SELECTIVE FEEDING, INGESTION AND ASSIMILATION RATES,
AND DISTRIBUTION OF THE COPEPOD *ACARTIA*
IN CHESAPEAKE BAY

Stephen E. Storms

Chesapeake Bay Institute
Johns Hopkins University
Baltimore, Maryland 21218

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ABSTRACT

Acartia was found to be the numerically dominant copepod genus in Chesapeake Bay from February through December 1973; in early spring *Eurytemora affinis* was numerous in the upper bay and both *Temora longicornis* and *Centropages* sp. were found in substantial numbers in the lower bay and adjacent shelf waters. Rotifers were also abundant in the upper bay in spring, but their numbers were underestimated because of inefficient retention on the sampling mesh.

Selective ingestion by *Acartia* of different phytoplankton cell sizes, as measured by Ivlev's electivity index E, was found to depend on total volumetric concentration or biomass in each algal cell size group, rather than on the numerical abundance of cells in a given size group or cell size alone. *Acartia* ingested cells as small as 4-5 microns equivalent spherical diameter, but more often preferred cells larger than 7-8 microns. Little evidence was found for selective ingestion of phytoplankton cells larger than 35 microns, except when algal biomass in this size group equalled or exceeded that in smaller size groups.

Ingestion and assimilation rates of late copepodite and adult *Acartia*, combined with data on numerical abundance of these organisms, suggest that mature *Acartia* do not ingest a significant portion of the phytoplankton standing stock or daily net primary production, except in the lower bay, and during the colder months.

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Rotifers, despite lower individual feeding rates, may ingest a larger portion of the daily algal production during their periodic increases in abundance. It is suggested that microzooplankton, including rotifers, protozoans, and immature copepods, may play a significant role in the utilization of primary production in Chesapeake Bay.

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CHAPTER 1.

GENERAL INTRODUCTION

The groups of animals forming the phylum Arthropoda are important in aquatic and terrestrial environments, not only because of the diversity of ecological niches occupied, but also because of the sheer numbers of individuals and species involved. Barnes (1963) estimated that more than 800,000 species of arthropods have been described, comprising about 80% of all known animal species. Of the three largest classes of arthropods, two, Insecta and Arachnida, are largely terrestrial, with a few groups secondarily adapted to fresh-water environments. The third major arthropod class, Crustacea, is primarily aquatic; although there are a considerable number of fresh-water species, most crustacean species are marine.

Within the marine environment, one of the most important groups both ecologically and in terms of absolute numbers of individuals is the crustacean sub-class Copepoda. Copepods are the dominant members of the zooplankton in most oceanic and neritic environments, forming a link in the food chain between the planktonic primary producers and the higher animals. Nemoto (1970) reports that copepods of the genus *Calanus* are a major source of food for the fin, sei, and right whales. Marshall, Nicholls, and Orr (1937, 1939) have demonstrated the importance of *Calanus* in the feeding habits of all life stages of the herring, a commercially important oceanic fish.

Copepods are also abundant in the zooplankton of the Chesapeake Bay. Wilson (1932) published a comprehensive species list of the copepods in the bay; he found copepods of the genus *Acartia* to be numerically dominant, comprising about two-thirds of the entire collection. Rupp (1969) elucidated the seasonal and spatial distribution of *Acartia* in the upper bay, north of the Potomac River; she found *A. tonsa* to be present and dominant year-round except for winter months, when *A. clausi* becomes numerous.

Another calanoid, *Eurytemora affinis*, is abundant in lower salinity waters during the winter and early spring. Two other calanoids, *Pseudodiaptomus coronatus* and *Pseudocalanus* sp., are reported by Heinle (1972) to be common but not abundant in the plankton. Other copepods, such as *Scottolana canadensis* and *Oithona brevicornis*, are epibenthic as adults and are taken only infrequently in routine plankton samples.

Because of their abundance in the zooplankton of the Chesapeake Bay, copepods in general and *A. tonsa* and *A. clausi* in particular, are a vast reservoir of food for the carnivorous animals of the plankton and nekton. The carnivorous ctenophore, *Mnemiopsis leidyi*, has been shown to account for a major portion of the daily mortality of *A. tonsa* in the Patuxent River (Bishop, 1967); both *M. leidyi* and other zooplankton are a major dietary constituent of the sea-nettle *Chrysaora quinquecirrha* (Calder, 1972). The smaller dominant fish of the Chesapeake Bay, such

as the silverside (*Menidia menidia*) and the bay anchovy (*Anchoa mitchilli*), depend heavily on zooplankton, possibly including rotifers and tintinnids, for food; these smaller fish then serve as forage for the predaceous striped bass and bluefish which are of prime importance to both sport and commercial fisheries in the bay area (Musick and Wiley, 1972). *A. tonsa* and other species of zooplankton have been shown by Kjelson et al. (1974) to account for up to 99% of the gut contents of post-larval stages of spot (*Leiostomus xanthurus*) and Atlantic menhaden (*Brevoortia tyrannus*) in the Newport River estuary in North Carolina; a major commercial fishery for the Atlantic menhaden also exists in the Chesapeake Bay.

In the oceanic food chain, *Calanus* has been shown to be of prime importance in the flow of food material and energy from the primary producers to higher trophic levels. The purpose of this dissertation is to determine whether *Acartia* occupies a similar dominant role among the herbivores of the estuarine ecosystem of the Chesapeake Bay.

This study can be divided into three main parts: First, the measurement of the numerical abundance of *Acartia* and other planktonic herbivores at representative stations in Chesapeake Bay throughout the year. Second, the determination of the ability of *Acartia* to ingest the phytoplankton cells which comprise the major source of food in the bay; an investigation into feeding selectivity of *Acartia* toward certain segments of

that phytoplankton assemblage; and a comparison of feeding behavior of *Acartia* with other major herbivores in the bay.

Third, the measurement of the ingestion and assimilation rates of *Acartia* and other herbivores; and the calculation of the relative effects of the grazing of these organisms on the standing stock and net production of phytoplankton in the Chesapeake Bay. This dissertation is divided into three chapters which correspond to the three main divisions mentioned above.

CHAPTER 2

DISTRIBUTION OF *ACARTIA* AND OTHER COPEPODS IN CHESAPEAKE BAY*Introduction*

Copepods of the genus *Acartia* are among the most numerous and widely distributed zooplankton in the nearshore and estuarine waters of the eastern coast of North America. *A. clausi* has been reported from the Gulf of Maine by Bigelow (1926), while both *A. tonsa* and *A. clausi* were found to be abundant in the Woods Hole region (Fish, 1925; Wilson, 1932a; Anraku, 1964a). Deevey (1952a, 1952b) noted *A. tonsa*, and to a lesser extent *A. clausi*, in the waters of Block Island Sound. *Acartia* spp. have been found to be the dominant zooplankton in Narragansett Bay (Martin, 1970), Long Island Sound (Conover, 1956; Deevey, 1956), Sandy Hook Bay (Sage and Herman, 1972), Delaware Bay (Deevey, 1960; Cronin, Daiber, and Hulbert, 1962), Newport River estuary, North Carolina (Thayer et al., 1974) and Biscayne Bay (Woodmansee, 1958; Reeve, 1970).

The earliest survey of the copepods of Chesapeake Bay was that of Wilson (1932b), but the proper identification of the dominant copepod in this estuary did not occur until Davis (1944) found *A. tonsa* in samples taken throughout the year, and *A. clausi* only in winter samples. While Davis postulated a change in copepod species in the Bay since Wilson's earlier survey, Bowman (1961) discovered that species identified by Wilson as *A. clausi* and *A. longiremis* were truly *A. tonsa*.

