

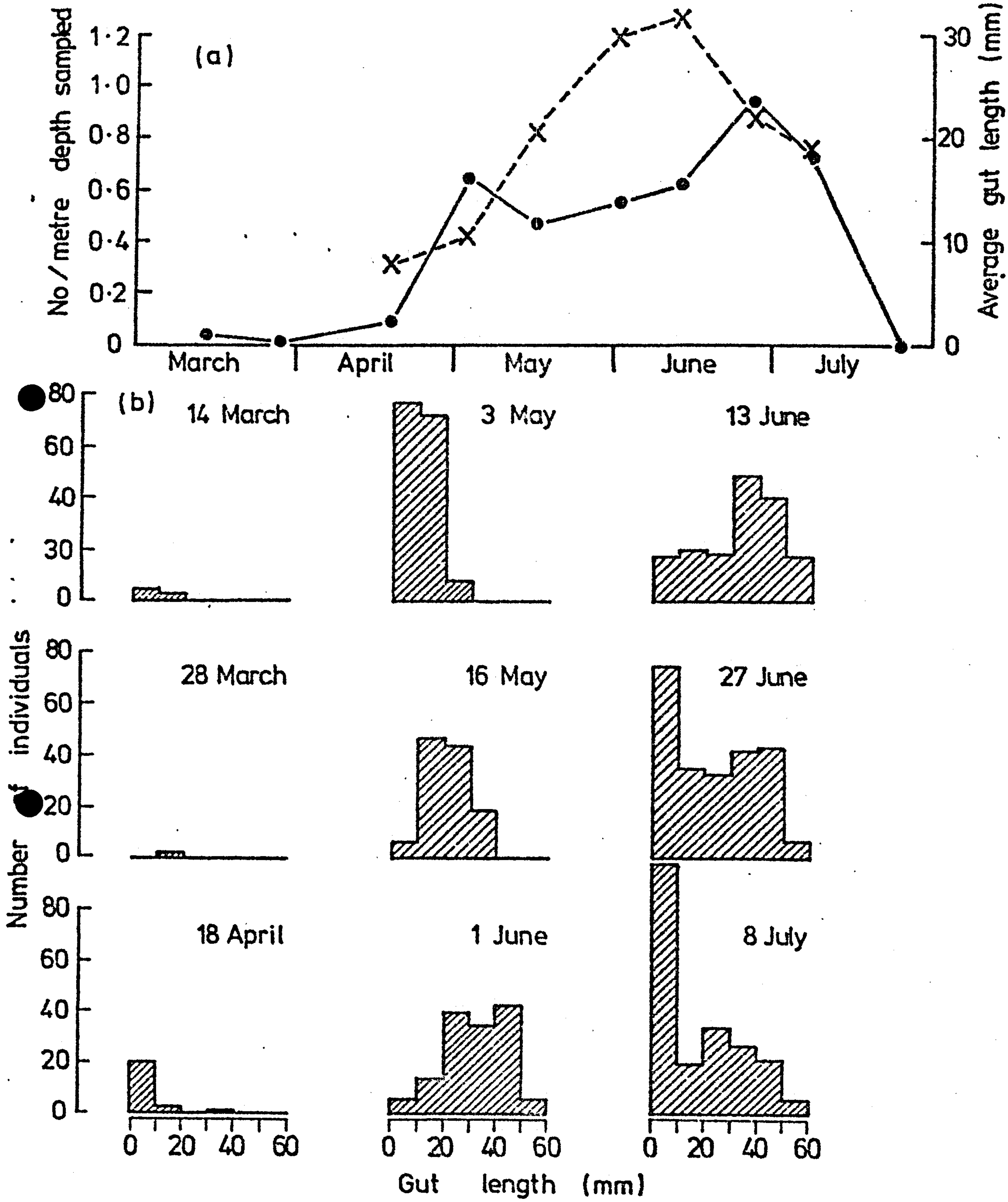

Fig. 2 Growth and development of the 1977 Bolinopsis population as sampled with a 1 m plankton net. (a) Abundance (dots) and average size of samples (crosses), (b) Size group histograms.

