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Trophic interactions and production processes in natural zooplankton communities in enclosed water columns. I. Results of CEPEX Foodweb I

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ABSTRACT

Detailed studies of the population dynamics of herbivorous and carnivorous zooplankton were made during the first 40 days of an experiment in two 1300 m3 (CEPEX) enclosures with divergent populations of primary producers, one dominated by diatoms and the other by flagellates. Changes in age structure and vertical distribution are described for the second and third trophic levels, respectively, comprising calanoid copepods, and ctenophores and chaetognaths. Improved sampling methods were used to quantify young Pleurobrachia and all sizes of Bolinopsis, which were previously poorly sampled. Population variations in time and (vertical) space are described for the major herbivore species (calanoid copepods) and their food (phytoplankton), and for the major carnivores (ctenophores and chaetognaths) and their prey (copepods). These field observations within the enclosures were complemented by laboratory experiments to determine growth, feeding rates, and feeding behavior of animals obtained from the enclosures, and from animals maintained in laboratory culture. Analyses of the gut contents of chaetognaths and ctenophores in the enclosures were combined with laboratory observations to provide estimates of food consumption by the enclosure populations. Based on this experimental work, quantitative estimates of trophic interactions between the herbivore and carnivore populations are presented for a period of intense ctenophore predation. Detailed observations of the size distribution of the dominant copepods through time were used to estimate their growth and mortality rates, secondary production, and transfer efficiencies. These data are used to assess the functional role of the dominant zooplankton species in the production ecology of the two systems.

INTRODUCTION

The Foodweb I Experiment was designed to test the hypothesis that the structure of the phytoplankton community determine the type and number of links in the food chain and controls the transfer efficiency from primary production to upper trophic levels. The experiment lasted for 111 days and an overall account of it is given by Grice et al. (1980). This paper is a detailed account of the first 40 days of the experiment a period characterized by 16-18 days of rapid herbivore growth followed by a period of intense predation on herbivores by rapidly growing carnivores.

METHODS

Two 1,300 m^3 Controlled Experimental Ecosystems (CEEs) each 9.5 m in diameter by 23.5 m deep were employed in the experiment. The CEEs were in Saanich Inlet, Canada. Manipulations to encourage the maintenance of a diatom-dominated population in CEE 2 included intermittent gentle bubbling from a depth of 8.5 m, nutrient additions and the placement of a removable screen over the CEE to reduce incident light radiation. A nutrient mix (nitrate, silicate, phosphate) was initially added to the upper 8 m of CEE 2 in a ratio to maintain nitrogen as the limiting nutrient at 7 µg at l^{-1}. Additions were made subsequently whenever this value fell below 1 µg at l^{-1}. Nutrients were initially added to CEE 3 at four times this concentration but silicate was withheld. This massive addition to CEE 3 was intended to stimulate a bloom of the diatoms captured in turn removing all the existing silicate in the water column and binding it in the sediment as the population sank to the bottom.

Phytoplankton and particulate organic matter were sampled with a peristaltic pump. Routinely, 5 depth intervals (0-4, 4-8, 8-12, 12-16, 16-20 m) were sampled three times a week. Primary productivity was estimated by ^{14}C technique (four hour incubations, 1000-1400); composition of particulate matter was investigated by microscopic enumeration and measurement of phytoplankton, particulate organic carbon and chlorophyll a determinations (see Grice et al. 1980) and by particle size analysis with a model TA II Coulter Counter.

Mesozooplankton samples for herbivore population assessment were obtained using the large-volume (200 $l\text{-}min$) pumping system described by Beers, Reeve and Grice (1977). During the period covered by this report pump samples were collected three times a week from 2 (0-16, 16-20 m) or three (0-8, 8-16, 16-20 m) depths each sampling day. Concentrating nets were 80 µm for the post nauplii copepodids fraction and 35 µm for nauplii.

Experimental investigations on herbivore feeding were performed using calanoid copepods collected from vertical net tows from the CEEs, and phytoplankton collected from the 4-8 m depth range using methods detailed by Harris (1980). Copepods fed overnight at 10 or 15°C in 1-l bottles rotated at 0.5 rpm on a wheel. Comparisons, using a Coulter Counter, between control bottles and those containing known numbers of copepods, were used to estimate the particle size composition of the diet. Animals were recovered for weight and organic carbon determinations.

Several different sampling and enumeration techniques were employed for carnivores because different problems were involved in adequately describing all the populations. Three times each week, a standard vertical haul was made from 20 m to the surface at the center of the CEE, using paired nets of 40-cm mouth diameter 200-μm mesh. Once each week, a single 1-m mouth diameter 500-μm mesh net was employed; its contents were examined alive in the laboratory. To enumerate larvae (< 2 mm) a vertically integrated 20-l water sample was obtained weekly (beginning the second week) by lowering a hose attached to a small diaphragm pump through the water column. These collections were returned immediately to the laboratory unpreserved. In order to investigate the vertical distribution of carnivores in CEE 3, on five occasions at weekly intervals the paired 200 μm nets were used to obtain day and night sets of samples through the same depth intervals used for the micro- and mesozooplankton study. Since the samples were preserved no estimate of the vertical distribution of Bolinopsis could be obtained from them.

Because we were unsure of the validity of our estimates of newly-hatched ctenophores from water samples, we made a further check on fecundity, using ctenophores collected from the CEEs in the weekly 1-m net tows. Animals were isolated without food individually in 1,500 ml sea water at 13°C for two days, after which any eggs and larvae produced were counted.

Gut contents of Pleurobrachia and Sagitta from preserved paired-net samples were dissected out and examined at 50-200 X to identify prey species and developmental stage. The average number of prey per carnivore was calculated for each sampling date and for a number of size classes.

Live Sagitta and Pleurobrachia held overnight in filtered seawater (12°C) were subsequently fed in the laboratory to determine digestion times of prey as detailed by Reeve (in press). Using digestion times and the total number of prey per predator, a daily ration for each size class of predator was calculated as described by Sullivan and Reeve (in prep.). The calculation was made separately for a 12 hour day time and 12 hour night time feeding period and summed.

For Pleurobrachia, estimates of total population feeding activity over the first 40 days of the experiment were also obtained by a method which relied on a relationship between clearance rate and size. This relationship, which was assumed to be independent of food concentration, was based on laboratory feeding experiments reported by Reeve and Walter (1976). The volume swept clear of food by an individual of each size class was multiplied by the total numbers in each size class, and the products summed to estimate the volume swept clear of food items by the total population of Pleurobrachia in units of liters m^{-3} day^{-1} (Sullivan and Reeve, in prep.).

The food consumption rate of the Bolinopsis population could not be estimated directly. Indirect estimates were made, based on the untested and arbitrary assumption that on any given day Bolinopsis of equivalent carbon weight had the same clearance rate as Pleurobrachia, or the same gut contents.

The detailed series of observations of captured animal populations, provides the opportunity to estimate quantities such as stage residence times, mortalities, and herbivore and carnivore production directly from the population data. This is done by assuming that there is a model, with a (preferably small) number of parameters, which predicts a complete history of the population. The parameters are then adjusted until the model predictions match the observations as closely as possible. This technique, known as systems identification, has been applied by Parslow et al. (1979) and Sonntag and Parslow (MS) to estimating growth and death rates, and total production of copepod populations.

RESULTS

Phytoplankton:

Nutrient concentration, phytoplankton production, chlorophyll a, herbivore biomass and carnivore biomass over the first 40 days are shown in Fig. 1. The four fold initial difference in nutrient addition to the CEEs is reflected in the correspondingly higher standing crop of nitrate, chlorophyll a and phytoplankton production during the first 10 days in CEE 3.

Following the initial nutrient induced phytoplankton bloom in CEE 3 the vertical distribution of primary productivity, chlorophyll a, total particle concentration and the proportion of diatom biomass in the phytoplankton population are illustrated in Fig. 2, which gives mean values for five depth intervals for the period from day 9 to day 39. The majority of primary production occurred in the upper 4 m and rates were very similar at corresponding depths in both CEEs during this period. Particulate carbon, particle volume, and chlorophyll a, all measures of potential food for filterfeeding zooplankton, were relatively uniformly distributed from surface to bottom in both CEEs. All three variables had higher average values after the first nine days in CEE 2 than in CEE 3, with the exception of carbon concentrations below 8 m. Also, after day 9 there was a clear difference in the composition of the phytoplankton populations in the two enclosures, diatoms forming 75% on average of the total phytoplankton carbon in CEE 2 compared with 11% for CEE 3. In both CEEs the proportion of diatom biomass increased with depth, probably due to the sinking of the initial bloom. In the upper 8 m, 70% of the phytoplankton carbon was attributable to diatoms in CEE 2 but only 3.5% in CEE 3. During the entire period (day 9-39) a background population of μ-flagellates persisted in both CEEs, dominating in numerical abundance, and in CEE 3 some diatoms persisted at depth, presumably utilizing residual silicate. The major difference in phytoplankton composition is reflected in the differing particle size distributions in the two CEEs (Fig. 3). In CEE 3 mixed flagellate and dinoflagellate populations resulted in relatively uniform particle size distributions with small peaks at 5-6 μm at the surface and at 20 μm at greater depths. Species of Gymnodinium, Gyrodinium, Dinophysis and Amphidinium dominated. In contrast, at all depths in CEE 2 a pronounced biomass peak at 64 μm was the characteristic feature, reflecting the bloom of the large chainforming diatom Stephanopyxis turris, which dominated throughout the period and composed the major part of the phytoplankton biomass.

Zooplankton Vertical Zonation:

Evidence of pronounced vertical zonation of the zooplankton in the CEEs is illustrated in Figs. 4 and 5 from pump and paired net samples respectively. The dominant copepod species, with the exception of Oithona, were all concentrated in the upper 8 m during daytime (Fig. 4). This distribution was most marked for Paracalanus. Pseudocalanus and Acartia, however, were more likely to be found in either of the two upper ranges. The distribution pattern for Oithona was the inverse of the other species, most animals occurring in the deeper levels. The copepods in the 200-μm mesh net showed no diurnal vertical movement, the averaged daytime distribution, with over 50% in the upper 8 m, being almost identical at night. Distributions in both CEEs were very similar and there was no evidence that the bubbling in the upper 8 m in CEE 2 affected the vertical zonation of either nauplii or later development stages.

Since numbers of ctenophores and chaetognaths in the three vertical samples (0-8, 8-16, 16-20 m) were small, and only five night time series were taken at weekly intervals over four weeks up to day 32, the results were pooled and expressed as percentages in Fig. 5. The bulk of the ctenophore population was collected below 16 m during the day. At night the situation was reversed with over 60% of the animals larger than 1 mm in the upper 8 m. The smallest larvae, on the other hand, remained near the bottom. The highest concentrations of chaetognaths of all sizes were at the mid depths (8-16 m) both day and night, although an upward night time trend is evident.

Herbivore Population Dynamics:

The herbivore biomass (Fig. 6) here defined as including adult and copepodid copepods, larvaceans, gastropod veligers and cyphonautes, ranged in the CEEs from less than 10 mg m^{-3} to about 60 mg C m^{-3} in CEE 2 to about 100 mg C m^{-3} in CEE 3. The maximum in each enclosure occurred on day 18. Nauplii biomass on day 4 was less than 2.0 mg C m^3. It did not exceed 3.0 mg C m^3 during the first 40 days.

Although 12 copepod species and 14 other taxa were identified from samples obtained in the CEEs, only four species of mesozooplankton contributed a significant proportion of the biomass during the first 40 days of the experiment. These were the copepods Paracalanus, Pseudocalanus, Oithona and Corycaeus. Lesser contributions to the overall biomass were made by larvaceans, gastropod veligers and cyphonautes larvae.

The biomass of Paracalanus and Pseudocalanus in comparison to the total herbivore biomass is shown in Fig. 7. Reproduction during the early days was rapid and successful. Two Paracalanus cohorts were distinguished from inspection of the population data (Fig. 8). Members of the first cohort were spawned from no more than about 200 females per cubic meter which had been captured or matured during the early days of the experiment, giving a generation time of about 12 days from first naupliar stage to maturity.

Pseudocalanus accounted for the largest part of the mesozooplankton biomass during the first 15 days (Fig. 7). By day 23 its biomass was less than that of Paracalanus and by day 27 it was insignificant. At the

beginning of the experiment two cohorts of Pseudocalanus present in Saanich Inlet plankton were captured in the water columns as indicated by dotted lines on Fig. 9. A third cohort was apparently spawned by adults between days 13 and 16. Large numbers (> 3,500 m^{-3}) of first and second stage nauplii were observed on days 13 and 15, but mortality was high and the cohort was not recognizable beyond the early copepodid stages (day 20).

Adults and copepodids of Oithona reached maximum abundance during the first nine days then rapidly declined until day 25 beyond which relatively few adults (approximately 100 m^{-3} or less) were present in either CEE (Fig. 10).

Unlike the preceding three species, the number of all stages of Corycaeus generally increased through the first 40 days (Fig. 11). Beyond day 30 this was the only copepod species that was important numerically.

There were two peaks in larvacean abundance during the experiment, but only one occurred during the first 40 days. Nudibranchs and bryozoans were presumably captured as larvae. They attached to the inner walls of the enclosures, and grew to adults and produced large numbers of larvae after day 30.

Carnivore Population Dynamics:

Size frequency distributions for Pleurobrachia, Bolinopsis and Sagitta are represented in Figs. 12, 13 and 14, respectively.

The initial capture of ctenophores at the beginning of the experiment was low and consisted mainly of older animals. The numbers of Pleurobrachia and Bolinopsis of reproductive age were about 1 m^{-3} with similar numbers of smaller animals. There were no young ctenophores in the water column initially. By the middle of the third week reproductive activity of Pleurobrachia had reached a peak, as evidenced by numbers of newly-hatched larvae (< 1 mm), which reached at least 4,500 m^{-3} in both CEEs. The occurrence and duration of this reproductive activity was confirmed in the fecundity tests (Fig. 15) which indicated that the largest animals could produce over 500 eggs over 48 hours of the test. By day 27, no eggs were produced by any of the animals from either CEE, and this situation did not change up to day 72, beyond which testing stopped because there were no animals of reproductive size remaining. A similar pattern was seen for Bolinopsis, although numbers never exceeded 100 eggs $animal^{-1}$.

Numbers of Pleurobrachia larvae (< 1 mm) reached a peak on day 19, then declined rapidly between days 20 and 30. As would have been predicted from the fecundity test, no more of these smallest larvae were seen for the rest of the experiment. Their decline was due to a cessation of reproduction, growth into the next size category, and mortality. Reduction of numbers between the first two size classes indicated the youngest larvae suffered the highest mortality rate, with less than 10% of the < 1 mm animals reaching the next size class. The effect was particularly severe in CEE 2 where there were only about a third as many 1-2 mm animals as in CEE 3. This differential mortality was reflected in lower biomass levels throughout the rest of the experiment in CEE 2. It appears that virtually no members of this cohort grew to reproductive age except for a

few between days 35 and 50 which may have achieved the > 8 mm size class. If this is a correct interpretation, their growth from hatching to maturing took a minimum of 25 days.

The recognition of cohort structure in Bolinopsis (Fig. 13) is less certain than for Pleurobrachia, particularly in CEE 2. There were very few larvae recorded from water samples, but it is more likely that Bolinopsis larvae were destroyed in the pumping and handling process.

Laboratory tests showed that reproduction in Bolinopsis is initiated in the 8-16 mm size class and, as with Pleurobrachia, egg production rate increases rapidly with size. Compared to CEE 3, mortality of young Bolinopsis was severe in CEE 2, resulting in a permanently reduced biomass in that CEE for the rest of the experiment. Virtually no animals of this cohort grew beyond the 8-16 mm size class, no further cohorts were produced, and the progenitors of the cohort had nearly all died out by day 60.

The CEE populations of Sagitta (Fig. 14) show no clear cohort of animals growing up through the experiment, although there are indications that the populations, initially predominated by immature animals, were growing slowly and maturing. Larger size classes, some with mature (large) eggs in their ovaries, became prominent between days 20 and 40. Peaks in the 3-6 mm size class over the same period may have been their offspring. The gradual elimination of Sagitta could have been due to predation by ctenophores (particularly the mucous ciliary feeding of the lobate Bolinopsis), as well as to assault by the increasing numbers of the cyclopoid copepod Corycaeus, which is known to be capable of attacking chaetognaths as well as other copepods.