Bowman (1961) suggested a seasonal distribution of *A. tonsa* and *A. clausi* for the Chesapeake Bay, based primarily on the results of seasonal surveys of copepods in Long Island Sound (Conover, 1956) and Delaware Bay (Deevey, 1960). Additional data on the changes in abundance with season of *A. tonsa* and *A. clausi* were provided by Heinle (1966) and Herman, Mihursky and McErlean (1968) for the Patuxent River, a tributary of the Chesapeake Bay. The seasonal and spatial distribution of the two species of *Acartia* in the upper Chesapeake Bay north of the Potomac River was elucidated by Rupp (1969).

The purpose of this investigation into the abundance of *Acartia* in Chesapeake Bay was two-fold. First, few of the previous surveys of copepods in the Chesapeake Bay area contained quantitative data on the numerical abundance of *Acartia*, and none covered the entire bay. The quantitative collections of Herman et al. (1968) were taken with a 370 μ m mesh net which would necessarily retain only the largest copepodites and adult copepods. It was felt that to obtain a complete picture of the abundance of copepods in the estuarine system, a net which would retain at least all of the copepodites as well as adults should be utilized. Although ideally it would have been desirable to sample nauplii as well as later stages, it was found that the use of smaller mesh nets resulted in extensive clogging. Heinle's (1966) study of the production of *A. tonsa* did include nauplii, copepodites and adults, but both his study and that of Herman

et al. (1968) were confined to the Patuxent River estuary of the Chesapeake Bay, and it was thought that copepod abundances might differ markedly between the Patuxent estuary and the open waters of the Chesapeake.

Rupp's (1969) study of the seasonal and spatial distribution of *Acartia* in the Chesapeake Bay was concerned primarily with copepods north of the Potomac River, although one station in the lower bay was sampled for a period of one year. It was felt that the present study, which covered the entire bay somewhat less intensively would complement the data collected by Rupp, especially in the lower bay. In addition, while Rupp's data lumped copepodites and adults into one group, it was thought advisable in this study to further separate the developmental stages of *Acartia*.

The second and perhaps more important purpose of this study of copepod abundance in Chesapeake Bay was to obtain estimates of the numbers of animals present at a particular station at a given time to accompany ingestion and assimilation experiments performed at that station. Since in the majority of copepod feeding experiments ingestion rates are expressed on a per animal basis, and the animals were concentrated with respect to nature to some degree, it is necessary to know the natural abundance of the animals in order to convert ingestion per copepod to ingestion by the population of copepods at a particular station.

Methods

Procedures for quantitative and qualitative sampling of copepods during these cruises (code name Procon) generally followed the methods of Bosch and Taylor (1973a). Eight stations along the longitudinal axis of the Chesapeake Bay, and one station over the continental shelf approximately 25 km offshore, were sampled at eight-week intervals during 1973 (Figure 1).

Qualitative samples for species identification, and for purposes detailed in later chapters, were taken by vertical haul. A 26 cm diameter plankton net (160 μ m mesh) was lowered to approximately 12 m and retrieved. Additional tows were made as necessary to collect sufficient material.

Quantitative samples were collected by a submersible pump (Whaley, 1958) which was lowered to the desired depth. The pump capacity with 20 m of 26 cm inside diameter hose was approximately 100 liters per minute. Fifty liters of water from each depth were collected in calibrated polyethylene carboys which were then allowed to drain through 160 μ m mesh Nitex screen. The animals were washed off the screen and preserved in buffered 5% formalin-seawater for subsequent counting and identification.

All samples were collected between the hours of 1100 and 1300. Quantitative samples were taken at four depths: just below the surface, 4, 8 and 12 meters. These depths were chosen largely to correspond with those sampled during recent zooplankton studies in the Chesapeake Bay by Rupp (1969), and

Figure 1. Location of Chesapeake Bay stations.

Bosch and Taylor (1973a, b). Deeper samples were collected when station depth permitted if qualitative vertical plankton hauls indicated that significant numbers of zooplankton were to be found below the routine sampling depths.

The copepods which were utilized in the feeding experiments described in later chapters were separated into three size classes by filtering through 405 μm and 253 μm mesh screens. It was desirable therefore to obtain estimates of the abundance of each of these three size classes at every depth sampled. In order to facilitate this size classification, groups of copepods which had been retained by each of the three mesh sizes were measured for body length with a binocular microscope equipped with an ocular micrometer. Thereafter, copepods in quantitative samples were separated into three size categories by visual reference to the established body length for each mesh size. *Acartia* were not identified to species in these samples, as *Acartia tonsa* and *A. clausi* had not been separated for feeding experiments.

Subsamples for enumeration were taken from a well-mixed preserved sample with a wide-mouth pipet. An attempt was made to count in excess of 100 individuals of each genus; however, it was frequently not possible to count 100 individuals of each size class. On some occasions when zooplankton numbers were low, the entire preserved sample was counted to obtain maximum possible precision.

The precision of the pump sampling method, using the same equipment as was used in this study, was discussed by Bosch and Taylor (1973a). In subsamples containing more than 100 animals, the coefficient of variation was found to tend toward a constant value of 25%. In order then to be considered significantly different, the count in one sample should be less than one-half or more than double the count found in another sample, assuming that at least 100 animals were counted in each sample.

Although naupliar stages of *Acartia* did appear in the preserved samples, they were not enumerated. All stages of copepodites and mature females and males were counted. Heinle (1966) found that a #10 net (150 μ m mesh opening) captured *A. tonsa* naupliar stages V and VI; it is therefore thought that the 160 μ m mesh used in this study retained even the youngest copepodite stages of *Acartia* quantitatively.

The 160 μ m mesh net used in this study would not have quantitatively retained microzooplankton such as rotifers and tintinnids. Large rotifers were retained at times on the 160 μ m mesh net, but the retention efficiency of this net in sampling these organisms was not determined, so these estimates of rotifer abundance should be considered minimum values. Recent studies in the Chesapeake Bay (Loftus, Subba Rao and Seliger, 1972) have indicated that rotifers and tintinnids can be quite abundant in this estuary; the possible significance of these microzooplankton is discussed in later chapters of this dissertation. It should

be noted that the smaller zooplankton have generally been neglected in studies of zooplankton abundance in the marine environment, especially in oceanic studies where large mesh sizes were traditionally used in zooplankton sampling. Beers and Stewart (1969) have found microzooplankton (less than 202 μm) to comprise a significant portion of the total zooplankton volume in the oceanic environment, and the data of Loftus et al. (1972) indicate that microzooplankton may be even more important in the estuarine environment. The vast majority of zooplankton studies cited earlier in this chapter would not have detected microzooplankton because of the relatively large mesh sizes utilized.

Results

Numerical abundances of *Acartia* at nine stations sampled during six cruises are shown in Figures 2 through 4. Abundance is expressed in number of copepods of each of three size classes per cubic meter; this was calculated by taking the mean of the number of copepods per cubic meter at the four sampling depths.

In interpreting these figures, it should be noted that the three size classes used to separate the copepods into groups do not correspond exactly to body length of the copepods, but rather to the mesh size of the screen used to separate the animals. However, after examining numerous groups of separated animals, a useful relationship between mesh size and developmental stages did emerge. The largest size class (greater than 405 μm)

Figure 2. Abundance of *Acartia* adults and copepodites in Chesapeake Bay, February and April, 1973. Solid circles, *Acartia* ($>405\text{ }\mu\text{m}$). Half-filled circles, *Acartia* ($250\text{--}405\text{ }\mu\text{m}$). Open circles, *Acartia* ($160\text{--}250\text{ }\mu\text{m}$).

Figure 3. Abundance of *Acartia* adults and copepodites in Chesapeake Bay, June and August, 1973. Symbols as in Figure 2.