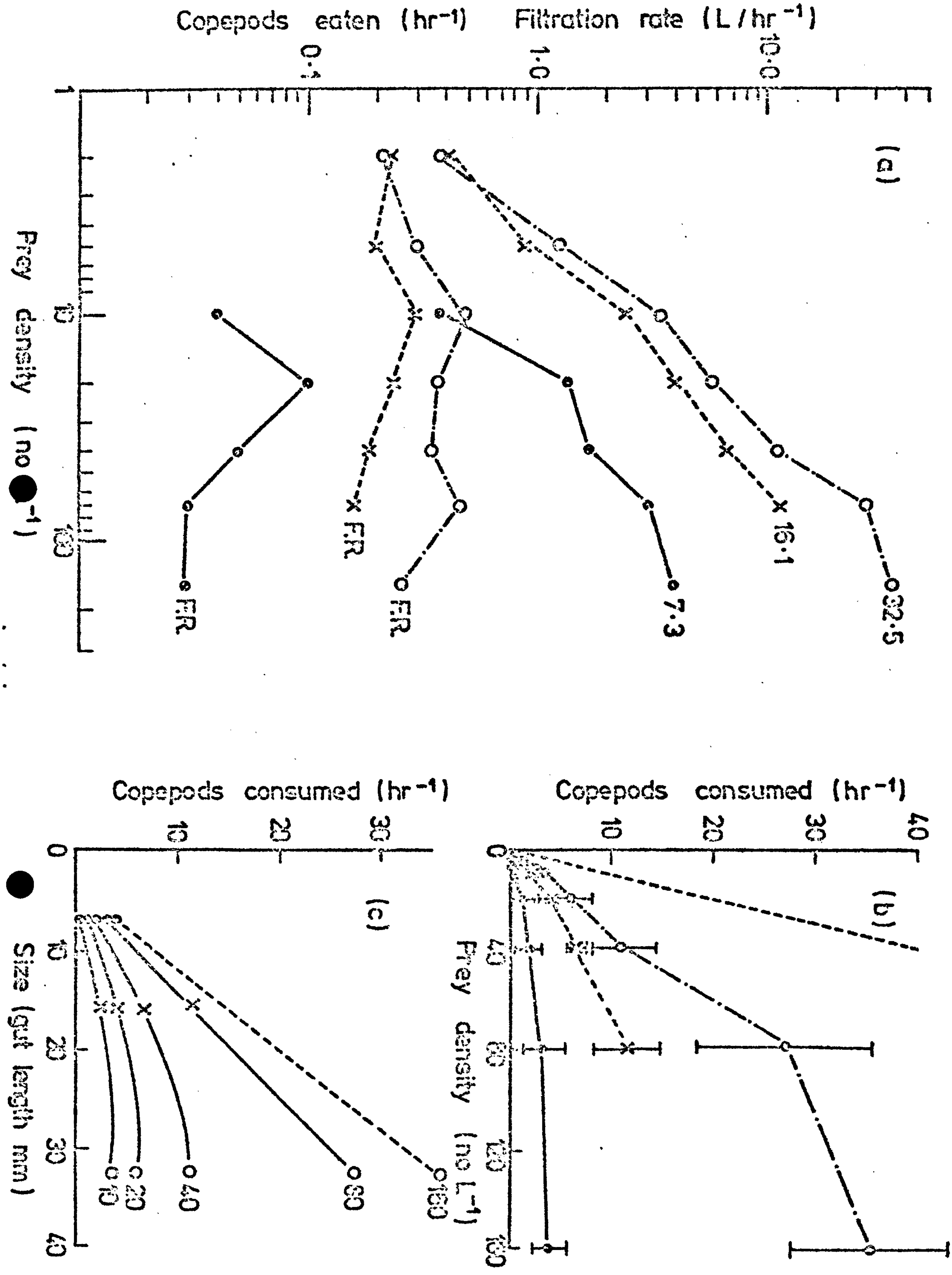

Fig. 3 Feeding rate of Bolinopsis on 250 µ mesh caught copepods. (a) Log plot of consumption rates of three size groups (mm gut length indicated) with their respective filtering rates (F.R.) (b) Linear plots of consumption rates showing means and standard deviations. (c) Consumption rate in relation to size at different copepod concentrations (No. l^{-1} indicated).