The relative importance of the carnivore populations may be summarized by biomass changes of the populations. The peak biomass of ctenophores in both CEEs occurred around day 25 (Fig. 16), and the pattern of gradual decline throughout the rest of the experiment was similar.

Food Consumption of Herbivores:

Because of their relevance to the central hypothesis of the FOODWEB I experiment emphasis was placed on the study of possible interspecific differences in particle size composition of the diet of the dominant herbivorous copepods. This experimental work, in particular that on comparisons between Calanus and Pseudocalanus, is described in detail elsewhere (Harris, 1980). In the present context selected examples of the results of these experiments will be given to illustrate the types of feeding behaviour observed during the first 40 days of the experiment and their significance in an assessment of the trophic interactions in the CEEs. In Fig. 17 a comparison is made of the particle size composition of the ingested ration for adults of three herbivores, Calanus, Pseudocalanus, and Paracalanus. The latter two species were numerically the dominant calanoids in both CEEs and the figure illustrates a date when both were near their maximum abundance and the differentiation between phytoplankton in the two enclosures was well developed, only 7.3% of the biomass in CEE 3 on this date being attributable to diatoms, flagellates and non-photosynthetic dinoflagellates dominating the population. The figure illustrates two points, firstly that the size frequencies of ingested food

were generally similar and as such is typical of a large number of experimental observations (Harris, 1980); interspecies differences were subtle rather than major and there was evidence for considerable interspecific competition. Secondly, even when small cells (< 10 μm, ≈ μ-flagellates) form a significant proportion of the particulate biomass they do not comprise a signficant percentage of the ingested ration; "small" copepods do not necessarily feed on "small" cells.

Fig. 18 illustrates intraspecific comparisons between developmental stages of Pseudocalanus previously raised in laboratory cultures feeding on natural particulate material collected from CEE 3, and adults collected directly from the CEE, when both are allowed to feed on CEE 3 phytoplankton under similar conditions. The day chosen (day 27) is a time when nauplii and copepodids of the second cohort developing in the CEE might be expected to be feeding actively. At this time photosynthetic dinoflagellates made up 42.9% of the population biomass with Dinophysis accuminata the dominant species. Fig. 18 indicates that all stages have competing food requirements in the range 10-30 μm. Again the < 10 μm fraction is shown to be relatively unimportant, and there is no major selection by the smaller stages of these small cells. Though the pronounced peak in the adult female diet at 64 μm corresponded to a minor peak in the environmental frequency distribution, this feature my simply be a result of counting variability because of the small number of cells present in the larger size channels.

Fig. 19 compares estimates of copepod ingestion rates expressed as μgC copepod^{-1} 24 h^{-1} for adult female Pseudocalanus and Calanus, with some points for Paracalanus, when feeding on phytoplankton collected from the 4-8 m depth interval. This depth was chosen as being representative of the region in which the majority of herbivorous copepods occurred (see section above). Calculation of mean ingestion rates for all observations after the initial diatom bloom shows a significant difference ($t = 2.87$, $p < 0.01$) between rates of ingestion by Calanus in CEE 2 ($x = 15.0$ μgC copepod^{-1} 24 h^{-1}) and CEE 3 ($x = 9.6$ μgC copepod^{-1} 24 h^{-1}). In contrast, there is no significant difference between the CEEs when Pseudocalanus is considered (1.7 for CEE 2; 1.8 for CEE 3). These differences are also reflected in the weight specific ingestion rates which for Pseudocalanus averaged 0.20 and 0.23 of the body carbon per day in CEE 2 and 3 respectively, and for Calanus were 0.19 and 0.13 for CEE 2 and 3. Hence, if the nutritive value of the phytoplankton is considered to be similar in the two CEEs, one would expect Calanus to have had relatively greater scope for adult egg production in CEE 2, whereas Pseudocalanus would show no similar difference. An explanation of the differences in feeding response of the two species is suggested by the average particle size distribution for the two enclosures during this period (Fig. 3). There is a significant difference ($p < 0.01$) in total concentration between CEE 2 (5.67 ppm) and CEE 3 (3.30 ppm). However, this difference mainly represents the predominance of diatoms of large cell size in CEE 2 (e.g., Stephanopyxis) as there was no significant difference in particle concentration summed for the channels below 40 μm.

Thus, the higher Calanus ingestion rates are probably a response to the high particle concentrations of the diatom peak in CEE 2, whereas Pseudocalanus, may not be able to exploit the large diatoms so effectively. Despite the evidence for a considerable degree of interspecific

competition, for example Fig. 17, Harris (1980) found that over a long series of experiments there was, in fact, a small difference in the size frequency distributions of the ingested rations; the median particle diameter for the diet of Calanus was 1.2 x that for Pseudocalanus.

Food Consumption of Carnivores:

Table 1 records the distribution of food items consumed by Pleurobrachia and Sagitta by size class of carnivore and category of prey. The smallest size groups of both carnivores ingested substantial proportions of ciliates (44 and 12% for Pleurobrachia and Sagitta respectively). It may be presumed that had the smallest chaetognath larvae (1 mm) been captured in the nets, the proportion of ciliates ingested would have approached closer to that of the 1 mm Pleurobrachia. During the first 25 days, copepodids and adults of the "small" copepods (mainly Paracalanus and Pseudocalanus, with a few Acartia) provided the food of as much as 80% of all chaetognaths above 4 mm, and 55% of all ctenophores above 1 mm, the proportion of adults in the gut predictably increasing with carnivore size. Most of the rest of the Pleurobrachia diet was composed of the cyclopoid copepods Oithona and Corycaeus (both copepodids and adults) which the chaetognaths seemed not to capture.

Beyond day 25, both carnivores relied heavily on Corycaeus for their food source. Although the percentage of Corycaeus was high, actual food consumption during this period was very much reduced in terms of total numbers of food items. This was in part because Corycaeus was an undesirable food species, as determined by observations where both ctenophore species virtually refused to consume Corycaeus over long periods in laboratory containers, and in part because the concentration of copepods in the CEEs was very much reduced by this time.

Fig. 20 shows the ratio of number of food items consumed to total numbers of guts dissected for individual Pleurobrachia and Sagitta of different size classes over the first 40 days in CEE 3. The Sagitta were divided into only two size classes because of the small numbers of chaetognaths in the samples. The number of food items per carnivore is highest over the first 20 days of the experiment, declining abruptly after that as copepod populations are rapidly reduced. In all cases, the ratio is highest in the night time samples, although the difference is least in the youngest animals and diminishes with time.

The methods by which daily feeding rates, both in terms of numbers and carbon weights of food items, were computed from these data, were detailed by Sullivan and Reeve (in prep.). Table 2 contains the total carbon computed to be ingested on a daily basis for all age classes of Pleurobrachia and Sagitta from gut content studies, and for Bolinopsis making assumptions referred to in the methods section. The total daily carbon ingestion rate for all carnivores is also calculated. This estimate may be compared with those for total copepod carbon biomass for the same day. Day 16 was the day of peak copepod biomass with 98.7 mg C m^{-3} available. At this time, the rapidly increasing carnivores had a consumption rate of 7% of that amount daily. By day 18, the copepod biomass was in decline as the carnivore consumption rate increased to 12% daily; and on the day of maximum consumption (day 25) the combined carnivores were removing 14.5 mg of a total 23 mg copepod biomass (63%), a

proportion computed to be maintained through day 32, when both carnivore and copepod populations were in rapid decline. The chaetognath contribution was very small; only reaching 9% on its day of maximum biomass, (day 18), and being less than 1% of the total predatory activity beyond day 25.

Table 3 presents total population clearance rates for Pleurobrachia and Bolinopsis in terms of number of liters of water cleared by the animals in a cubic meter volume of CEE 3. The peak clearance rate was thus computed to occur about day 23 (94 l m^{-3}; i.e., 9.4% of the CEE volume) which decreased to 5.3% by day 37. Assuming that all copepods and ctenophores were distributed evenly in the CEEs and all ctenophores could completely remove all copepods in the volume assigned to them, the population carbon ingestion rate could be computed by relating the proportional volume to the carbon biomass contained in the total volume. On this basis, and ignoring the minor contribution of the chaetognaths, the carnivore consumption rate on the peak copepod biomass day was about 6%, which was very similar to the value obtained on the basis of gut contents. Beyond that time, over the period when the gut contents method yielded a stable 62%, the clearance rate method provided a much lower estimate of about 10%. This discrepancy may be accounted for by the food selection preferences of ctenophores which showed that animals over 1 mm body diameter progressively selected larger food items than the average for the water column thus greatly increasing their estimated food intake rate as documented by gut contents.

Secondary Production:

We chose to model only the copepodid and adult stages of Paracalanus and Pseudocalanus, since nauplii contributed only a small amount (Fig. 5) of biomass or production.

The model describes both Paracalanus populations surprisingly well (Fig. 21), Pseudocalanus less well (Fig. 22). In CEE 2, recruitment to the first cohort in Paracalanus is 31,000 animals m^{-3} peaking on day 13; to the second, 43,000 m^{-3} peaking on day 25. Stage residence time is 1.0 days for first stage copepodid and 1.7 days for fifth stage copepodid. Instantaneous mortality rate is 0.06 per day on day 10 and 0.35 per day (corresponding to 30% mortality over a day) on day 20. Secondary production from day 4 to day 39 is 75 mg C m^{-3}. Results of applying the model to other populations are summarized in Table 5. We excluded the day 11 from the computations for CEE 3 populations; if it is included, the estimates change very little but the associated variances increase by half.

Attempts to describe Pleurobrachia populations by a similar model, with a continuous size variable instead of discrete stages, failed. Considering the data presented in Fig. 12 for CEE 3, it would seem that the reason for failure is the large variation in individual growth rates, so that the size classes 1-2, 2-4 and 4-8 mm all reach their maximum abundance at approximately the same time. If it is assumed that mortality of animals larger than 1 mm is negligible (this seems consistent with the population history after day 20) then Pleurobrachia production can be estimated as equal to the greatest observed biomass, or 6.2 mg C m^{-3}.

Estimates of herbivore production (Table 4) can be compared to the calculated phytoplankton production throughout the experimental period considered here (40 days) and during a shorter period (day 4-18) when there was relatively little predation on the herbivores by ctenophores. Over the entire 40 days primary production in CEE 2 and CEE 3 was 1,725 and 2,102 mg C m-3 respectively. (These are values averaged over the whole enclosure volume.) During this period the production of Paracalanus and Pseudocalanus the two dominant copepods, was 116 and 138 mg C m-3 in CEEs 2 and 3 respectively. As indicated earlier there was little herbivore production beyond day 18 in either CEE (Fig. 6). Considering only days 4-18, a period characterized by early nutrient addition followed by development of copepod cohorts, the net primary production in CEEs 2 and 3 was 661 and 993 mg C m-3 respectively. In the same period the production of Paracalanus and Pseudocalanus in CEEs 2 and 3 was 78 and 106 mg C m-3 respectively. For about one half of the experiment the food chain efficiency between producers and major herbivores was 12% in CEE 2 and 11% in CEE 3 while for the first 40 days it was about 4.5% in both CEEs. The productivity of Pleurobrachia in CEE 3 was estimated earlier to be about 6.2 mg C m-3. Thus, the transfer efficiency between herbivores and carnivores was at least 5% and if the combined production of Bolinopsis and Sagitta were equivalent to that of Pleurobrachia the transfer efficiency between herbivores and carnivores would be about 10%.

DISCUSSION

The central hypothesis of the FOODWEB I experiment was that the different phytoplankton populations would determine the number and type of links in the food chain as a result of the effects of cell size on herbivore trophodynamics (Greve and Parsons, 1977; Steele and Frost, 1977). The predatory impact (Fig. 23) of ctenophores prevented longer-term implications of phytoplankton population structure being followed up the food-chain as was the original intention (Grice et al., 1980). There was, however, a period after the initial phytoplankton bloom, during which there was a major difference in the phytoplankton populations (Figs. 2 and 3) and when herbivores had not yet been significantly affected by ctenophore predation (Fig. 1). Over this period evidence for differences at the herbivore level in the two CEEs might be sought. This time interval coincides with the development of Paracalanus and Pseudocalanus cohorts. As has already been noted there was no significant differences between the CEEs in stage residence time or mortality for these cohorts. The most obvious difference in the copepod populations in the two CEEs over this period was the larger biomass (Fig. 1) and production (Table 4) of Paracalanus and Pseudocalanus in CEE 3. This difference could be attributed to a simple chain effect proceeding from a similar difference in phytoplankton production, itself promoted by the initial difference in nutrients (Fig. 1). Other than this, there were no indications of differential copepod population structure, and little experimental support that any would be expected on the basis of feeding preferences. Paracalanus, however, was not intensively studied experimentally. Thus, the original hypothesis of FOODWEB I, relying as it did on the supposition that small copepods eat small cells and larger copepods eat larger cells, may be too simplistic.

REFERENCES

Beers, J. R., M. R. Reeve, and G. D. Grice. 1977. Controlled ecosystem pollution experiment: Effect of mercury on enclosed water columns. IV. Zooplankton population dynamics and production. Mar. Sci. Comm. 3(4): 355-394.

Greve, W. and T. R. Parsons. 1977. Photosynthesis and fish production: Hypothetical effects of climatic change and pollution. Helgo. wiss. Meeresunters. 30: 666-672.

Grice, G. D., R. P. Harris, M. R. Reeve, J. F. Heinbokel and C. O. Davis. 1980. Large scale enclosed water column ecosystems. An overview of Foodweb I, the final CEPEX experiment. J. Mar. Biol. Ass. U.K. 60: 401-414.

Harris, R. P. 1980. A comparison of the feeding behaviour of Calanus and Pseudocalanus in two experimentally manipulated enclosed ecosystems. (In preparation).

Parslow, J., N. C. Sonntag, and J. B. L. Matthews. 1979. Technique of systems identificatin applied to estimating copepod population parameters. J. Plank. Res. 1: 137-152.

Reeve, M. R. Comparative experimental studies on the feeding of chaetognaths and ctenophores. Limnol. Oceanog. (in press).

Reeve, M. R. and M. Walter. 1976. A large scale experiment on the growth and predation potential of ctenophore populatins. In: Coelenterate Ecology and Behavior. Ed. G. Mackie, Plenum Press, New York, 187-199.

Steele, J. H. and B. W. Frost. 1977. The structure of plankton communities. Phil. Trans. Roy. Soc. (B), 280: 485-534.

Table 1. Pleurobrachia Diet: percent composition of different size classes of prey, data from CEE 2 and 3 combined.

	TOTAL ITEMS	CILIATES	NAUPLII	OITHONA	COPEPODITES	SMALL ADULTS	CORYCAEUS HARPACT	CALANUS	BARNACLE	OTHER
SAGITTA size										
2–4	66	12	44	5	25	–	2	–	–	10
5–8	90	–	9	4	45	30	3	–	–	5
9–12	81	–	–	6	24	59	–	6	–	5
> 12	91	–	–	5	10	72	7	4	–	2
PLEUROBRACHIA to day 25										
< 1	65	44	11	11	15	2	2	–	–	15
1–2	177	12	14	11	23	19	14	1	–	6
2–4	155	5	7	12	16	36	17	1	4	2
> 4	284	–	3	17	5	50	13	5	18	1
day 30–52										
1–2	37	8	8	3	3	11	43/19	–	–	5
2–4	128	–	2	–	–	–	39/57	–	–	2
> 4	18	–	–	–	–	–	22/72	–	–	6

Table 2. Mg C m^{-3} computed from gut contents analysis to have been consumed by the carnivore populations in CEE 3.

DAY	PLEUROBRACHIA	BOLINOPSIS	SAGITTA	TOTAL
4	.45	.47	.12	1.04
11	2.54	1.47	.11	4.12
18	3.97	3.51	.70	8.18
25	7.17	7.29	.12	14.58
32	1.62	1.31	.02	2.95
39	.26	.24		.50
44	.60	.61		1.21
51	.36	.22		.58
58	.31	.41		.72

Table 3. Total population clearance rates in liters m^{-3} for Pleurobrachia and Bolinopsis in CEE 3.