Figure 4. Abundance of *Acartia* adults and copepodites in Chesapeake Bay, October and December, 1973. Symbols as in Figure 2.

generally contained only adult female *Acartia*. The two smaller size classes (250-405 μ m and 160-250 μ m) usually contained copepodite stages IV and V and copepodite stages I through III, respectively. Naupliar stages also appeared in the smallest size class, but these were not counted. There was of course some overlap in these size classes, especially since *A. clausi*, when present, tends to be slightly smaller than *A. tonsa*. In addition, adult *Acartia* males were usually found in the middle size category; males, however, were relatively rare and so were not distinguished except when specifically used in a feeding experiment.

Acartia in the middle size category (copepodites IV and V) were always more numerous than or at least equally numerous with the adult females; the smallest copepodites also sometimes exceeding adults in abundance.

All stages were low in abundance in February and April (Figure 2) in the upper bay, but increased in number going south as far as 724, after which abundance again decreased at the southernmost bay station and the shelf station (Ø707V). *Acartia* was virtually undetected at the three northernmost stations in April. Peaks in abundance of *Acartia* were found in both the upper and lower bay in June (Figure 3); the highest mean number of an *Acartia* size category occurred in this month at 707Ø. Relatively low numbers of *Acartia* were found at 804C in June.

In August (Figure 3), however, abundance of *Acartia* was higher at 804C than any other station except 904M. Adults and

larger copepodites were particularly numerous at these two stations. Adults decreased in number southward from 804C, but juveniles increased, reaching another peak at 707Ø.

In October (Figure 4), *Acartia* in the largest size class were abundant only in the upper bay, but larger copepodites were relatively numerous throughout the bay. *Acartia* in the smallest size categories, the earliest copepodites, were especially abundant at three mid-bay stations.

All stages decreased in abundance in December, especially at lower bay stations (Figure 4). Adult *Acartia* were present in the bay, but with the exception of the three northernmost stations, their numbers were too low to permit precise estimates of abundance. Older copepodites were also found only in small numbers in the lower bay. Overall abundance for all stages was the lowest of all six cruises in December.

Figures 5 and 6 show the mean number of animals per liter at each station for zooplankton other than *Acartia*. *Eurytemora affinis* was encountered only in February and April (Figure 5) in the upper bay. In February, *Acartia* and *Eurytemora* were about equal in abundance, but in April *Eurytemora* far exceeded *Acartia* in number at the four northernmost stations.

Rotifers were also very abundant in the upper bay in February and April. Numbers for rotifers in February should be considered minimum estimates since the rotifers were collected on a 160 µm screen probably did not sample the smaller forms quantitatively.

Figure 5. Abundance of zooplankton other than *Acartia* in Chesapeake Bay, February and April, 1973. Solid squares, *Eurytemora affinis* ($>405\ \mu\text{m}$). Open squares, *E. affinis* (250-405 μm). Solid triangles, *Centropages* sp. ($>405\ \mu\text{m}$). Open triangles, *Centropages* sp. (250-405 μm). Inverted solid triangles, *Temora longicornis* ($>405\ \mu\text{m}$). Inverted open triangles, *T. longicornis* (250-405 μm). Crosses, rotifers ($>160\ \mu\text{m}$).

Figure 6. Abundance of zooplankton other than *Acartia* in Chesapeake Bay, June 1973. Solid diamonds, *Temora longicornis* and *Centropages* sp. ($>405\ \mu\text{m}$). Open diamonds, *T. longicornis* and *Centropages* sp. ($250\text{--}405\ \mu\text{m}$).

At 904N and 854G in February, rotifers were quite abundant but were not counted. At 834G and 818P, however, the sampling screen clogged partially with chain-forming diatoms, thus increasing retention efficiency of the net and allowing a greater proportion of the rotifers to be sampled. For the April cruise, the 160 μ m mesh was replaced with a 35 μ m mesh in an attempt to retain all rotifers; these values could be considered better estimates of rotifer abundance than the February values.

Two neritic copepod genera common to the continental shelf were encountered in February, April and June at lower bay and continental shelf stations. In February, *Centropages typicus* and *C. hamatus* were abundant at Ø707V and present but not numerous at 707Ø and 724R. *Temora longicornis* was noted in April at Ø707V, but not at stations inside the bay. In February or April *Acartia* outnumbered both *Temora* and *Centropages*. In June a mixture of *T. longicornis* and *Centropages* sp. exceeded *Acartia* in number by a factor of 10 at station Ø707V, but the shelf copepods were not encountered in the bay (Figure 6).

Figures 7 through 9 show the vertical distribution of copepodites and adult *Acartia* along the longitudinal section of the bay and the shelf station for six cruises in 1973. Values are expressed in animals per cubic meter at each of the four (occasionally six) sampling depths; numbers of copepods in the different size classes were summed for each depth to give the total of adults and copepodites. Figure 7 shows the relatively

Figure 7. Distribution of *Acartia* adults and copepodites in Chesapeake Bay, February and April, 1973. Number of organisms per cubic meter.

Figure 8. Distribution of *Acartia* adults and copepodites in Chesapeake Bay, June and August, 1973. Number of organisms per cubic meter.

Figure 9. Distribution of *Acartia* adults and copepodites in Chesapeake Bay, October and December, 1973. Number of organisms per cubic meter.

uniform distribution of *Acartia* found in February in the middle bay, with decreasing numbers up-bay especially in shallow depths, and increasing numbers toward the lower bay and greater depths.

In April (Figure 7) the low abundance of *Acartia* at upper bay stations (also noted previously in Figure 2) was shown to be confined mostly to the shallow depths; animal densities increased down-bay to a maximum in the upper 8 meters at 724R. The extent of the high abundance of copepods seems less widespread than in February.

Large numbers of *Acartia* continued to be found below 8 meters in the upper bay in June (Figure 8); abundance decreased in mid-bay as was reflected also in Figure 3, then increased further down-bay to a maximum at the southernmost station in the bay.

Distribution of *Acartia* in August and October (Figures 8 and 9) was relatively uniform. Maximum animal densities in August were encountered below the surface waters at 904N; a record maximum for a single depth was found in mid-bay at 8 meters. Animal densities continued to be slightly elevated at lower bay stations, but had decreased considerable from the maximum found in June. Abundance of *Acartia* at 818P, 834G and 854C was generally low.

The maximum abundance of *Acartia* in October was found at 4 meters at 818P and 834G; the rest of the upper bay population had also increased in number, except that the maximum at 904N

found in August has disappeared. Animal densities in the lower bay were slightly lower than in the previous cruise.

A more varied distribution of *Acartia* existed in December (Figure 9). Maximum concentrations were again found in the upper bay from 834G northward. Minimum abundance was encountered at 804C, especially in the upper layers where *Acartia* was virtually undetectable. Samples taken at greater depth than usual revealed a higher density of animals extending from 804C southward in the lower depths. Densities in the shallower depths of the lower bay were much lower than during the previous cruise.

Discussion

This study covered a wider geographic area than Rupp's previous (1969) survey of the distribution of *Acartia* in Chesapeake Bay, but our stations were more widely spaced and were sampled less frequently. Because of this, direct comparisons between the two studies are difficult to draw, especially in hypothesizing movement of *Acartia* within the bay from changes in copepod densities during the eight-week intervals between sampling. It should be remembered that the primary purpose of this quantitative sampling was to provide data on copepod abundance to accompany feeding experiments performed during the cruises, not to duplicate Rupp's upper bay study or to extend it into the lower bay. Had this in fact been the goal of our survey, more frequent sampling as well as identification of

individual *Acartia* species in each sample would, of course, have been necessary. The study as it was carried out, however, satisfied the need for information on total copepod populations in Chesapeake Bay.