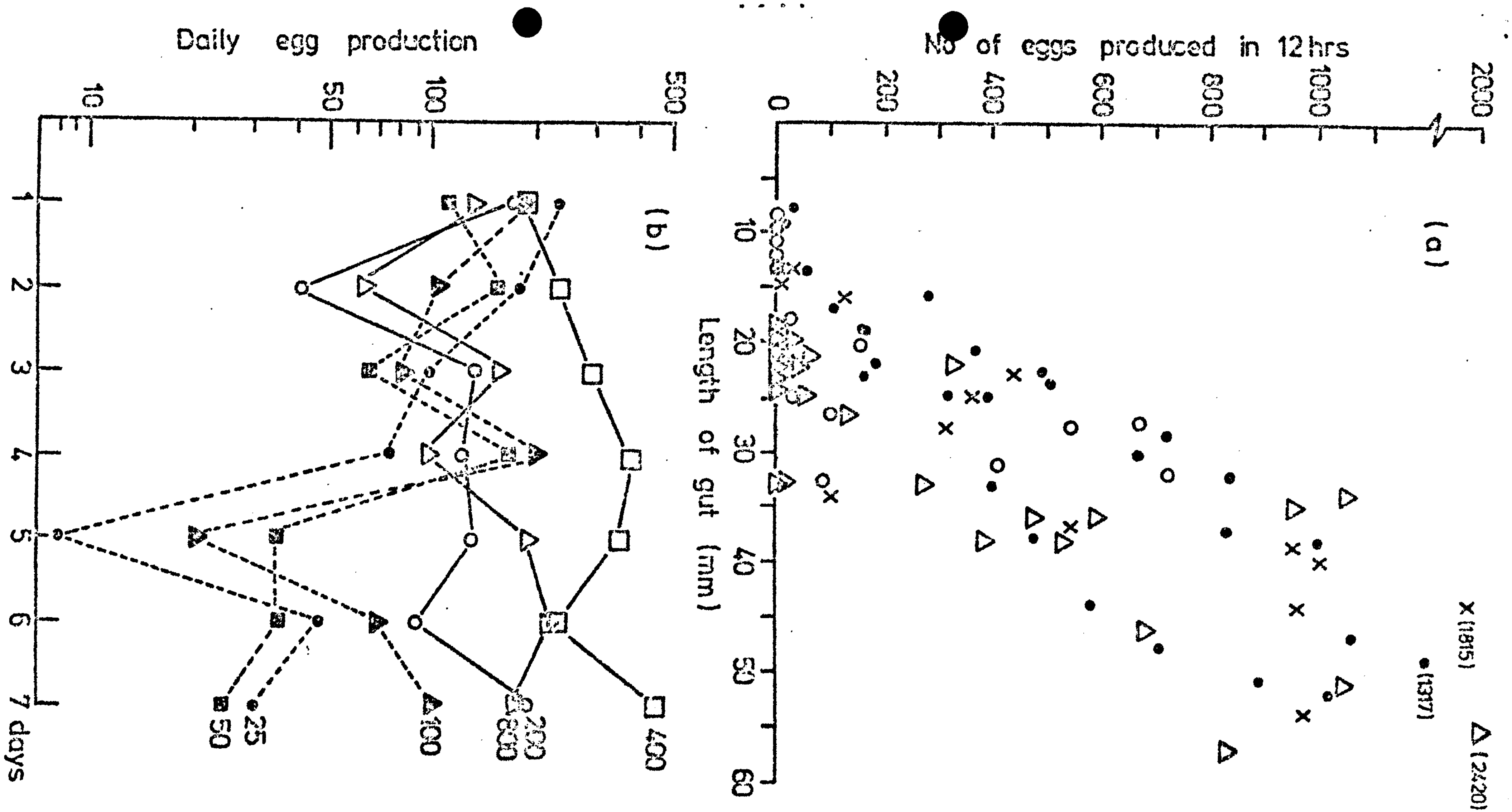

Fig. 4 Egg production of Bolinopsis. (a) Monthly 12 hr experiment; April – dots, May – triangles, June – crosses and July – open circles. (b) Effect of dietary regime on daily egg production of 20 mm (gut length) individuals. (Initial daily food concentration indicated, No. 5 l^{-1}).