DAY	PLEUROBRACHIA	BOLINOPSIS	TOTAL
9	29.6	2.1	31.7
16	50.8	7.1	58.0
23	64.3	29.3	93.6
30	56.0	24.3	80.3
37	39.7	14.9	52.6
43	40.1	10.6	50.7
51	17.5	7.3	24.8

Table 4. Model estimates of population parameters and secondary production for copepods, expressed as estimate ± one standard deviation.

Population	Recruitment to CI		Residence time		Mortality rate		Production
	Thousands	Peak Time	CI	CV	Day 10	Day 20	
CEE 2	31 ± 3	13.0 ± 0.1	1.0 ± 0.1	1.7 ± 0.2	0.06 ± 0.09	0.35 ± 0.12	75 ± 12
Paracalanus	43 ± 3	25.2 ± 0.2					
CEE 2	1.7 ± 0.7	-0.6 ± 0.9	1.9 ± 0.6	3.4 ± 1.0	0.07 ± 0.08	0.30 ± 0.11	41 ± 14
Pseudocalanus	3.6 ± 0.6	7.9 ± 0.7					
CEE 3	40 ± 5	12.5 ± 0.2	1.2 ± 0.2	1.6 ± 0.3	0.05 ± 0.09	0.32 ± 0.12	82 ± 18
Paracalanus	20 ± 2	22.8 ± 0.2					
CEE 3	2.3 ± 0.7	0.8 ± 0.6	1.9 ± 0.2	3.1 ± 0.3	0.03 ± 0.07	0.25 ± 0.11	56 ± 18
Pseudocalanus	3.2 ± 0.6	8.2 ± 0.5					

Figure Legends

Fig. 1. Nitrate concentration, phytoplankton chlorophyll *a* and production, herbivore and carnivore biomass in CEEs 2 and 3 during the first 40 days.

Fig. 2. Average vertical profiles for day 9-39 excluding initial bloom. Horizontal lines are one standard deviation.

Fig. 3. Size composition of particulate matter, average values for days 9-39.

Fig. 4. Vertical distribution of copepod species, based on mean numerical abundance, for days 18, 25 and 32. Daytime collections in CEE 3 (pump samples).

Fig. 5. Average day and night distribution of copepods, *Sagitta* and *Pleurobrachia* in CEE 3 for days 18, 25 and 32 (Paired net samples).

Fig. 6. Biomass of mesozooplankton (copepodid and adult stages) and nauplii for CEEs 2 and 3.

Fig. 7. Biomass of mesozooplankton (copepodid and adult *Paracalanus* and *Pseudocalanus*) for CEEs 2 and 3.

Fig. 8. *Paracalanus* abundance in CEEs 2 and 3 by developmental stages. Note scale change between nauplii and copepodids.

Fig. 9. *Pseudocalanus* abundance in CEEs 2 and 3 by developmental stage. Note scale change between nauplii and copepodids.

Fig. 10. *Oithona* abundance in CEEs 2 and 3.

Fig. 11. *Corycaeus* abundance in CEEs 2 and 3.

Fig. 12. *Pleurobrachia* abundance in CEEs 2 and 3 by size class.

Fig. 13. *Bolinopsis* abundance in CEEs 2 and 3 by size class.

Fig. 14. *Sagitta* abundance in CEEs 2 and 3 by size class. Darkened areas shows number of specimens with mature ovaries.

Fig. 15. *Pleurobrachia* fecundity. Number of eggs produced per animal over two days in the laboratory after removal from CEEs on day specified.

Fig. 16. *Bolinopsis*, *Pleurobrachia* and *Sagitta* biomass, CEEs 2 and 3.

Fig. 17. Composition of the diet of three co-occurring adult female copepod species feeding on phytoplankton from 4-8 m depth from CEEs 2 and 3 on day 18.

Fig. 18. Comparison of size composition of the diet of naupliar, copepodid and adult *Pseudocalanus* in CEE 3 on day 27. Phytoplankton from 4-8 m.

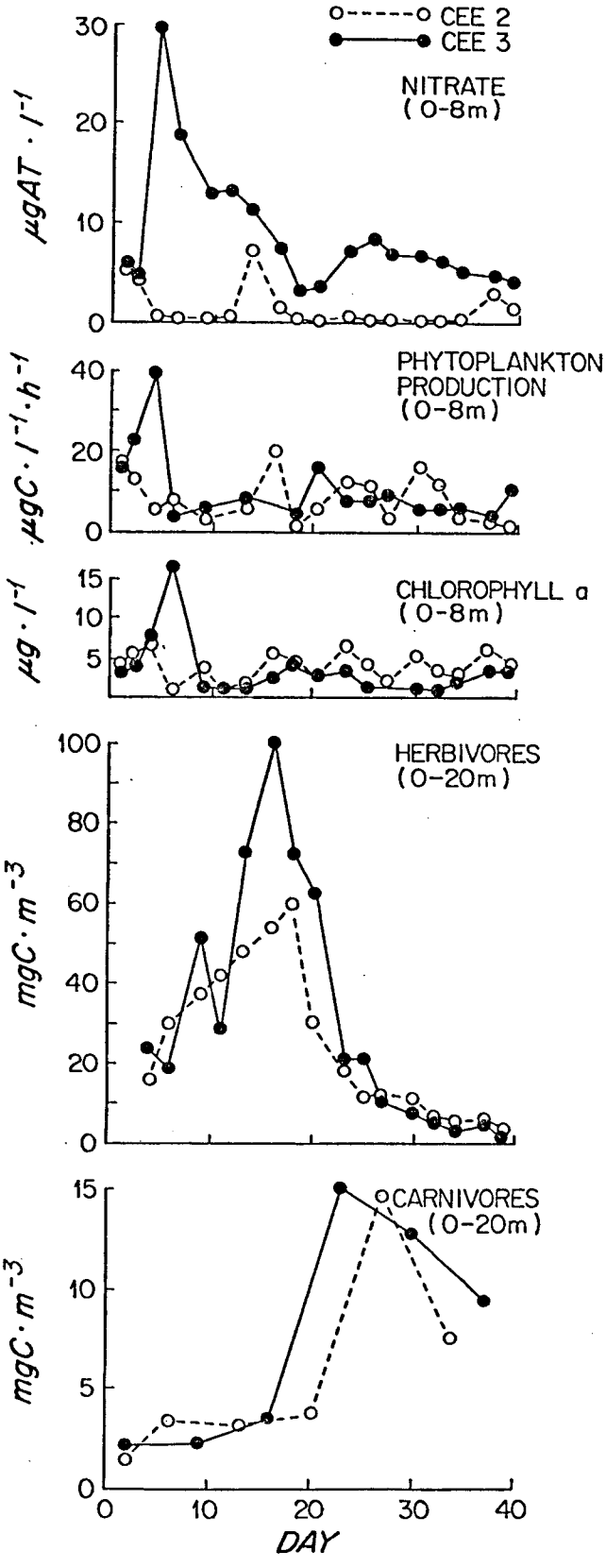
Fig. 19. Ingestion rates for adult female herbivorous copepods feeding on phytoplankton obtained from 4–8 m.

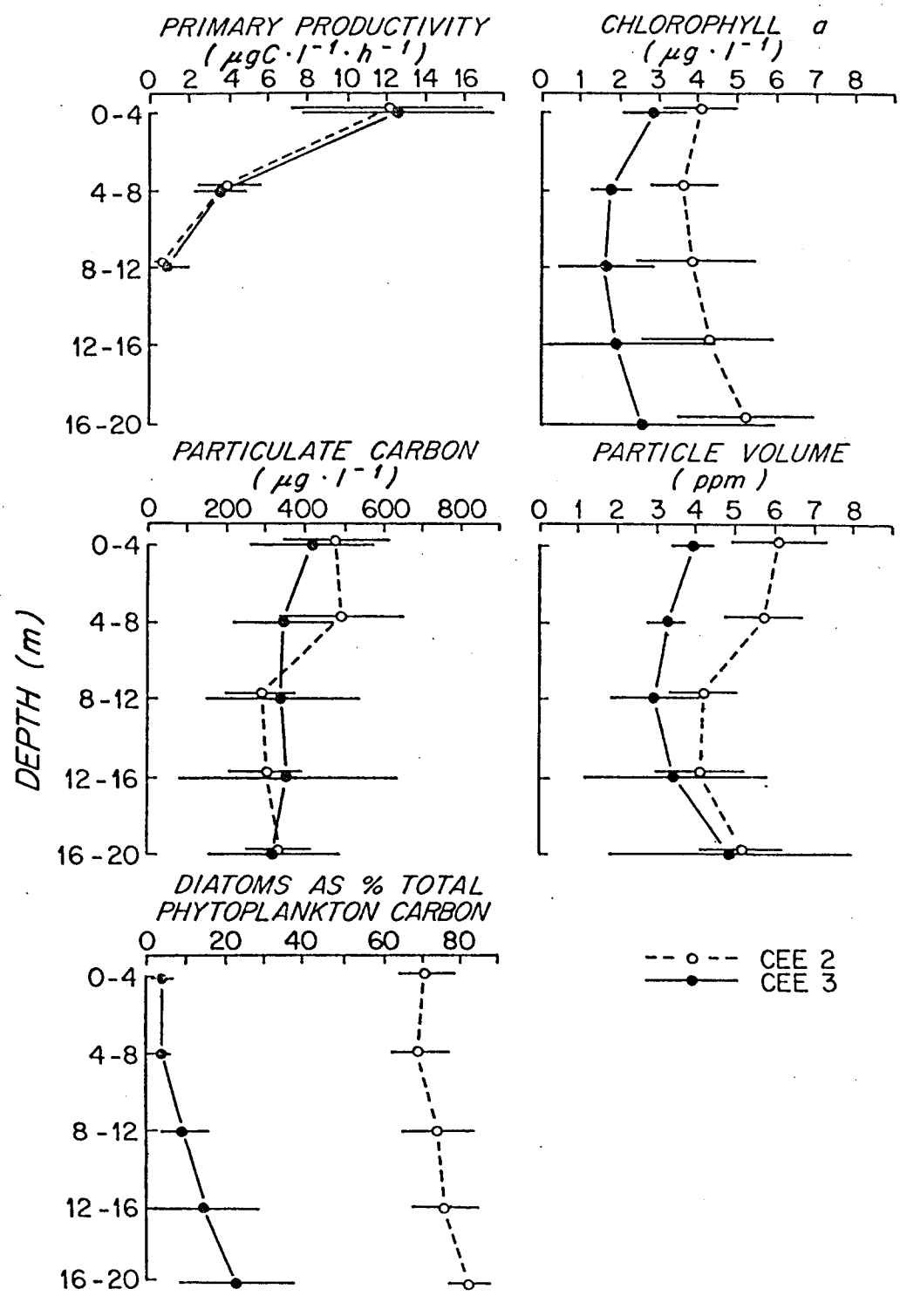
Fig. 20. Food items present in Pleurobrachia and Sagitta guts during day and night in CEE 3.

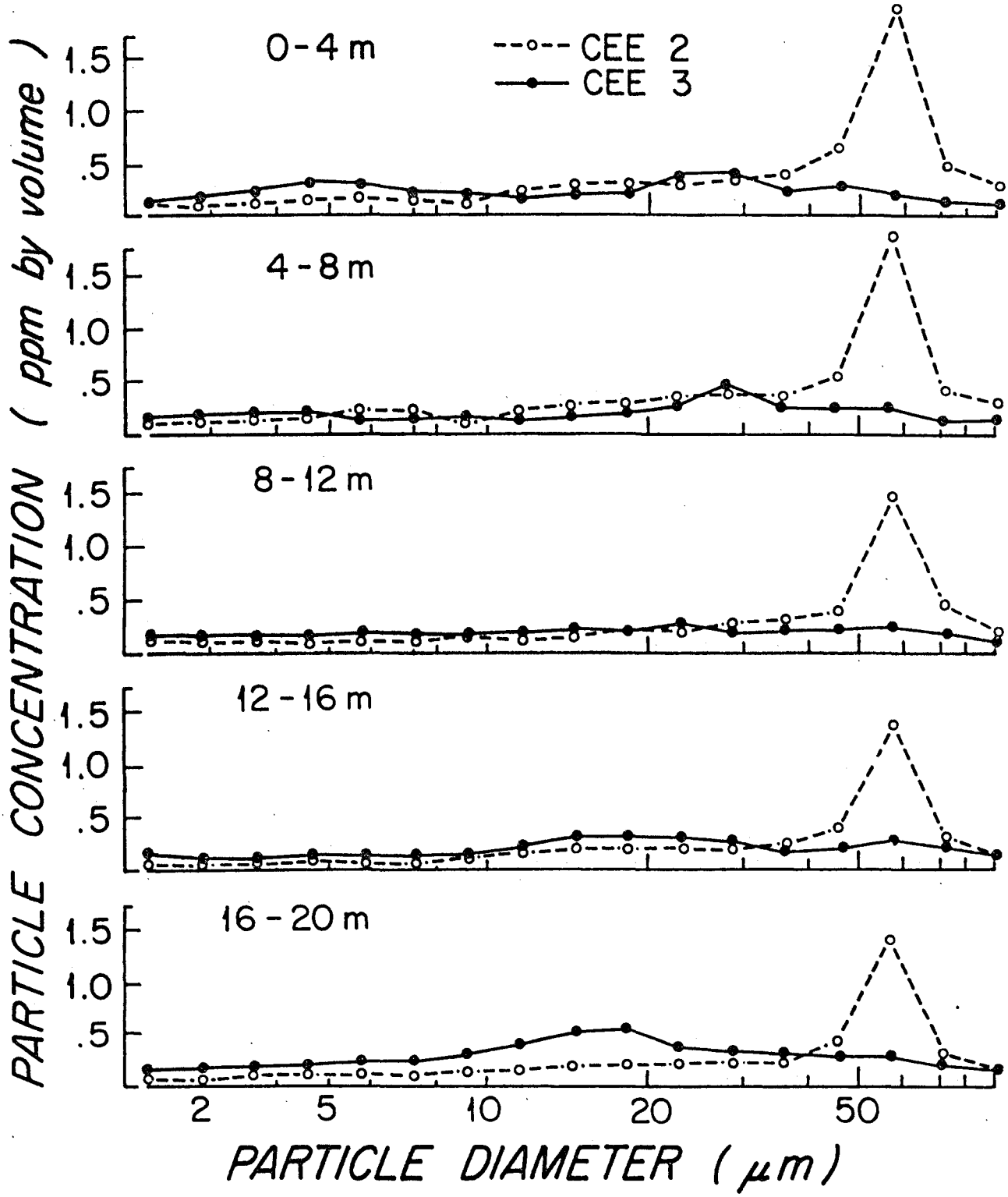
Fig. 21. Paracalanus population model. Day 11 data for CEE 3 ommitted (see text).