Rupp's (1969) samples of the upper bay zooplankton were collected with a 70 μ m mesh and her later series of samples from the lower bay at 724R were collected with a 103 μ m mesh; both of these nets retained *Acartia* nauplii to some extent, but as she did not enumerate or identify these nauplii they do not enter into the estimates of *Acartia* abundance shown in her figures. My samples were collected on a 160 μ m mesh which, as discussed by Heinle (1966), would retain all stages of *Acartia* copepodites. Thus as far as copepodite and adult abundance are concerned, our estimates of numbers of *Acartia* should be directly comparable to those of Rupp.

The largest standing crops of *Acartia* in our study were encountered in the lower bay during February; these were reduced in number and geographic extent slightly in April and more so in June. Rupp (1969) found that *A. clausi* was the dominant copepod at 724R during the period February through April in 1968 and 1969, reaching densities in excess of 10,000 individuals per cubic meter. These densities are of the same order of magnitude as our observations in the lower bay. In the upper bay in February, Rupp observed both species of *Acartia* in numbers generally between 1000 and 10,000 per cubic meter,

similar in magnitude to our study. *A. clausi* attained maximum abundance in the upper bay in March and April, according to Rupp, declined in numbers in June, then was not detected again until the following January. In the lower bay at 724R, *A. clausi* disappeared at about the same time, but reappeared one month earlier, in December. This seasonal change in abundance of the two species agrees with the suggestion of Jeffries (1962b, 1967) that *A. clausi* is less tolerant than *A. tonsa* of reduced salinities; elimination of *A. clausi* results from interaction of the two species in the spring in the upper bay even before temperatures reach a level which would limit the reproductive success of *A. clausi*. Replacement of *A. clausi* might be expected to be delayed in the lower bay where more favorable osmotic conditions for this species would prevent its replacement until limiting temperatures were reached (Jeffries, 1962b).

If the general trends of species distribution in the bay have not changed since Rupp's study, we can then surmise that in February and April my samples from the upper bay were a mixture of *A. tonsa* and *A. clausi*, while those from the lower bay would have been primarily *A. clausi*. In June, only the lower bay samples would have contained significant numbers of *A. clausi*. August and October samples throughout the bay would have contained *A. tonsa* almost exclusively, since *A. clausi* was undetected at all stations during these months in Rupp's study. In December, the upper bay samples would still be free of

A. clausi, but lower bay samples, especially those from greater depths, might be expected to contain progressively larger numbers of *A. clausi*.

Maximum animal densities encountered in this study were in excess of 10,000 copepods per cubic meter; one isolated count slightly in excess of 50,000 per cubic meter was recorded. These numbers are in general agreement with those of Rupp (1969), although she encountered numbers greater than 50,000 per cubic meter more frequently than did I. Mean numbers of copepodites and copepods per cubic meter for all stations in this study was 5200; means for each cruise range from a high of 7700 in February to a low of 2100 in December. This is comparable to Heinle's study of standing crops in the Patuxent, where most of his data for numbers of *Acartia* adults and copepodites fell between 1000 and 10,000 per cubic meter. Heinle's (1972) comment that *Acartia* population densities are commonly 100,000 to 200,000 per cubic meter takes into account nauplii, which he found were an order of magnitude more numerous than copepodites in samples taken with a #20 net (Heinle, 1966). Herman et al. (1968), who sampled primarily mature copepods with a #2 (370 μ m mesh) net, obtained a mean of about 800 *A. tonsa* individuals per cubic meter.

Eurytemora affinis, which we found in numbers exceeding 3000 per cubic meter at upper bay stations in February and April, has also been found to dominate the upper Patuxent River in lower salinity water, where Herman et al. (1968) found mean

numbers of 500 per cubic meter in samples taken with a #2 net. Rupp (1969) noted that *E. affinis* was abundant in low (less than 3 ‰) salinity waters in the Chesapeake Bay, but gave no numerical estimates of abundance. *Eurytemora* spp. have been shown to be an important and sometimes dominant copepod in low salinity portions of Raritan Bay (Jeffries, 1964) and other Middle Atlantic and New England estuaries (Jeffries, 1962a).

Rotifers were also encountered by Rupp (1969) during the months of April and May in the upper bay, but again no estimates of abundance were given. In this study rotifers outnumbered both *Acartia* and *Eurytemora* in February and April in the upper bay; even more impressive is the fact that these estimates of rotifer abundance are probably underestimates as a result of inefficient net retention. Jeffries (1964) found an unidentified rotifer in numbers ranging up to 130,000 per cubic meter in Raritan Bay, coincident with the spring diatom bloom. Loftus et al. (1972) encountered the rotifer *Euchlanis* sp. at concentrations up to 60×10^6 per cubic meter in the mouth of the Rhode River in Chesapeake Bay, while, closer to mid-channel, in a bloom dominated by *Oxytoxum* sp., rotifer concentrations ranged from 2×10^5 to 10×10^6 per cubic meter.

Centropages typicus, *C. hamatus* and *Temora longicornis* are neritic copepods which though seldom encountered at stations in the Bay, were common at the continental shelf station in February, April and June. Deevey (1960) found the same three species at

stations outside the Delaware Bay, although *C. hamatus* was more abundant inside the bay than outside. Jeffries (1962c) also found these species occasionally inside Raritan Bay; he considered them not to be indigenous to the estuary but rather to be recruited from areas outside the bay more favorable in terms of salinity for reproductive success.

CHAPTER 3

SELECTIVE FEEDING OF *ACARTIA* AND OTHER HERBIVORES*Introduction*

Many species of planktonic copepods in the marine environment are herbivorous or omnivorous filter feeders; their primary source of food is the particulate material suspended in the oceans, ranging in size from bacterioplankton and nanoplankton to the "net" phytoplankton. Copepods feeding in the natural marine environment are presented with a wide spectrum of particle sizes from which to choose; this particle size distribution may vary from oceanic to neritic to estuarine phytoplankton assemblages, and in addition in any particular geographic area the distribution may change with the seasons or with any one of a number of other environmental variables.

Most filter-feeding copepods are not able to retain efficiently all sizes and shapes of cells available in the environment; their filtering ability depends to a large extent on the morphology of the structures associated with feeding. The extent to which filter-feeding copepods are limited in the size of cells which can be retained efficiently, and the extent to which a preference is shown for certain sizes or species of phytoplankton within that filterable range, has been the subject of numerous studies since Marshall (1924) undertook the first extensive investigation of the food of *Calanus* in the natural environment.

Most of the early work in selective feeding of copepods was done with the oceanic copepod *Calanus* and mixed laboratory cultures of phytoplankton. Harvey (1937) established that larger diatoms were removed preferentially from a suspension of two phytoplankton species; Raymont and Gross (1942) established that while survival of *Calanus* feeding on flagellates was poor, survival could be improved if diatoms were added to the culture. Data from Marshall and Orr (1955a) suggested a minimum filterable particle size of 10 μm for *Calanus*, but revealed no significant differences in grazing rates with different sizes of diatoms large enough to be filtered effectively.

The results of Mullin's (1963) experiments, however, suggested that not only does *Calanus* consistently prefer the larger of two species of phytoplankton, but that longer chains of diatoms such as *Asterionella* were also grazed more heavily than shorter chains. Anraku and Omori (1963) confirmed that *Calanus* was primarily a herbivore, but could capture *Artemia* nauplii if plant food was scarce. Mullin and Brooks (1967), working with *Rhincalanus*, observed both a preference for larger cells among adults and an increasing preference for larger cells with age in copepodites. Richman and Rogers (1969) demonstrated that size alone was the determining factor in the selectivity of *Calanus* grazing more rapidly on paired cells of *Ditylum* than on single cells.

Recently, studies have been completed in which selectivity of copepods feeding on natural phytoplankton assemblages has

been investigated; these studies (Martin, 1970; Hargrave and Geen, 1970; and Poulet, 1973) suggest that in coastal waters with variable particle size distributions, the grazing behavior of smaller copepods such as *Acartia tonsa* and *Pseudocalanus minutus* may not be as easily described as that of *Calanus* and other oceanic herbivores. Neritic copepods may in fact be able to respond to changes in phytoplankton size distributions with corresponding changes in their ability to ingest certain cell sizes more efficiently than others. The purpose of these experiments was to investigate the relative preferences of *Acartia* and other filter-feeding zooplankton for different sizes of phytoplankton in the natural environment, and to determine whether these preferences changed with the varying availability of cells of a particular size.

Methods

Feeding experiments were performed at stations on the longitudinal axis of Chesapeake Bay during a series of cruises run at six-week intervals from February 1973 (Procon 8) through December 1973 (Procon 13).

Zooplankton Collection

Zooplankton were collected with a 160 μ m mesh plankton net towed vertically through the water column. Vertical tows were generally made from the surface to 12 meters, but if few copepods were noted in this portion of the water column, additional tows were made to greater depth if the total water depth permitted.

The animals in the cod-end were diluted with 35 μ m filtered bay water and placed in a large beaker in a darkened incubator at ambient water temperature. Ctenophores, coelenterates, and mysid shrimp, if present, were removed by large-mouth pipette to prevent loss of copepods by predation during the holding period. After a short interval to allow debris and dead or injured animals to settle to the bottom of the container, the animals were further diluted with fresh bay water after transfer to another container.

Qualitative samples for species identification were taken at this time by decanting a portion of the plankton catch into a sample jar. Plankton were preserved in 5% formalin-sea water of appropriate station salinity, buffered with sodium tetraborate to pH 7.2. No attempt was made to retain ctenophores or coelenterates in these plankton samples, although at times these organisms can become quite numerous in tributaries of the Chesapeake Bay (Herman et al., 1968). Similarly, mysid shrimp and decapod larvae which were caught infrequently were not retained.

Zooplankton were separated into three size classes by filtering successively through nylon screens with mesh sizes 405 μ m and 253 μ m. The filtration was accomplished by gently pouring the suspended animals into a polyvinyl chloride cylinder covered at the lower end with a nylon mesh of appropriate size. While pouring, the cylinder was submerged in a polyethylene beaker whose drainage holes were higher than the level of the mesh on

the inner cylinder. This arrangement ensured that the animals retained by the mesh were never physically trapped against the mesh and were not exposed to air. Gentle pouring enabled the copepods to swim upwards in the cylinder and to remain suspended in the water. Observations of copepods segregated by size in this manner showed that negligible mortality resulted from the handling; this technique was probably less harmful to the animals than would be the collection from the water column by vertical haul in a rough sea. The animals were then returned to the darkened incubator for storage until needed for an experiment.

After this preliminary size classification, the zooplankton were further sorted to genera for use in feeding experiments. Groups of animals in a size class were poured into a shallow petri dish; individuals chosen for the experiment were removed with a wide-mouth eye dropper. Smaller animals were picked with the aid of a binocular microscope. Animals to be used in a single experimental bottle were counted into a beaker containing 100 ml of glass-fiber (Whatman GF/C) filtered water, so that, except to ensure that no animals had died since sorting, no further enumeration of the animals was necessary before the start of the feeding experiment. Counting and sorting of animals was not performed in a temperature-controlled room, but the containers were immersed in a tray of flowing seawater if ambient water temperature was significantly below room temperature.

In picking animals for these feeding experiments, *Acartia tonsa* and *A. clausi* were not distinguished. It was suggested in the first section of this dissertation that, according to Rupp's (1969) data, situations in which large numbers of both species occurred together would be found primarily in the winter months.

Following this final counting and sorting, the beakers containing the groups of selected animals were again returned to the darkened incubator. The animals remained in this food-free water for 1-3 hours before the beginning of a feeding experiment.

Phytoplankton collection

Water samples containing the natural phytoplankton suspension were collected at each station as soon as possible after the zooplankton collection was completed. A plastic bucket was used to sample water from just below the surface layer. The water was stored in large translucent polyethylene carboys which were immersed in a flowing seawater bath on the ship's fantail and exposed to natural illumination. Before being used in a feeding experiment, the water in the carboy was mixed gently by swirling, then filtered through a 35 μ m nylon screen to remove the largest phytoplankton cells and all zooplankton. Phytoplankton samples were not concentrated in any manner for feeding experiments.

Use of Coulter Counter in feeding experiments

Zooplankton grazing experiments were performed following the method of Sheldon and Parsons (1967a), in which a Coulter Counter is used to determine the phytoplankton cell concentration and size distribution in feeding bottles before and after grazing by herbivores.

The Coulter Counter, an electronic cell counting device, was originally designed for use in the medical field as an improvement over the traditional method of blood counts by hemocytometer. Blood counts by this electronic method were found to be both less time consuming and more precise than visual counts with a hemocytometer (Brecher, Schneiderman, and Williams, 1956; Mattern, Brackett, and Olson, 1957). The Coulter Counter was soon found to provide a quick and accurate method for the counting and sizing of unicellular marine organisms in suspension in seawater (Hastings, Sweeney, and Mullin, 1962; Maloney, Donovan, and Robinson, 1962) and has since been used in a wide variety of other fields of marine research (Sheldon and Parsons, 1967a).

The Coulter Counter has frequently been employed in zooplankton feeding experiments using algal cultures as food organisms (Mullin, 1963; Paffenhofer, 1971), but its use in counting natural populations of phytoplankton for grazing experiments has been restricted to recent studies. The Coulter Counter was used in Saanich Inlet, British Columbia, during a *Chaetoceros* bloom

to measure feeding rates of two species of copepods (Parsons, LeBrasseur, and Fulton, 1967); when my study was initiated, the Coulter Counter had not been used to measure grazing rates in non-bloom conditions in natural marine waters. However, two studies have recently been published (Poulet, 1973, 1974) involving just such an application.

Experimental Procedure

Samples of water containing the natural suspension of phytoplankton passing a 35 μ m mesh were distributed into a number of identical bottles. A known number of animals was added to each bottle by filtering the pre-counted animals from their holding beakers on to a 160 μ m nylon mesh as described previously, then immersing the net and cylinder in the experimental phytoplankton suspension. No food-free water was added to the experimental bottles. One or two bottles to which no animals were added served as controls.

For copepod ingestion experiments, approximately 100 animals were suspended in 500 ml of natural seawater. In other experiments, rotifer concentrations of up to 1000 animals per 500 ml of water were used.

The animal densities used in the experiments were similar on an animal weight per unit volume of water basis to recent experiments using small neritic copepods (Poulet, 1973, 1974). Mean weight of *Acartia tonsa* adults is about 7 μ g (Heinle, 1966); using a factor of 0.4 for conversion of dry weight to organic

carbon content (Beers, 1966), animal densities used in these experiments would not have exceeded $600 \mu\text{g C liter}^{-1}$, and were usually less since younger stages were frequently used. Animal densities in Poulet's (1973) experiments were about $350 \mu\text{g C liter}^{-1}$.

Animal densities had to be balanced against the length of the experiment in order to obtain a measurable change of cell concentration in a reasonable period of time. Since it was desirable to keep the animal concentration as low as possible, experiments were run for approximately 24 hours to assure a measurable change in cell numbers.

The cell size distribution in the experimental and control bottles was determined at the beginning of the feeding period with a Coulter Counter Model B (140 μm orifice diameter). The Coulter Counter had previously been calibrated by counting suspensions of paper mulberry pollen, after optical measurements of the pollen diameter had been made (Strickland and Parsons, 1968). The animals were allowed to feed for 24 hours in a dark incubator regulated to ambient water temperature. At regular intervals during that period the bottles were swirled gently but thoroughly to prevent phytoplankton cells from settling to the bottom of the container. Visual checks throughout the feeding period suggested that the rate of settling for cells in this size range is slow enough that occasional mixing is sufficient to keep the cells well suspended. Anraku (1964b) observed

grazing rates of *Acartia* which were 10-30% higher in feeding bottles mixed during an experiment, as compared to bottles left unmixed.