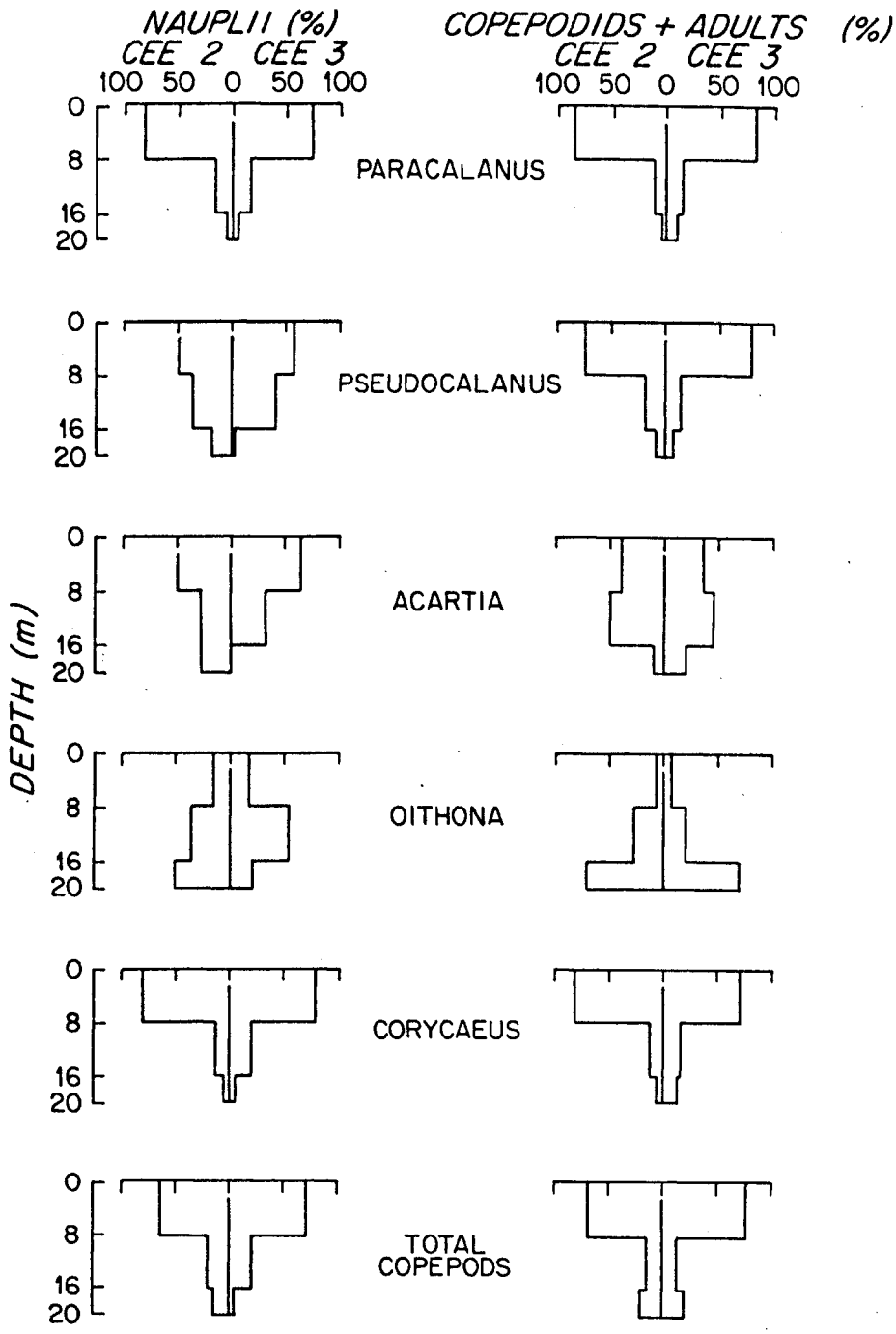
Fig. 22. Pseudocalanus population model. Day 11 data for CEE 3 ommitted (see text).

Fig. 23. Copepod and carnivore biomass.

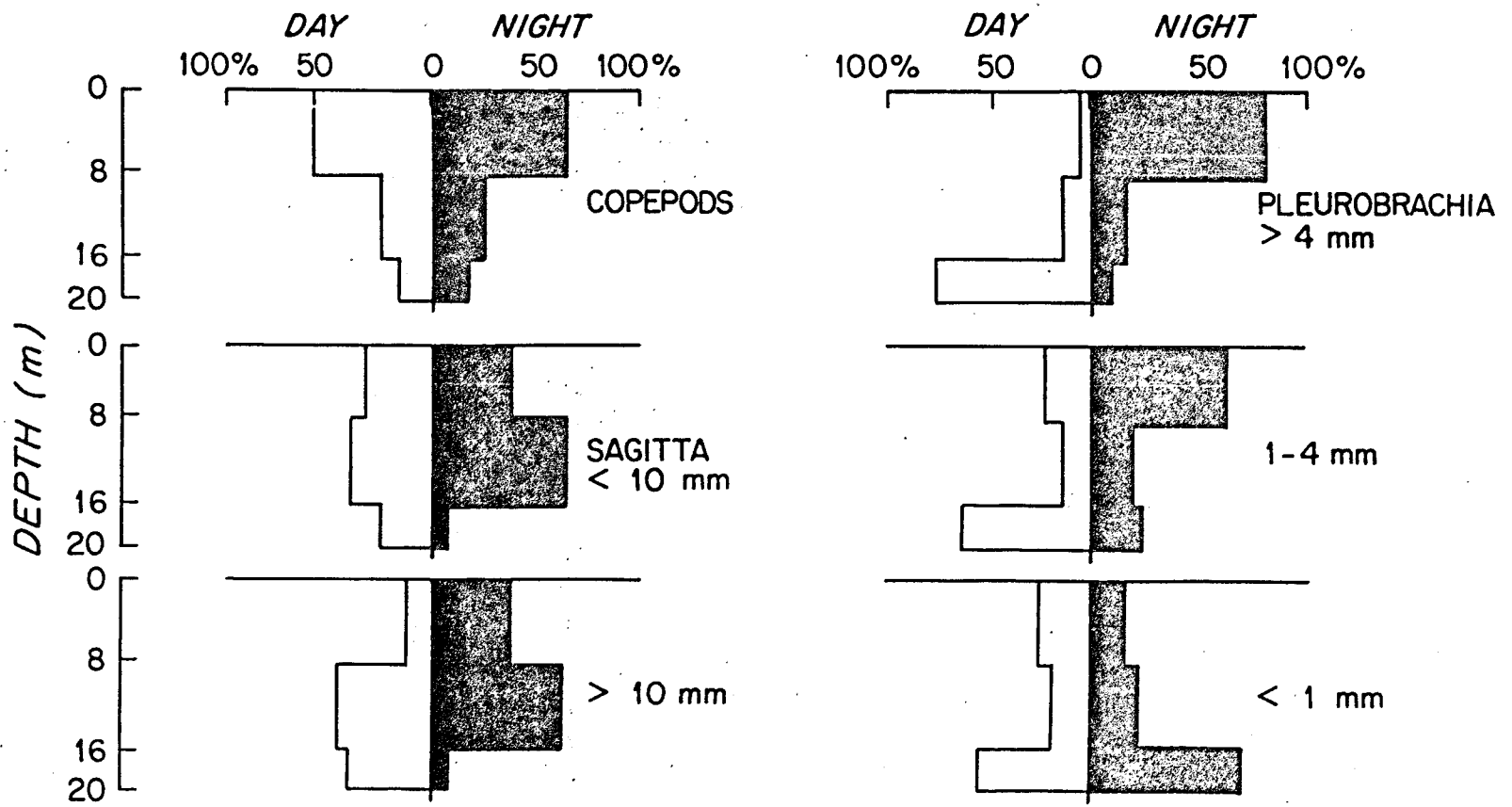

CEE 2
CEE 3
NITRATE
(0-8m)
µgAT · l⁻¹
PHYTOPLANKTON
PRODUCTION
(0-8m)
µgC · l⁻¹ · h⁻¹
CHLOROPHYLL a
(0-8m)
µg · l⁻¹
HERBIVORES
(0-20m)
mgC · m⁻³
CARNIVORES
(0-20m)
mgC · m⁻³
DAY

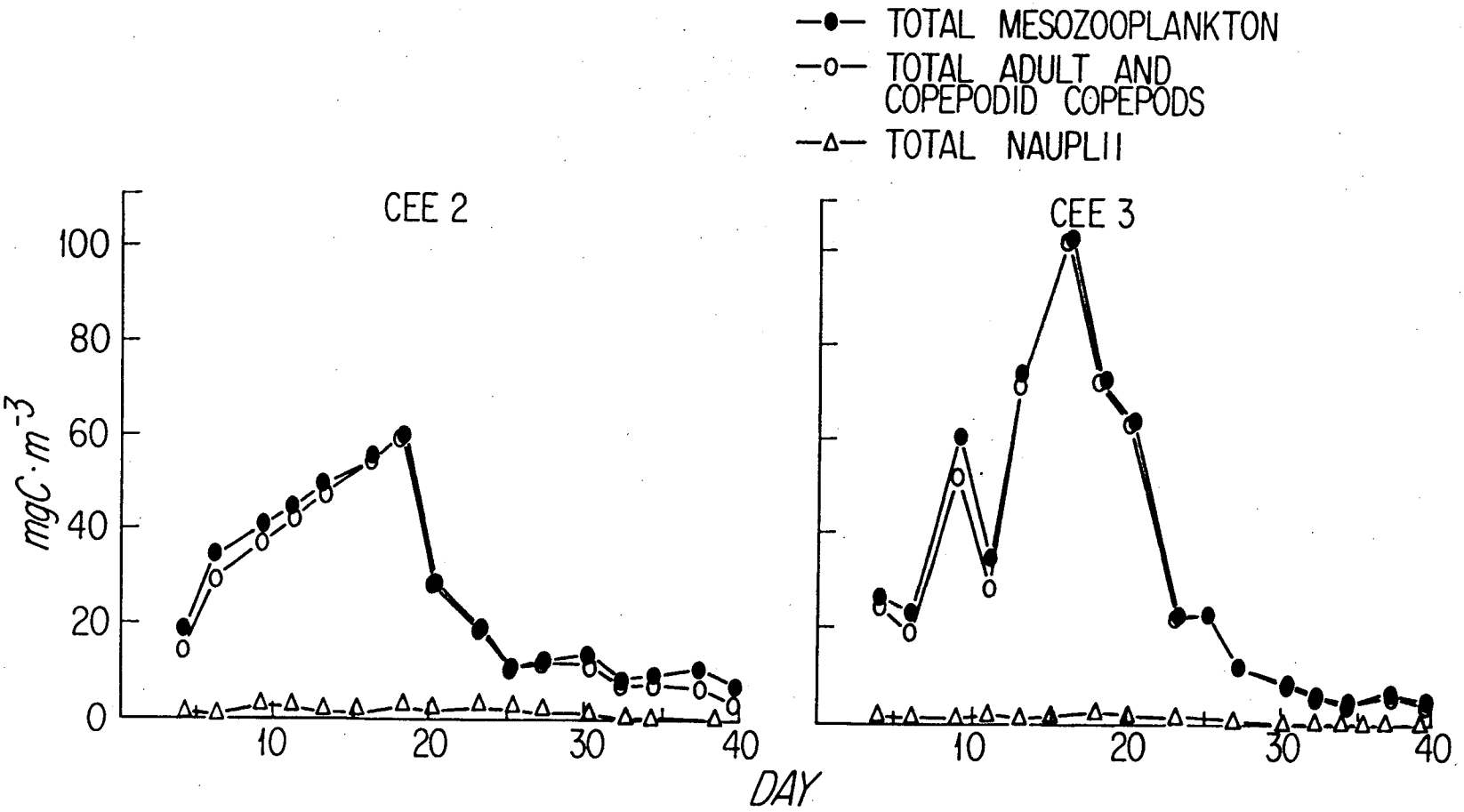

PRIMARY PRODUCTIVITY
(μgC·l⁻¹·h⁻¹)
0 2 4 6 8 10 12 14 16
CHLOROPHYLL a
(μg·l⁻¹)
0 1 2 3 4 5 6 7 8
PARTICULATE CARBON
(μg·l⁻¹)
0 200 400 600 800
PARTICLE VOLUME
(ppm)
0 1 2 3 4 5 6 7 8
DIATOMS AS % TOTAL PHYTOPLANKTON CARBON
0 20 40 60 80
DEPTH (m)
0-4
4-8
8-12
12-16
16-20
CEE 2
CEE 3

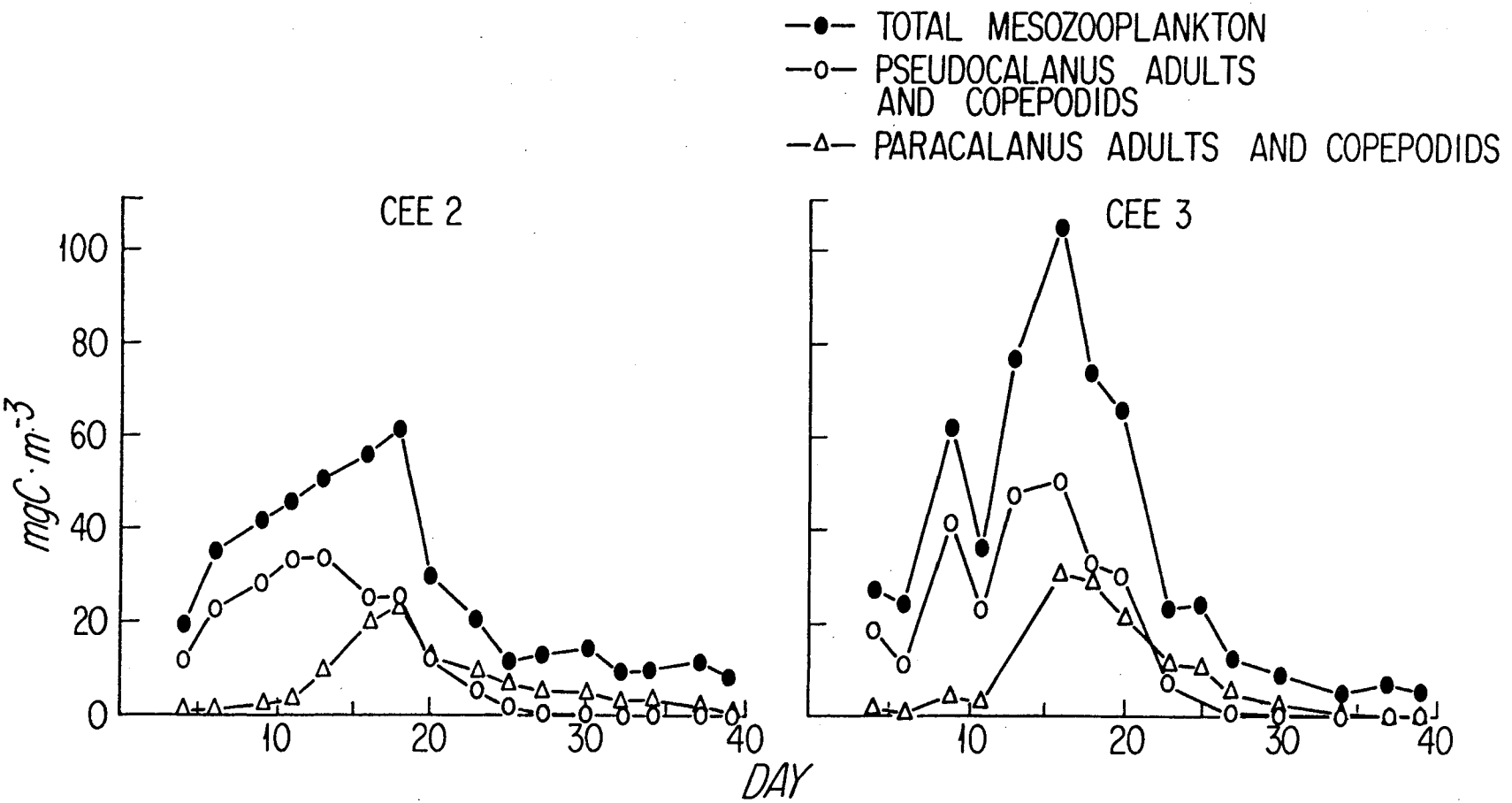

0-4 m
CEE 2
CEE 3
4-8 m
8-12 m
12-16 m
16-20 m
1.5
1.0
.5
PARTICLE CONCENTRATION (ppm by volume)
2
5
10
20
50
PARTICLE DIAMETER (μm)