At the termination of the feeding period, the cell concentration and size distribution were again determined for the control and experimental bottles. Duplicate counts were made in each size class. In these experiments, threshold settings were kept constant while multiplier (amplification and aperture current) settings were varied to obtain cell counts in each of eleven size fractions. The volume of a particle counted in a given size fraction was twice the volume of a particle in the next smaller size fraction. Particle volumes ranged from $23.8 \mu\text{m}^3$ to $24.3 \times 10^3 \mu\text{m}^3$, corresponding to a range of equivalent spherical diameters of $3.57 \mu\text{m}$ to $35.9 \mu\text{m}$. When a significant number of larger cells were noted in a whole water sample, an additional two size fractions were counted, extending the maximum size fraction to $97.1 \times 10^3 \mu\text{m}^3$ or $57.0 \mu\text{m}$ equivalent spherical diameter. Corrections for coincidence counting, which would have been less than 5%, were considered unnecessary because of the relatively low particle concentration and small sampling orifice used.

In order to compensate for changes in cell concentrations due to factors other than grazing, the final cell concentration in the control bottle is substituted in the calculation for the initial cell concentration in the feeding bottle (Sheldon

and Parsons, 1967a). Small increases in cell number (generally less than 10%) did occasionally occur in the darkened control bottle due to continued cell division in the dark.

The ingestion rate, I , is then calculated from the formula

$$I = \frac{V (C_0 - C_t) \cdot v}{t \cdot n}$$

where V is the volume of water in the experimental container, C_0 and C_t the initial and final cell concentrations in each size range, v the mean cellular volume for cells in that size range, t the duration of the feeding experiment in hours, and n the number of animals used in the experiment (Paffenhofer, 1971). The ingestion rate is expressed as cell volume (μm^3) ingested per animal per hour in each phytoplankton size fraction.

While microscopic examinations of the particles enumerated by the Coulter Counter were not made, indirect evidence indicates that most of these particles are in fact phytoplankton, not detritus or bacteria. Data collected concurrently with these experiments by Taft, Taylor, and McCarthy (1974) on chlorophyll a to particulate N and chlorophyll a to Particulate P ratios, indicate that most of the particulate N and P was associated with chlorophyll a containing organisms. ATP measurements from the same cruises (Loftus, unpublished data) and ATP to chlorophyll a ratios further suggest that virtually all measured ATP was contained in phytoplankton.

Electivity Index

The electivity index E was calculated for each particle size group from Ivlev's (1961) equation:

$$E = \frac{r - p}{r + p}$$

where r is the relative content of any size group in the total ration or assemblage of ingested cells, expressed as a percentage of the volumetric concentration, and p is the relative concentration of that size group in the natural phytoplankton assemblage, also expressed as a percentage value. Values for E range from +1.0, indicating strong preference for a size group, to -1.0, indicating avoidance or inability to remove that size particle from suspension (rejection).

Values of r were calculated from the amount of phytoplankton removed from suspension per animal on a daily basis, in terms of cellular volume, while values of p were based on phytoplankton volume concentrations in the control bottles at the end of the experiment.

Phytoplankton cell volume data used in both the phytoplankton concentration and size-dependent ingestion rate sections of the selective feeding chapter were derived directly from Coulter Counter measurements. The Coulter Counter measures the number of particles per unit volume of water in any given cell size category; the size characteristic to which the instrument responds is cellular volume. Phytoplankton concentration could then be

expressed in terms of numbers of cells of a given cell volume in a unit volume of water, but more meaningful results can be achieved by expressing the concentration in terms of total cell volume in any size category (cell numbers x mean cell volume) per unit volume of water. A convenient unit for phytoplankton concentration is parts per million (ppm) by volume, which is equivalent to $10^6 \mu\text{m}^3 \text{ ml}^{-1}$. In the particle size distribution plots, the values on the x-axis are given as equivalent spherical diameters, that is, the diameter of a sphere equal in volume to the cell detected by the instrument.

Results

February 1973 (Procon 8)

Particle size distributions and corresponding electivity indices E for selective feeding experiments performed on the February cruise (Procon 8) are shown in figures 10 through 12. With the exception of the shelf station (Ø707V), the particle size distributions for all stations on this cruise are similar; maximum phytoplankton concentrations occurred around $10 \mu\text{m}$ equivalent spherical diameter, with lower concentrations in size categories above $10 \mu\text{m}$ than in those categories below $10 \mu\text{m}$. At station 904N (Figure 10), however, the trend of particle distribution was reversed, with maximum phytoplankton concentrations occurring in the largest size categories. Because of the abundance of larger cells at this station, the usual $35 \mu\text{m}$ pre-screen was replaced with a $64 \mu\text{m}$ mesh. A minimum in particle concentra-

Figure 10. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. February 1973, station Ø707V. Symbols for electivity index diagrams, Figures 10 through 27:

- Open circles, *Acartia* (>405 μm).
- Solid circles, *Acartia* (>250 μm).
- Half-filled circles, *Acartia* (160-250 μm).
- Circles bisected with horizontal line, *Acartia* males.
- Circles bisected with vertical line, *Acartia* (160-405 μm).
- Solid squares, *Eurytemora affinis* (>250 μm).
- Open squares, *E. affinis* (250-405 μm).
- Open triangles, *Centropages* sp. (>250 μm).
- Solid inverted triangles, *Temora longicornis* (>405 μm).
- Open inverted triangles, *T. longicornis* (>250 μm).
- Solid diamonds, *Acartia* and *E. affinis* (>250 μm).
- Open diamonds, *T. longicornis* and *Centropages* sp. (>250 μm).
- Crosses, rotifers (>160 μm).

Figure 11. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. February 1973, stations 744, 804C, and 818P. Symbols as in Figure 10.

Figure 12. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. February 1973, stations 834G, 854G, and 904N. Symbols as in Figure 10.

tion occurred at 12 μm and concentrations gradually increased in size categories smaller than this; the biomass in the smaller categories did not approach that found in the 45-55 μm range.

Results of the selective feeding experiments performed at the shelf station (Figure 10), utilizing *Centropages* sp., demonstrates a feeding pattern typical of many oceanic copepods, that is, preference for larger cells. *Centropages* did not ingest particles smaller than 12 μm , and showed a slight preference both for cell sizes in the 45-55 μm range and in the 22-27 μm range.

Selective feeding experiments for stations inside Chesapeake Bay in February revealed a variety of feeding patterns. Copepods at stations 744, 804C, 834G and 854C displayed relatively high selectivity (positive electivity indices) for particles in the size category in which the maximum phytoplankton concentration occurred (12 μm), but also selected for the largest particles available (36 μm) even though the concentration of these large cells was low in comparison with the 12 μm particles. At station 834G, where both *Acartia* and *Eurytemora* were present, a mixture of the two genera did not display this preference for larger particles, although *Acartia* alone did. The minimum particle size which was ingested indiscriminantly ($E = 0$) was 6 μm at 744 and 804C, 7 μm at 854G, and 9 μm at 818P and 834G. At station 904N, where the particle concentration reached a maximum at a smaller size than at other stations, the minimum size ingested was also slightly lower for *Eurytemora* (5 μm).

At station 818P, the feeding patterns of *Acartia* and the rotifer *Brachionus* sp. were similar except for *Acartia*'s superior ability to ingest particles in the 23 μm range.

April 1973 (Procon 9)

In April, the pattern of particle size distribution changed slightly at both the shelf station and the rest of the bay stations (Figures 13 through 16). The cell size distribution at the shelf station was again characterized by a maximum phytoplankton concentration in the largest size category measured (45 μm), along with a secondary maximum at 23 μm . Cell size distributions at bay stations 724R, 744, 804C, 818P and 834G revealed phytoplankton concentration maxima in the 14-18 μm range, while at 904N, the size category in which the maximum occurred (9 μm) was again smaller than at stations to the south.

At stations on the shelf and in the lower bay, copepods showed greater preference for larger cells than small (Figures 13 and 14). *Temora longicornis*, found at station Ø70TV, displayed a positive selection toward particles in both the primary and secondary concentration peaks, while particles smaller than 15 μm were not selected. *Acartia* at the lower bay stations (724R, 744) selected most strongly particles larger than 28 μm , although particles in the 11-28 μm size range were also ingested. At station 804C, *Acartia* still showed preference for relatively large (14-28 μm) particles, but selection of particles larger than 28 μm was not evident, possibly because of the sharply

Figure 13. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. April 1973, station Ø707V. Symbols as in Figure 10.

Figure 14. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. April 1973, stations 724R and 744. Symbols as in Figure 10.

Figure 15. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. April 1973, stations 804C and 818P. Symbols as in Figure 10.

Figure 16. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. April 1973, stations 834G and 854G. Symbols as in Figure 10.

reduced concentration of cells in this size range as compared to lower bay stations.

In comparing feeding habits of *Acartia* and rotifers at 804C (Figure 15), *Acartia* shows higher positive selectivity than the rotifer in the 18, 23 and 28 μm size range. The rotifer, however, displayed a slightly higher selectivity when feeding on particles in the 4-7 μm size range. Plots of feeding habits of rotifers at stations 804C, 818P, 834G and 854C (Figures 15 and 16) were somewhat variable, although peaks in the electivity values seem to recur at 23 μm at all four stations, and 9 μm at the two upper bay stations.

June 1973 (Procon 10)

The particle size distributions at stations 707V and 707Ø in June (Figure 17) displayed maxima in the 18-23 μm range; this pattern continued up-bay, but at stations 724R and 744 (Figures 17 and 18) another peak developed at 9 μm and overshadowed the original maximum, although the distributions at these stations remained distinctly bimodal.

Plots of electivity values at these four lower bay stations were remarkably similar; strong positive selection was lacking in all size ranges, while rejection of particles occurred only in the extremely small and moderately large size ranges. The range of particle sizes which was ingested appeared to be bounded by the peaks in the bimodal size distribution curve.

Figure 17. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. June 1973, stations 0707V, 7070, and 724R. Symbols as in Figure 10.

Figure 18. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. June 1973, stations 744, 818P, and 834G. Symbols as in Figure 10.

Figure 19. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. June 1973, stations 854G and 904N. Symbols as in Figure 10.

The size distributions of particles at the upper bay stations were quite different from the lower bay stations in June. At 818P and 834G (Figure 18), the maximum concentrations of cells occurred in the smallest size range ($4\text{ }\mu\text{m}$); particle concentrations then decreased steadily with increasing size. At 854G and 904N, although the maximum still occurred in the $4\text{ }\mu\text{m}$ range, a secondary peak appeared between 14 and $18\text{ }\mu\text{m}$ (Figure 19).

Relatively high values of E were observed in *Acartia* at station 818P and 834G (Figure 18). At 818P, the positively selected range was 6 - $14\text{ }\mu\text{m}$; at 834G it was 11 - $14\text{ }\mu\text{m}$ and 23 - $28\text{ }\mu\text{m}$. Difference in feeding selectivity between *Acartia* males and a natural mixture of *Acartia* was insignificant at 834G and only slight at 818P.

Patterns of size selection at the two remaining upper bay stations, 854 and 904 (Figure 19), were similar to those encountered in the lower bay; no strong size selection occurred, and the range of particles ingested passively was 7 - $18\text{ }\mu\text{m}$ at 904N and 7 - $23\text{ }\mu\text{m}$ at 854G. No difference in size selection was observed between *Acartia* females and the natural mixture of *Acartia* at this station.

August 1973 (Procon 11)

At virtually all stations occupied in August, the size distributions of cells in the surface waters were characterized by maximum concentrations of particles in the smallest size categories. Phytoplankton concentrations generally decreased

with increasing cell size up to the 11 μm size range; at stations 724R, 744 (Figure 20), 804C, 818P (Figure 21), and 854G (Figure 22), concentrations then increased again to a secondary peak in the 14-18 μm range, of lesser biomass than the first. At station 854G, there was an additional concentration peak at 36 μm which in fact exceeded that found in the smaller size ranges; this was the only station in August in which the phytoplankton biomass maximum did not occur in the smallest size range. Particle concentrations decreased with increasing cell size at station 834G, except for a slight increase in biomass in the largest size range measured (28 μm). The size distribution of cells at 904N was relatively flat, although a small elevation of biomass was noted in the two smallest size ranges measured.

At five stations in August an attempt was made to compare cell size selection exhibited by *Acartia* females with that exhibited by the natural mixture of *Acartia* in the water column. At stations 707 $\emptyset$, 724R and 834G, females displayed slightly positive or neutral preference for cells in size ranges for which a mixture of developmental stages displayed strong rejection (negative electivity indices); this difference in selection occurred in the ranges 9-18 μm , 18-28 μm , and 11-28 μm at 707 $\emptyset$, 724R and 834G, respectively. A similar effect can be observed in plots for stations 744, and 804C, although the difference in electivity values is not as pronounced. In the electivity index plots for four of these stations, 707 $\emptyset$, 724R, 744 and 834G, the

Figure 20. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. August 1973, stations 707Ø, 724R, and 744. Symbols as in Figure 10.

Figure 21. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. August 1973, stations 804C, 818P, and 834G. Symbols as in Figure 10.

Figure 22. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. August 1973, stations 854G and 904N. Symbols as in Figure 10.

mixture of all developmental stages displayed greater positive electivity values than females alone in the smaller size ranges, although the difference in this case is relatively small.

At station 818P (Figure 21), a mixture of *Acartia* was separated into two size classes by screening through a 253 μm nylon mesh; the larger copepods at this station displayed greater positive selectivity toward particles in the 14-28 μm range, and slightly greater rejection of particles smaller than 6 μm .

A comparison of feeding selectivity between females only and a mixture of all stages retained on a 253 μm mesh at station 854G (figure 22) revealed little difference in feeding habits in any size range. Electivity values at this station were highest in the particle size range 28-36 μm , corresponding to the phytoplankton biomass maximum.

The plot of electivity values for station 904N included no extreme positive or negative values; the moderate rejection in the 23 μm particle size range coincided with the phytoplankton biomass minimum for this station.

October 1973 (Procon 12).

Phytoplankton cell size distributions were similar at all stations sampled in October (Figures 23 through 25). Maximum biomass occurred in the smallest (4 μm) size range, but a second concentration peak generally was found in a larger size class as well. This second peak, which was often comparable in magnitude to the main peak, occurred in progressively larger size ranges

going up-bay from 707Ø to 804C, after which it remained in the 18 µm size range. Station 854, the northernmost station sampled during this cruise, was unusual in that the cell size distribution was relatively uniform in concentration in the 4-23 µm range, after which phytoplankton concentration declined with increasing cell size as in stations further south.

Cell size selection by *Acartia* females alone and by a mixture of all stages of *Acartia* was again compared at three stations; differences in selection by different sizes of *Acartia* was investigated at three other stations. At stations 707Ø and 724R (Figure 23) *Acartia* females alone again displayed more positive selectivity toward larger particles (18-36 µm) than the natural mixture of all stages of *Acartia*, while in the smaller cell size ranges (407 µm), the mixture of stages displayed a more positive selectivity than the females (although both groups displayed moderate rejection in this smaller size range). A similar experiment at station 818P (Figure 24), however, did not result in significant differences in selectivity between the two groups.