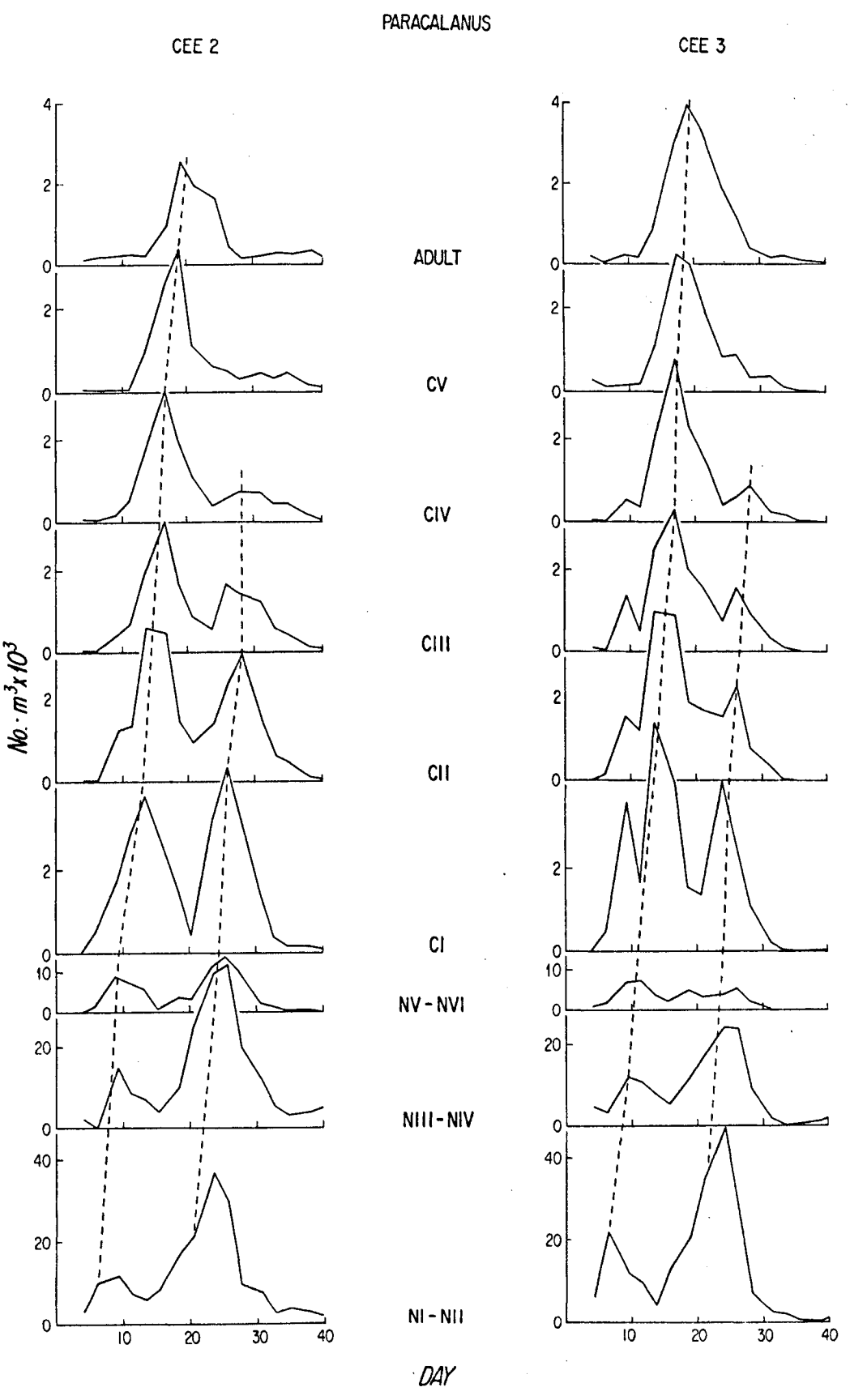

NAUPLII (%)
CEE 2 CEE 3
100 50 0 50 100
COPEPODIDS + ADULTS (%)
CEE 2 CEE 3
100 50 0 50 100
DEPTH (m)
0
8
16
20
PARACALANUS
PSEUDOCALANUS
ACARTIA
OITHONA
CORYCAEUS
TOTAL COPEPODS

CEE 3

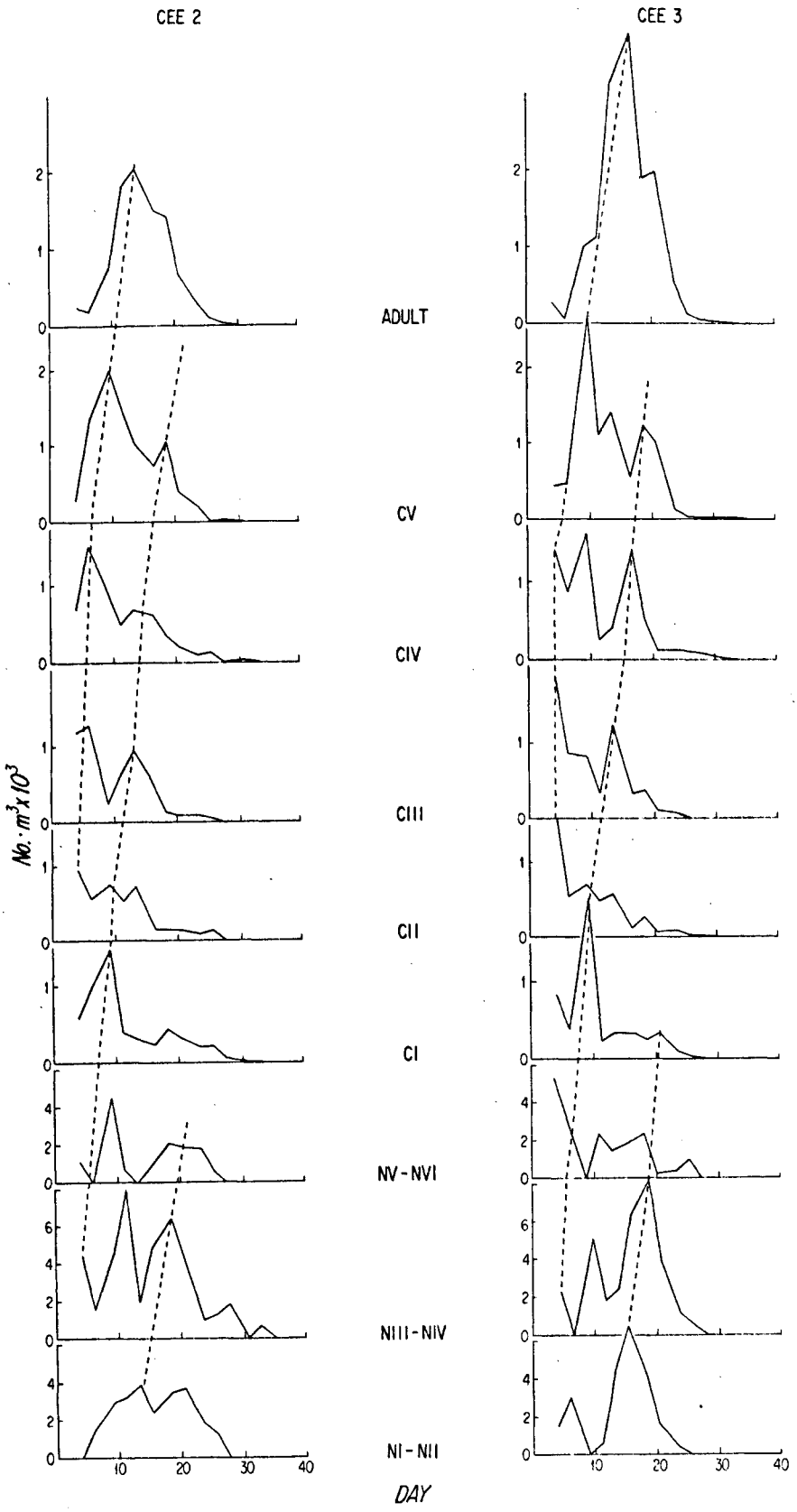

DAY
NIGHT
100% 50 0 50 100%
DEPTH (m)
0
8
16
20
COPEPODS
SAGITTA
< 10 mm
> 10 mm
PLEUROBRACHIA
> 4 mm
1-4 mm
< 1 mm

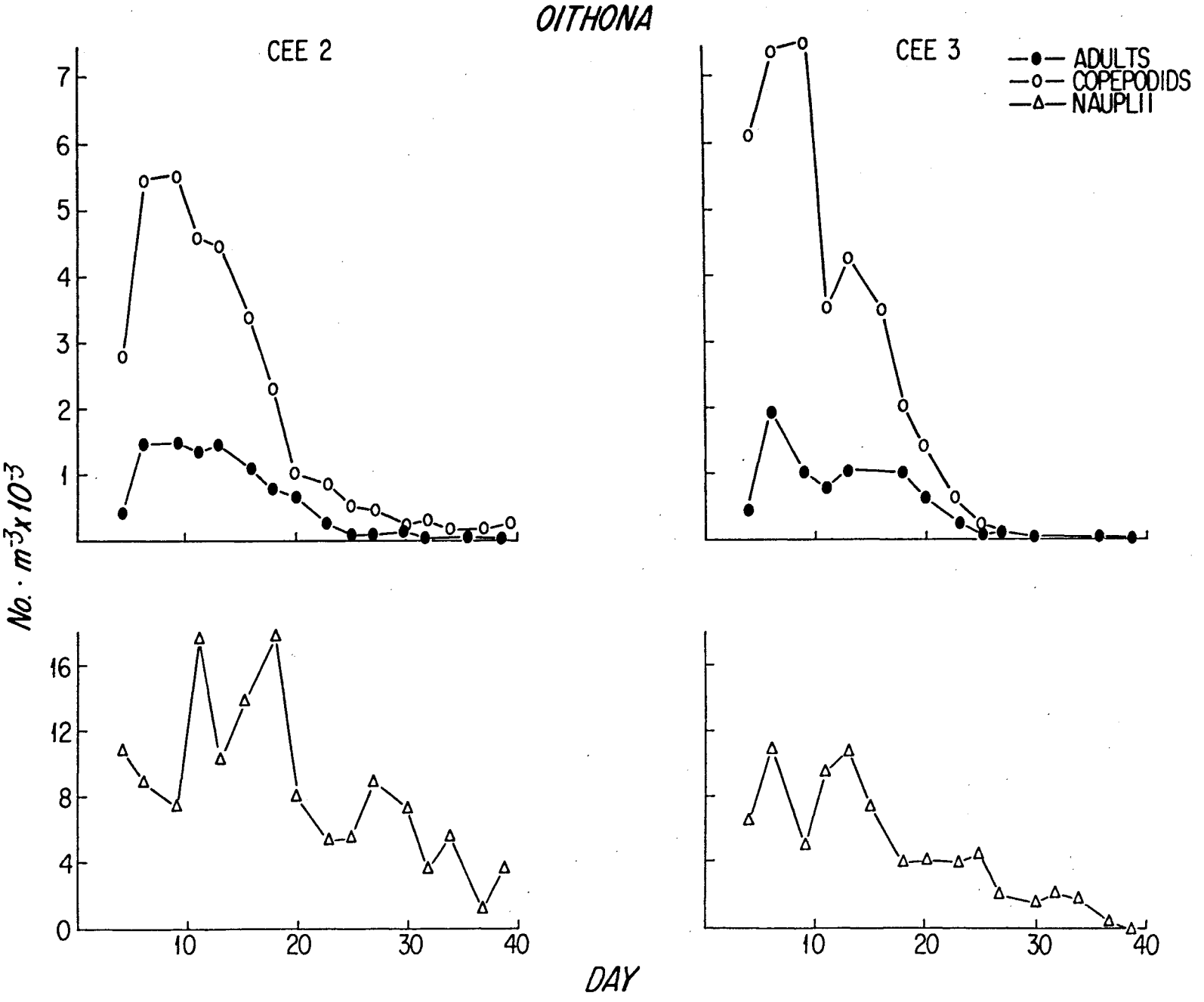

TOTAL MESOZOOPLANKTON
TOTAL ADULT AND COPEPODID COPEPODS
TOTAL NAUPLII
CEE 2
CEE 3
100
80
60
40
20
0
mgC·m-3
10
20
30
40
DAY

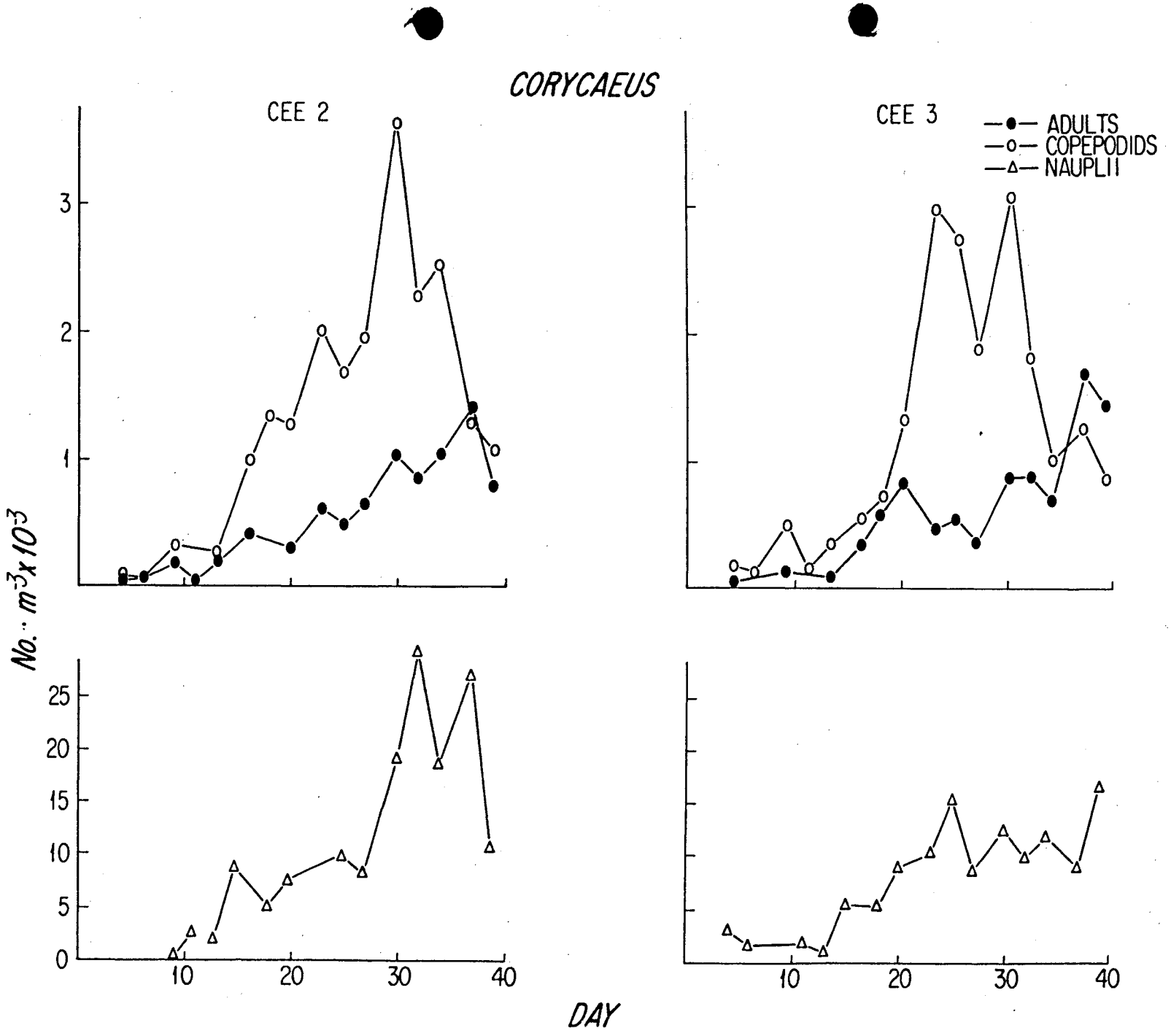

—●— TOTAL MESOZOOPLANKTON
—o— PSEUDOCALANUS ADULTS AND COPEPODIDS
—△— PARACALANUS ADULTS AND COPEPODIDS
CEE 2
CEE 3
mgC·m-3
100
80
60
40
20
0
10
20
30
40
DAY

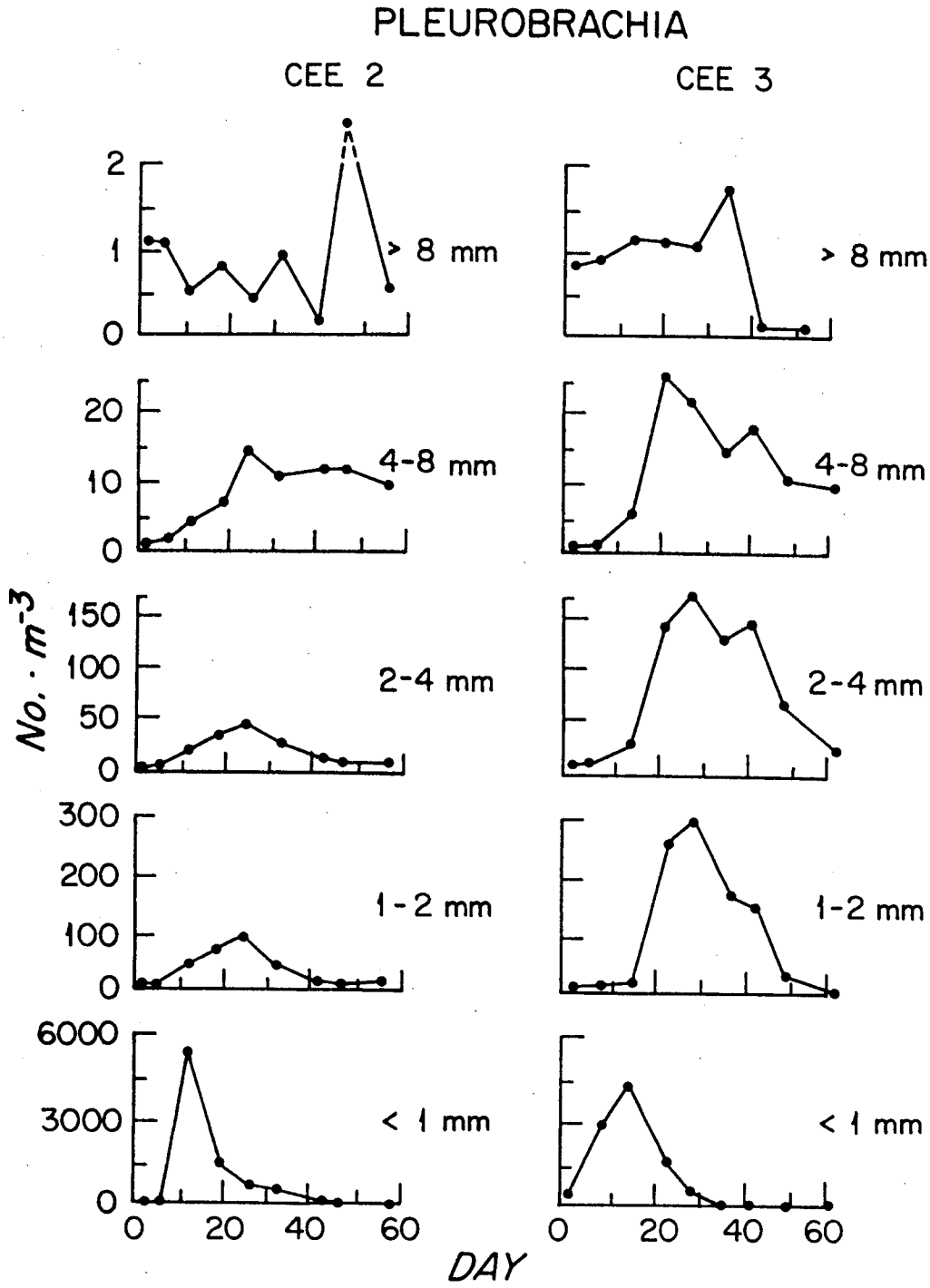

PARACALANUS
CEE 2
CEE 3
ADULT
CV
CIV
CIII
CII
CI
NV - NVI
NIII - NIV
NI - NII
No. $m^3 \times 10^3$
DAY

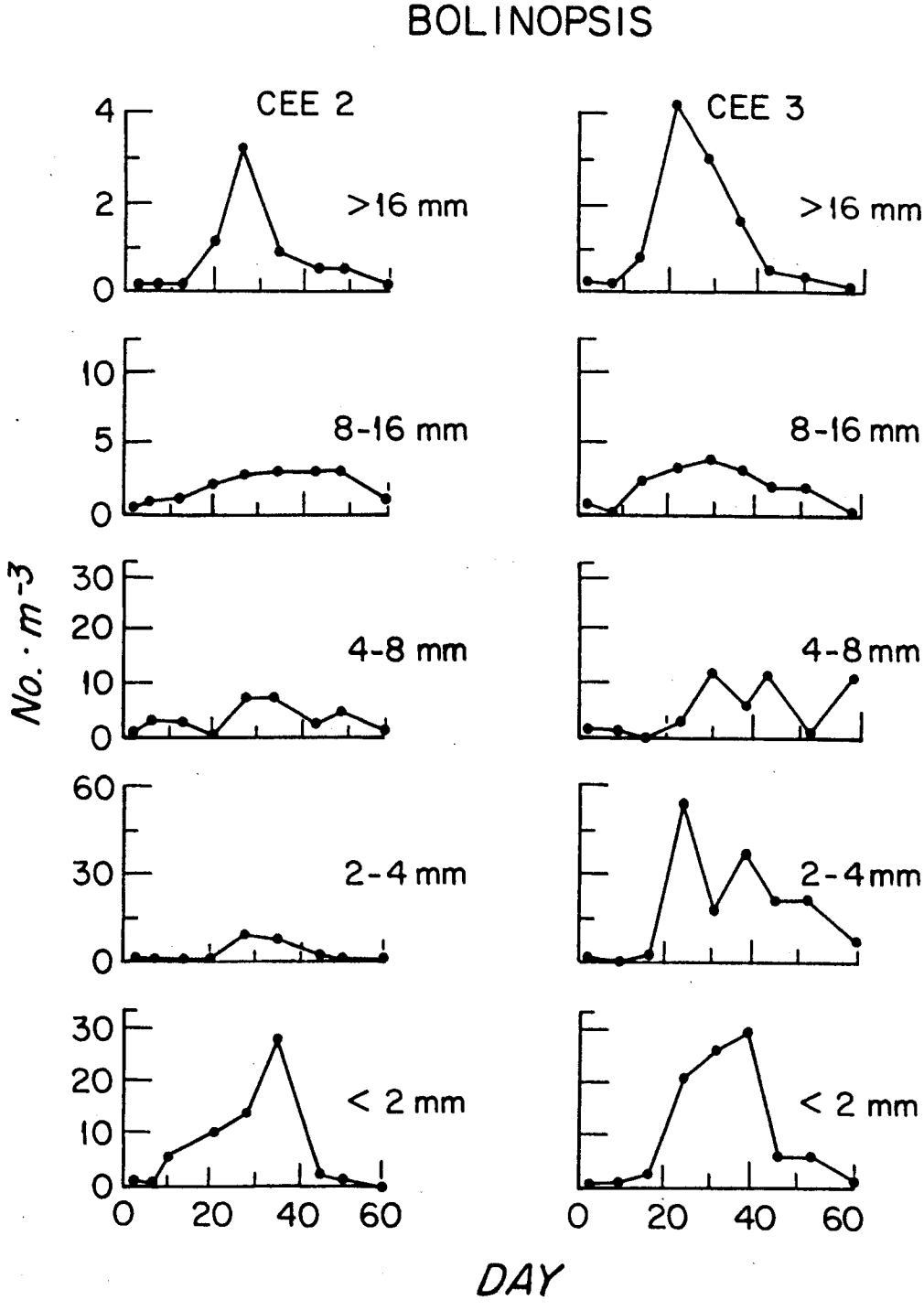
PSEUDOCALANUS

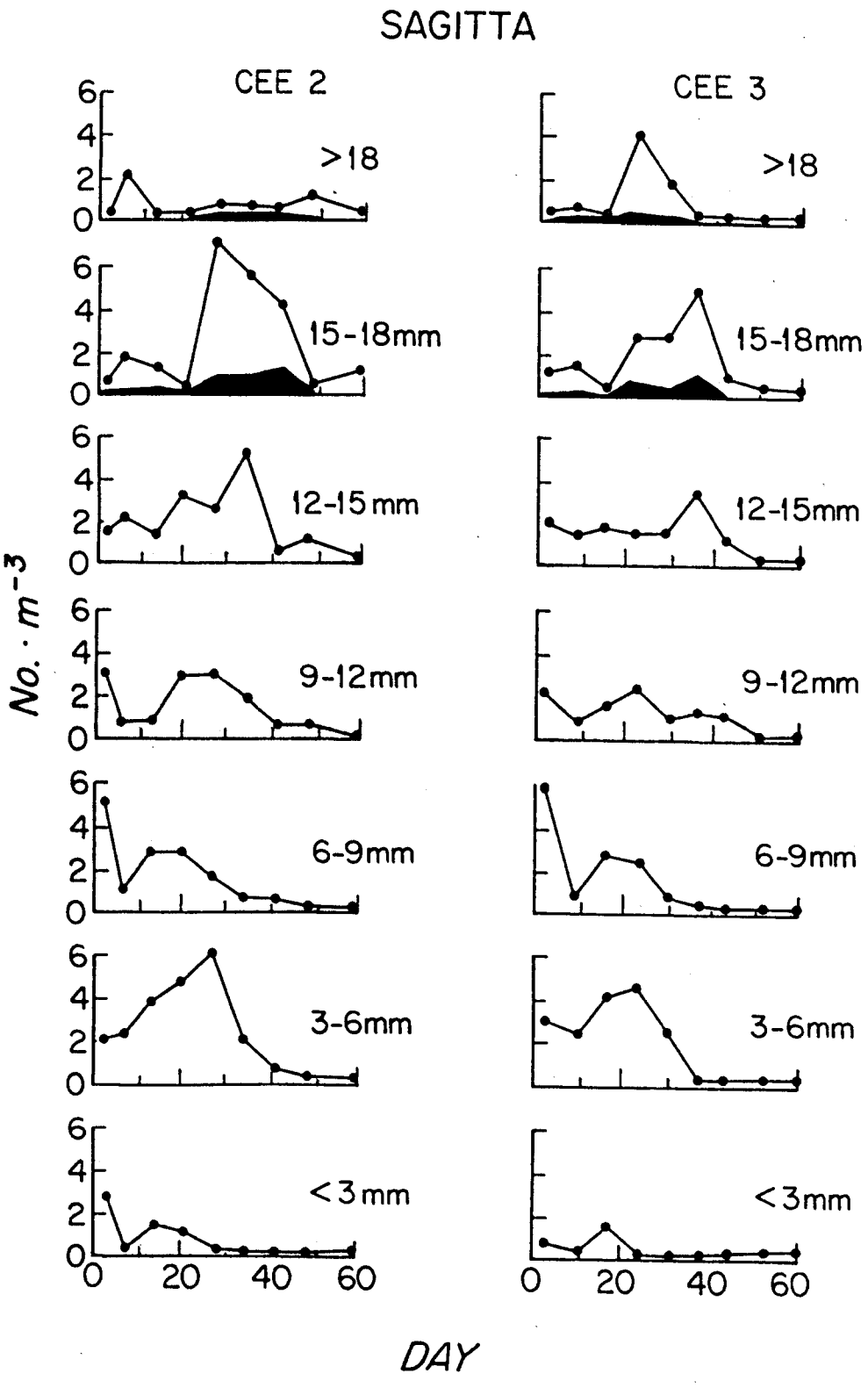


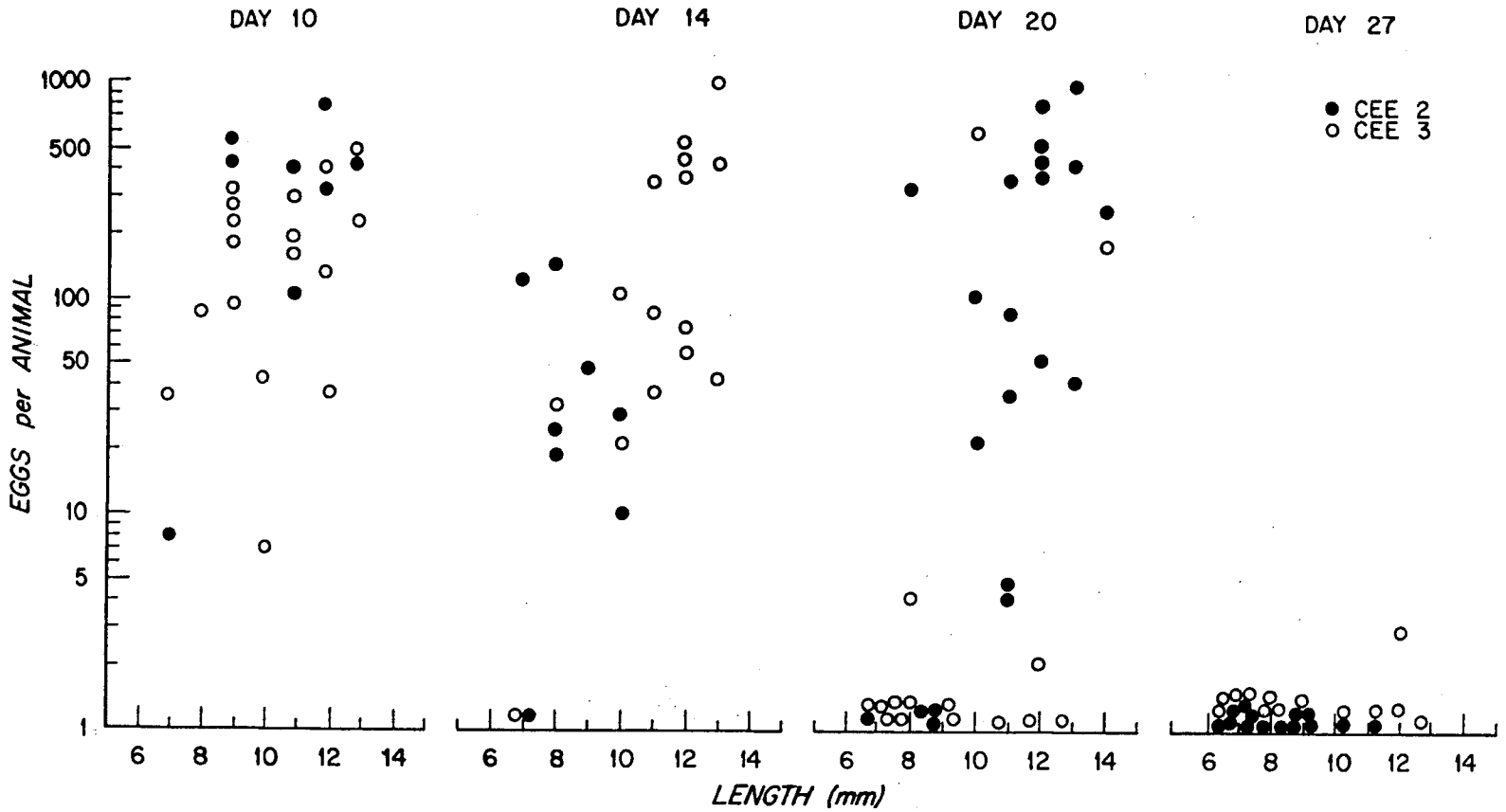

OITHONA
CEE 2
CEE 3
ADULTS
COPEPODIDS
NAUPLII
No. · m⁻³ x 10⁻³
DAY
0
1
2
3
4
5
6
7
4
8
12
16
10
20
30
40

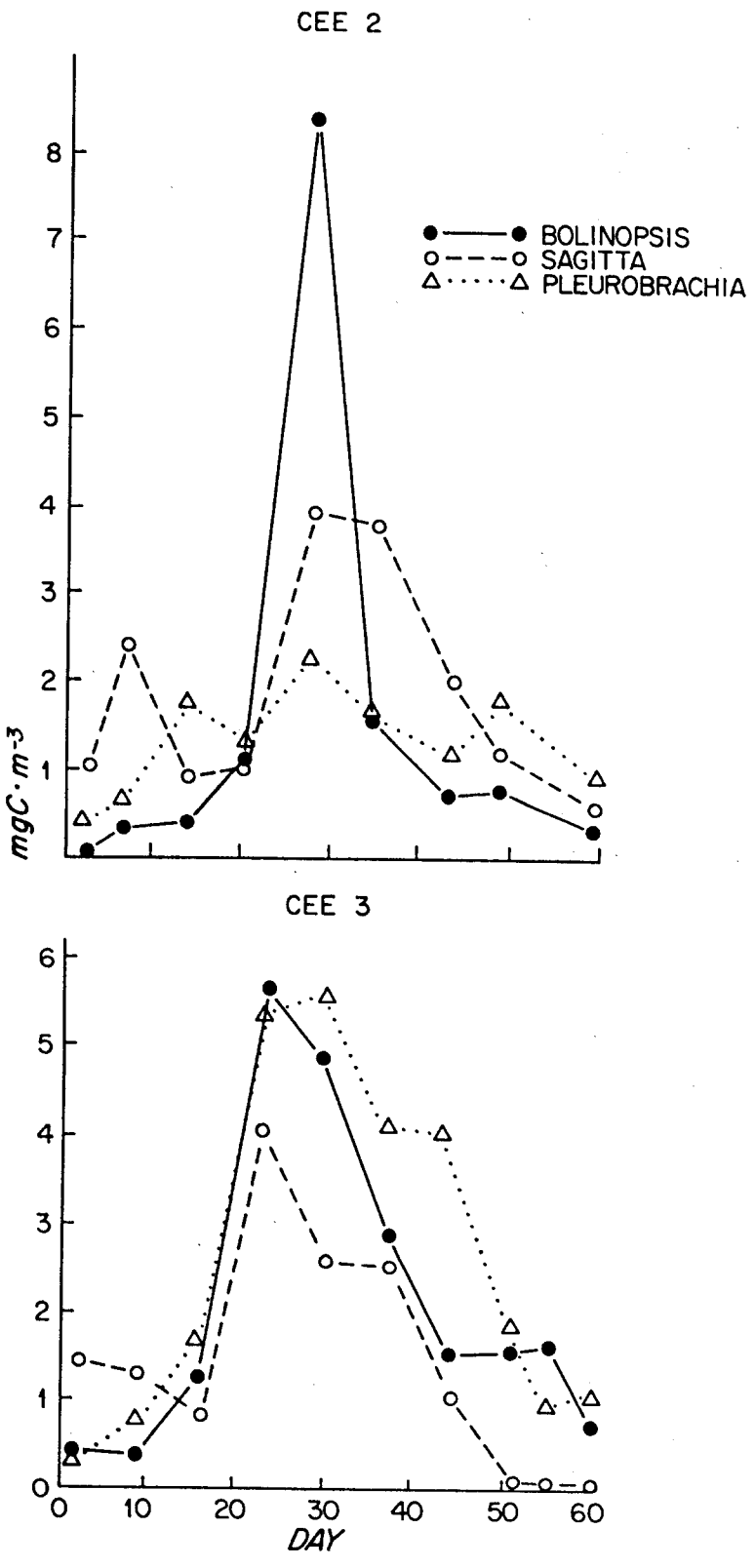

CORYCAEUS
CEE 2
CEE 3
ADULTS
COPEPODIDS
NAUPLII
No. · m⁻³ x 10⁻³
DAY
0
1
2
3
5
10
15
20
25
10
20
30
40

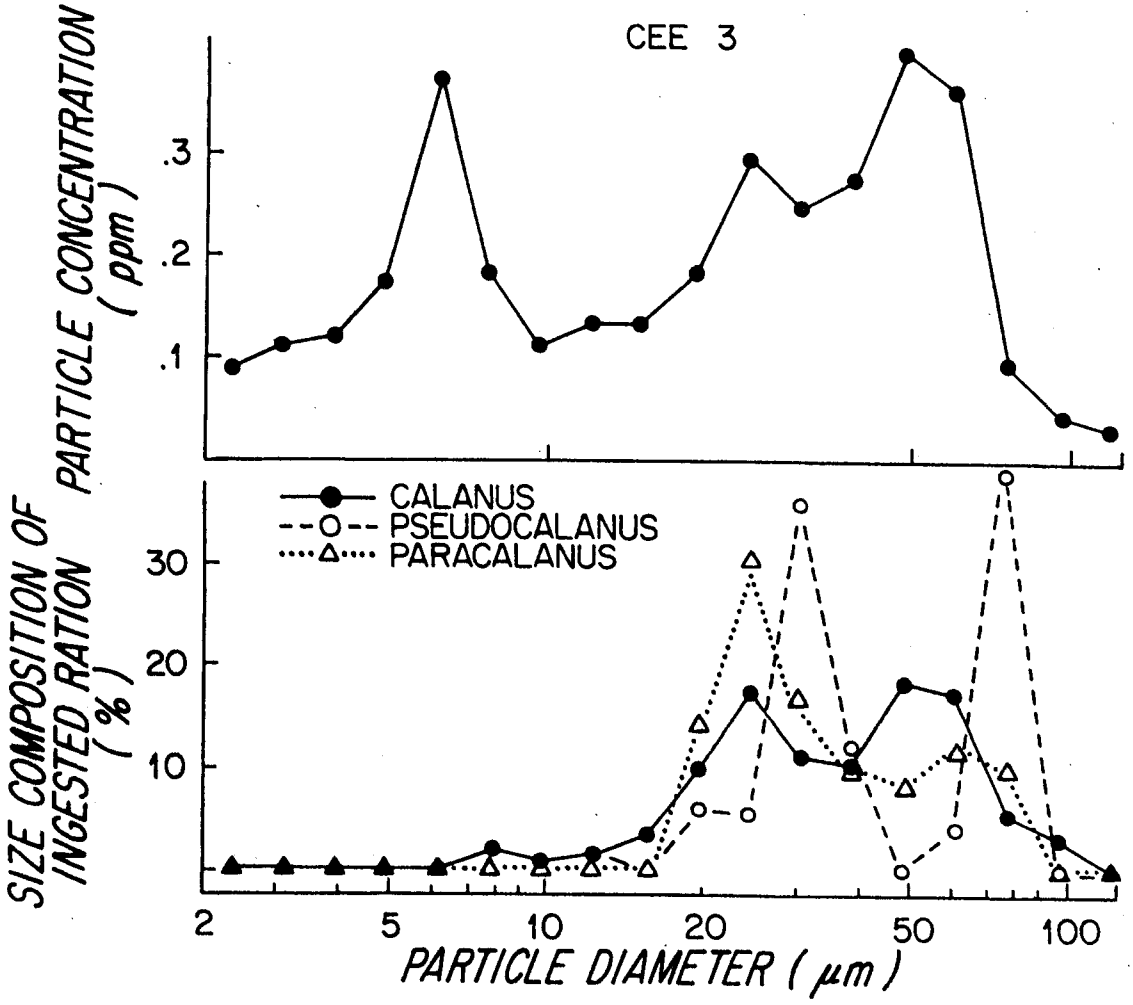

PLEUROBRACHIA
CEE 2
CEE 3
> 8 mm
4-8 mm
2-4 mm
1-2 mm
< 1 mm
No. · m-3
DAY
0
20
40
60

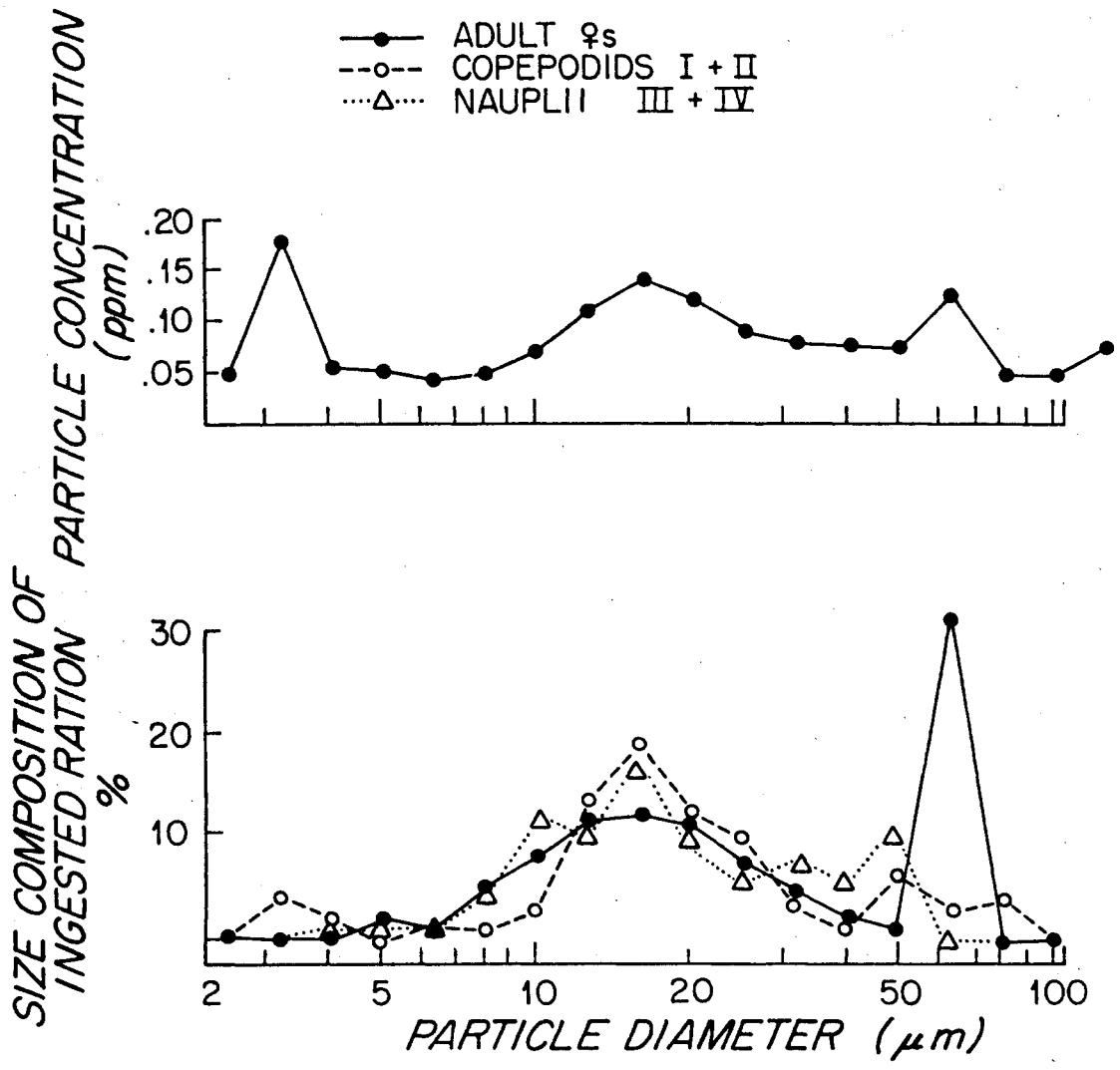

BOLINOPSIS
CEE 2
CEE 3
>16 mm
8-16 mm
4-8 mm
2-4 mm
< 2 mm
No. · m-3
DAY
0
20
40
60

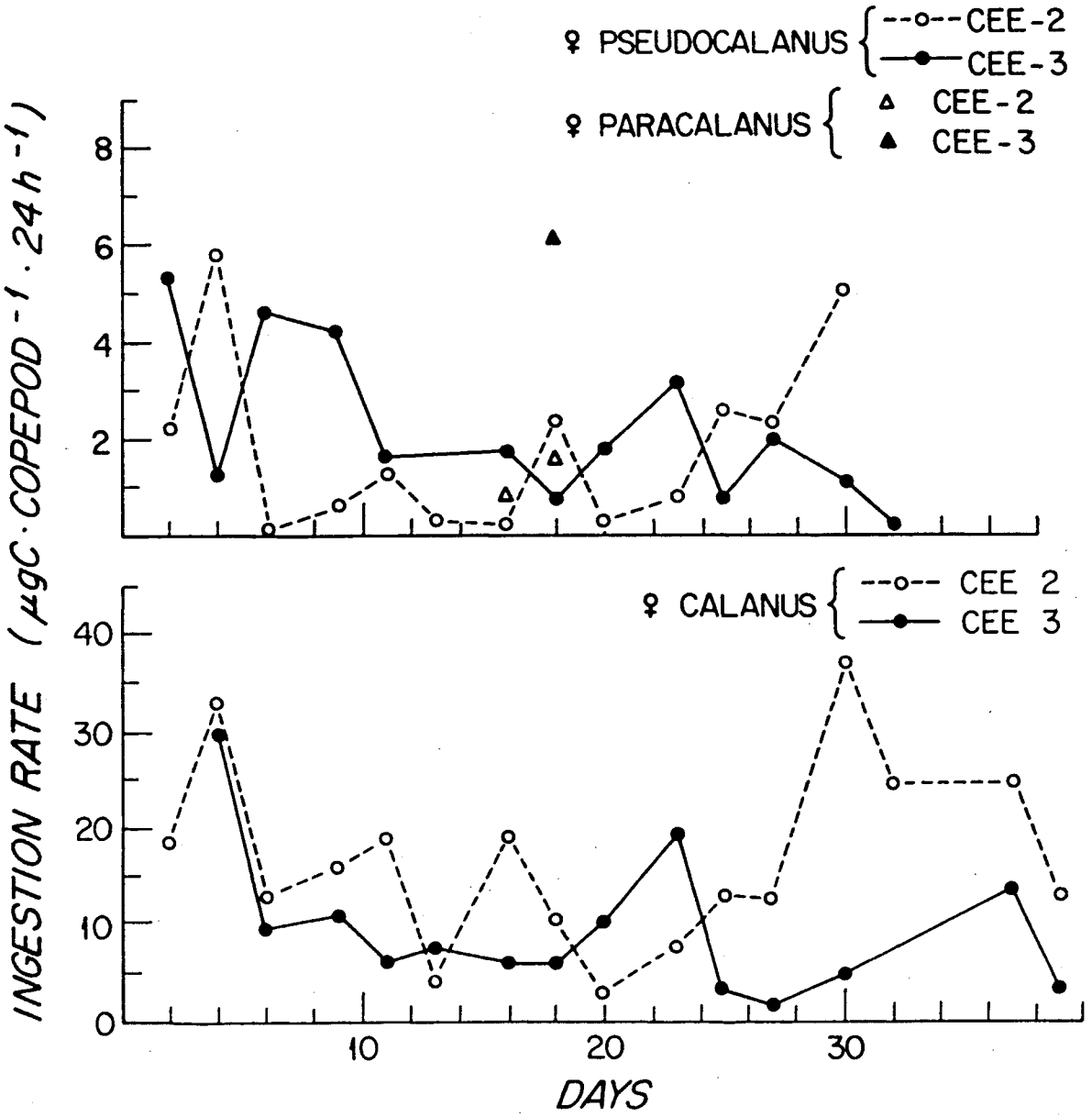

SAGITTA
CEE 2
CEE 3
>18
15-18mm
12-15mm
9-12mm
6-9mm
3-6mm
<3mm
No. · m⁻³
0
2
4
6
0
20
40
60
DAY

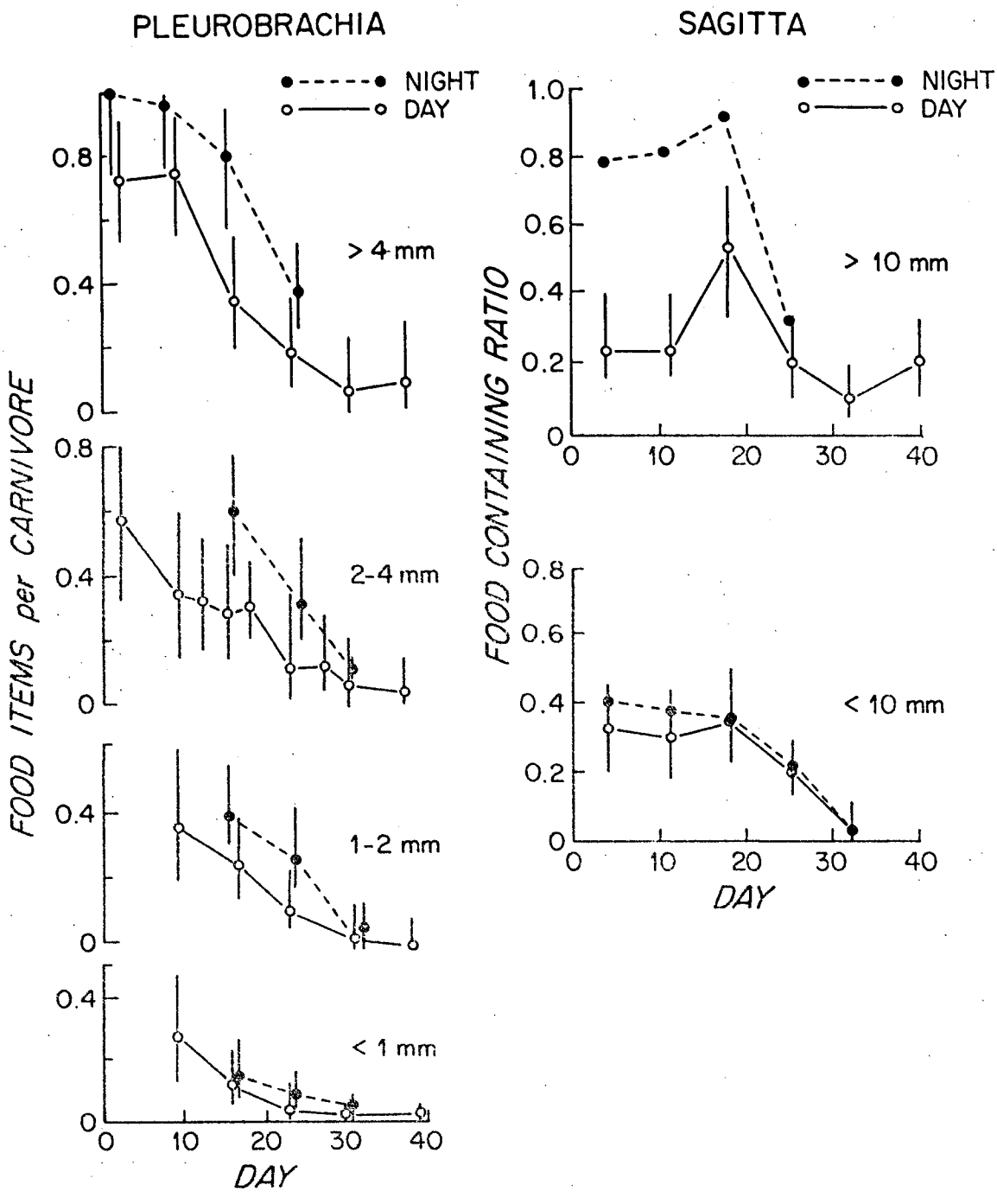

DAY 10
DAY 14
DAY 20
DAY 27
CEE 2
CEE 3
EGGS per ANIMAL
1000
500
100
50
10
5
1
6
8
10
12
14
LENGTH (mm)

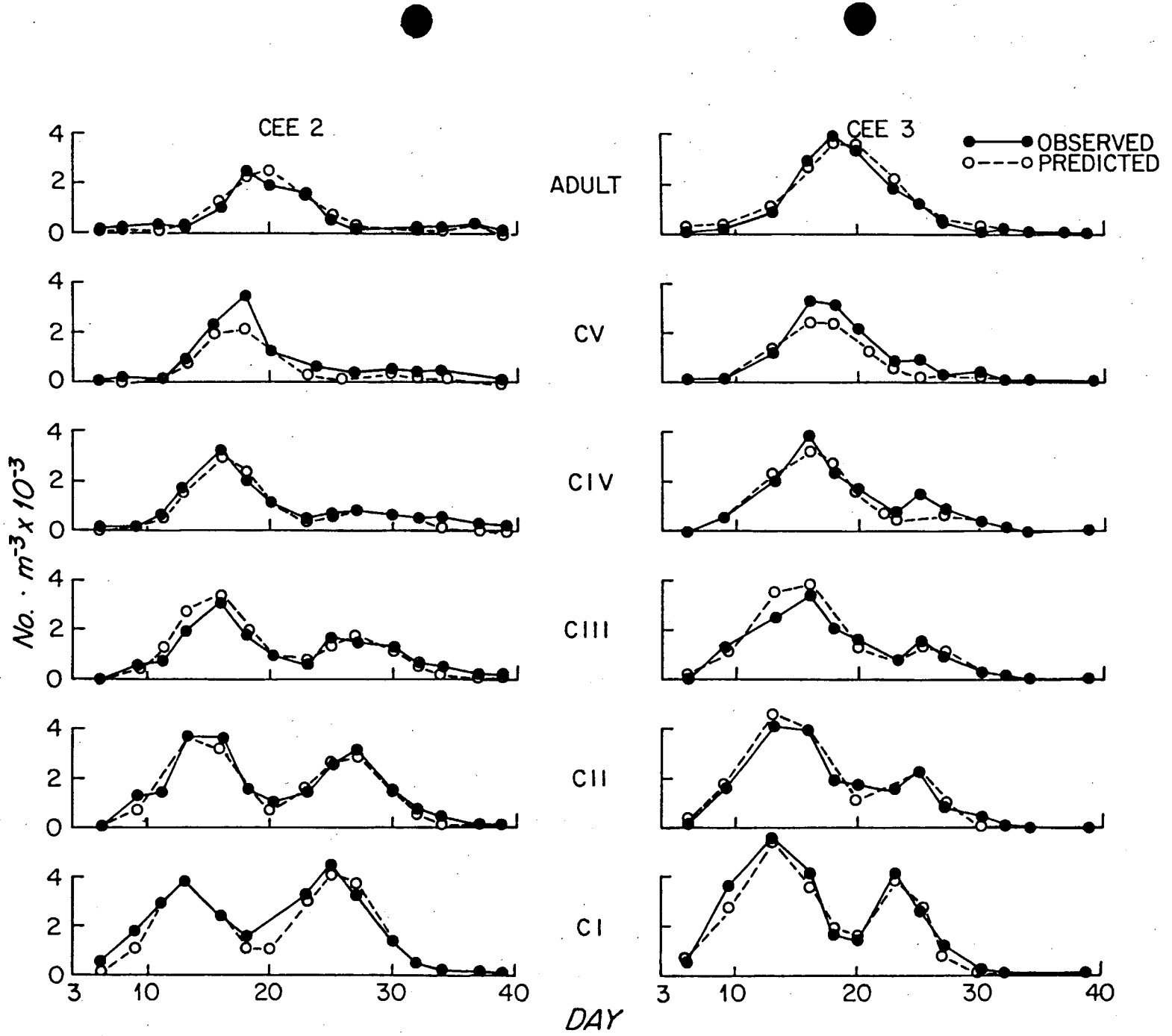

CEE 2
BOLINOPSIS
SAGITTA
PLEUROBRACHIA
mgC·m-3
0
1
2
3
4
5
6
7
8
CEE 3
0
1
2
3
4
5
6
0
10
20
30
40
50
60
DAY

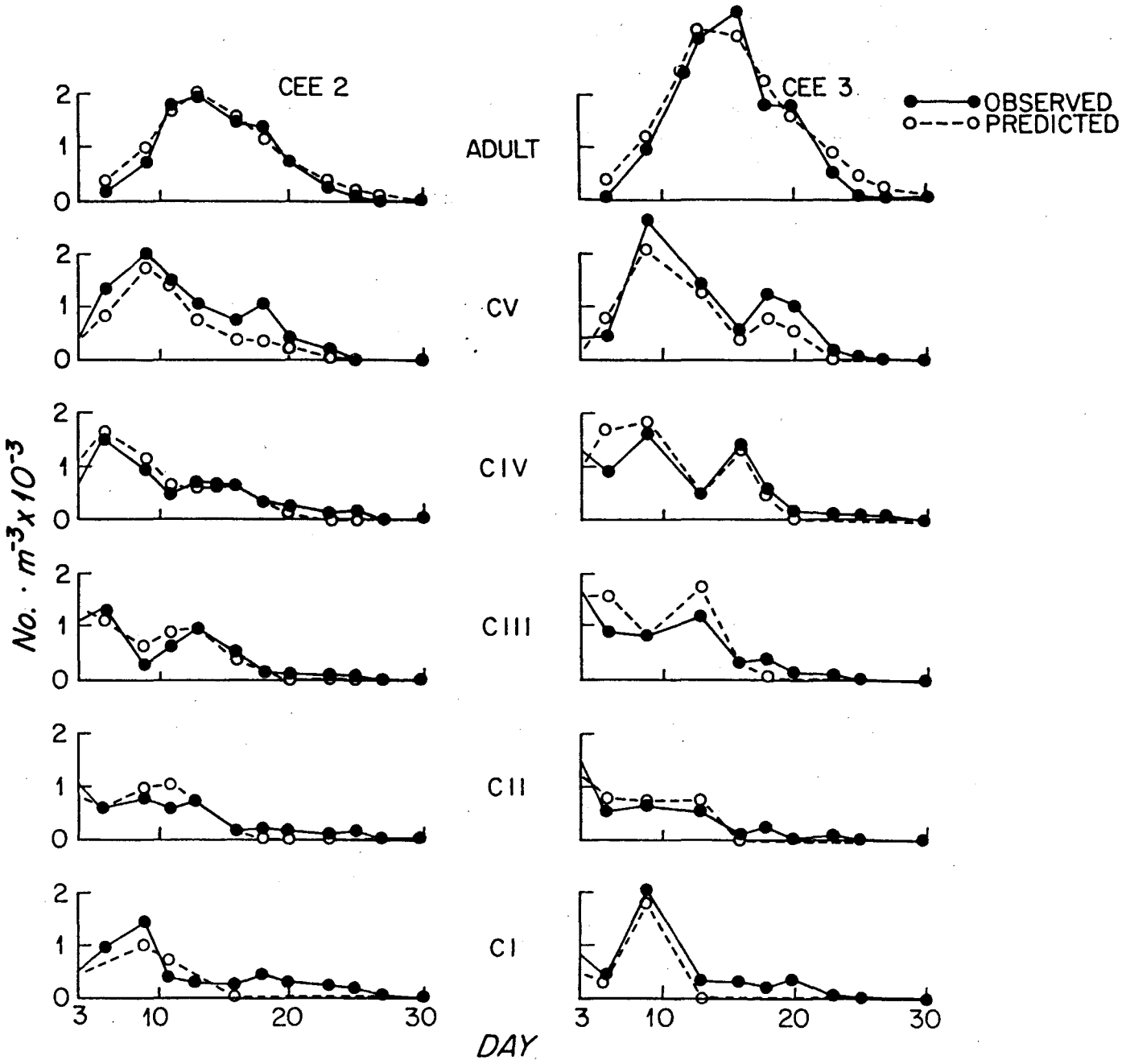

CEE 3
PARTICLE CONCENTRATION (ppm)
.3
.2
.1
SIZE COMPOSITION OF INGESTED RATION (%)
CALANUS
PSEUDOCALANUS
PARACALANUS
30
20
10
2
5
10
20
50
100
PARTICLE DIAMETER (μm)

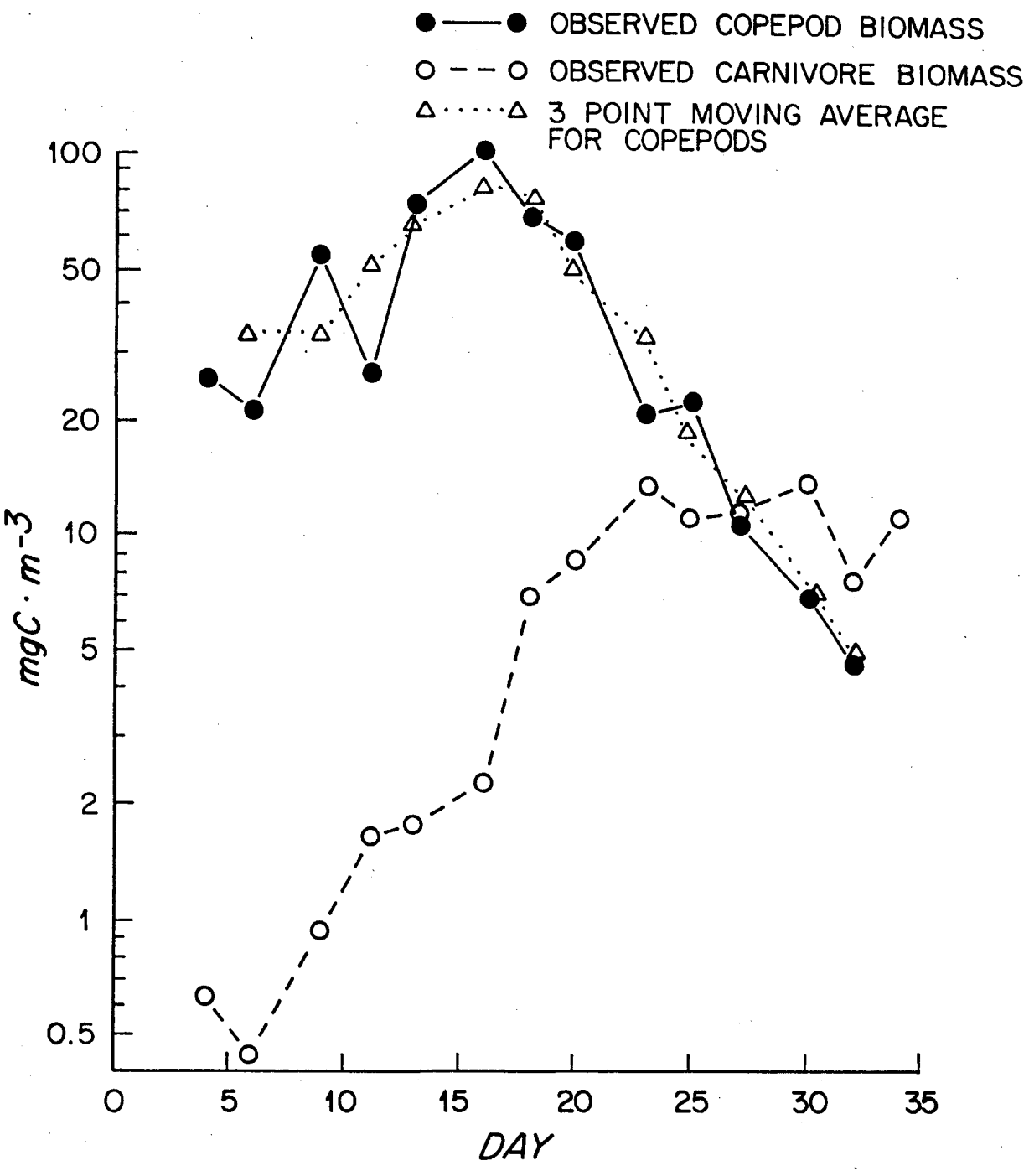

ADULT ♀s
COPEPODIDS I + II
NAUPLII III + IV
PARTICLE CONCENTRATION (ppm)
.20
.15
.10
.05
SIZE COMPOSITION OF INGESTED RATION %
30
20
10
2
5
10
20
50
100
PARTICLE DIAMETER (μm)


♀ PSEUDOCALANUS
CEE-2
CEE-3
♀ PARACALANUS
CEE-2
CEE-3
♀ CALANUS
CEE 2
CEE 3
INGESTION RATE (μgC·COPEPOD⁻¹·24h⁻¹)
DAYS
0
2
4
6
8
10
20
30
40
10
20
30


PLEUROBRACHIA
SAGITTA
NIGHT
DAY
> 4 mm
2-4 mm
1-2 mm
< 1 mm
> 10 mm
< 10 mm
FOOD ITEMS per CARNIVORE
FOOD CONTAINING RATIO
DAY
0
0.2
0.4
0.6
0.8
1.0
10
20
30
40


CEE 2
CEE 3
OBSERVED
PREDICTED
ADULT
CV
CIV
CIII
CII
CI
No. · m-3 x 10-3
DAY
0
2
4
3
10
20
30
40


CEE 2
CEE 3
OBSERVED
PREDICTED
ADULT
CV
CIV
CIII
CII
CI
No. · m⁻³ x 10⁻³
DAY
0
1
2
3
10
20
30


OBSERVED COPEPOD BIOMASS
OBSERVED CARNIVORE BIOMASS
3 POINT MOVING AVERAGE FOR COPEPODS
100
50
20
10
5
2
1
0.5
mgC · m-3
0
5
10
15
20
25
30
35
DAY