At stations 804C (Figure 24) and 834G (Figure 25), groups of *Acartia* differing only in size showed different patterns of cell size selection. At both stations, copepods displayed moderate positive selection for cells in the 5-14 µm size range, while larger cells were rejected. However, in the cell size range 11-23 µm, *Acartia* retained on a 253 µm mesh exhibited less rejection than *Acartia* passing a 253 µm mesh. This effect was

Figure 23. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. October 1973, stations 7070, 724R, and 744. Symbols as in Figure 10.

Figure 24. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. October 1973, stations 804C and 818P. Symbols as in Figure 10.

Figure 25. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. October 1973, stations 834G and 854G. Symbols as in Figure 10.

more pronounced at 834G than at 804C. At station 854 (Figure 25), *Acartia* retained on a 405 μm mesh showed slightly greater preference than those passing a 405 μm but retained on a 160 μm mesh, for cells in the 11-23 μm size range, but surprisingly showed less preference for 28-36 μm cells.

In general for the October cruise, smaller cell sizes (4-6 μm) were not selected positively at the three southernmost stations or the northernmost station, nor were larger cell sizes selected positively, with the exception of station 724R, where moderately positive selection by female *Acartia* occurred. Indeed, at 744, 818P, 834G and 854C, the three (two in the case of 854C) largest size classes of particles were the object of strong rejection.

December 1973 (Procon 13)

The phytoplankton cell size distributions at five stations (Figures 26 and 27) sampled in the bay in December were remarkably similar. Maximum biomass occurred in the 9 μm size range at all stations; minimum particle concentrations were found in the largest size range, 36 μm .

Plots of electivity values were also similar. Moderately positive selection was confined at most stations to the five size classes encompassing cells of medium size, such as 9-23 μm at 724R, 854G and 904N, or 11-28 μm at 834G. The positively selected range was narrower at 818P (11-23 μm). Cells of both size extremes were rejected at most stations in December. In no instance during this cruise did the highest positive selection coincide with the phytoplankton biomass maximum.

Figure 26. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. December 1973, stations 724R, 818P, and 834G. Symbols as in Figure 10.

Figure 27. Phytoplankton size distribution and zooplankton electivity index E for each cell size group. December 1973, stations 854G and 904N. Symbols as in Figure 10.

At station 904N (Figure 27) a comparison of selective feeding habits was made between *Acartia* retained on a 405 μm mesh and those passing the 405 μm . *Acartia* larger than 405 μm displayed selectivity similar to that found at stations further south in December, but selectivity in the smaller *Acartia* was quite erratic. Not only did selectivity values vary widely in some adjacent size ranges, but generally larger cells were selected more positively than was the case with larger *Acartia*. This result is quite different from that found in all other cruises when different size *Acartia* were compared.

Summary of Results of Selective Feeding Experiments

Patterns of selective feeding by *Acartia* and other copepods in Chesapeake Bay changed from month to month during 1973. In February, *Acartia* showed highest preference for cells in the size range of maximum phytoplankton biomass and also for the largest cells regardless of concentration. In April in the lower bay, this preference of *Acartia* for cells in the larger size classes continued, while the positive selection of cells in the high biomass per unit volume ranges was not as pronounced. In the upper bay, *Eurytemora* displayed moderate selection for the most numerous cells and did not select the less common larger phytoplankton. Rotifers in the upper bay in April did not ingest larger cells; selection in other size ranges was variable.

In February and April, *Centropages* sp. and *Temora longicornis* at the shelf station 0707V preferentially ingested the larger cells; in June the concentration of these larger cells had decreased and positive electivity indices were confined to smaller size ranges.

Acartia showed little positive selection in June, except for middle-sized cells at two mid-bay stations. Rejection of both large and small cells was evident at all stations, even when smaller cells were present in relatively high concentrations. Larger cells were not found in high concentrations in June.

In August, positive selection shifted toward the smaller cells which were present in the highest concentrations. At two upper-bay stations, however, increased selection of larger cells was observed, associated with increases in cell concentration in these size ranges.

Highest phytoplankton biomass continued to be found in the smaller size ranges in October; positive selection by *Acartia* was restricted to these ranges. Larger cells were generally rejected, except at two stations where slight increases in the concentration of these cells were observed.

In December, the size range in which the greatest concentration of cells was found had shifted to a slightly larger size; positive selection by *Acartia* began with this size range and continued in the larger ranges which were still relatively

abundant. Cells of a size smaller than those in the maximum biomass range were rejected; the largest cells available were similarly rejected.

At all stations where comparisons were made, *Acartia* females alone showed positive preference for larger cells than the natural mixture of copepodites and females; in smaller size ranges, the mixture of stages usually exhibited higher electivity values than females alone. Similarly, larger *Acartia* displayed higher electivity indices toward large cells when copepods were compared on the basis of size alone.

Discussion

The results of these selective feeding experiments have demonstrated that copepods of the genus *Acartia* are able to ingest a wide range of cell sizes in the natural estuarine environment. *Acartia* on many occasions ingested certain sizes of phytoplankton cells in a proportion greater than their abundance in the water column; this selective feeding behavior was usually associated with a higher concentration of that size cell with respect to other cells in the phytoplankton assemblage.

The minimum size cell which was ingested by *Acartia* in these experiments varied with the relative concentration of small cells in the water column. In August and October, when small cells were abundant, electivity values in the 4 μ m size range were frequently near zero, indicating that *Acartia* ingested

these particles but did not actively select them. Moderate positive selection was usually encountered in the next larger size range (5 μm), suggesting that these small cells could be retained efficiently.

In a recent paper dealing with food size selection among copepods, Wilson (1973) suggested that the minimum particle size ingested by *A. tonsa* was 14 μm . In his experiments, plastic beads of different sizes were ingested by *Acartia*; the smallest size presented, according to the text, was 7 μm , but his figures show that beads of this size represented less than 1% of the total number of beads. The maximum number of beads occurred in the 15 μm size range in this particular experiment; beads 11 μm in diameter were the smallest available in any substantial number (about 10% of the total). It is apparent that the ability to ingest small particles was not thoroughly explored in Wilson's experiments; his conclusions as to the minimum size particle ingested by *Acartia* should not be applied to the natural environment.

Hargrave and Geen (1970) demonstrated that *Acartia tonsa* was to ingest small (1-2 μm) cells when feeding on natural phytoplankton assemblages; feeding rates for these smaller cells was slightly higher than for 5 μm cells, although feeding rates for 10 μm cells were higher than for both smaller size ranges. In these experiments, the smaller cells were at least two orders of magnitude more abundant in numbers than the 10 μm cells, but were

only about three times more concentrated in terms of total cell volume per unit volume of water. In a similar experiment, Hargrave and Geen showed that *Pseudocalanus minutus*, a neritic copepod similar in size to *Acartia*, also can ingest cells as small as 1-2 μm , although at reduced rates compared to larger 5-10 μm cells.

Poulet's (1973) experiments with *P. minutus* likewise suggest that this copepod can ingest small cells efficiently. In situations where a large proportion of the phytoplankton biomass was present as small cells (smaller than 10 μm), ingestion of these cells was characterized by an electivity index near zero.

Thus the results of my experiments tend to support the findings of those workers who have suggested that *Acartia* and other small neritic copepods are able to ingest small (4-5 μm) cells efficiently. This fact is particularly significant in view of the abundance of and sizeable contribution to primary production by small (less than 10 μm) nanoplankton in Chesapeake Bay in summer (McCarthy et al., 1974).

Although the actual cell sizes ingested by *Acartia* in these experiments varied from station to station and month to month, the size range of cells most frequently ingested on the average was about 8-25 μm . This general pattern was encountered in about one-third of the experiments.

As previously mentioned, the range of ingested cells was frequently extended into smaller sizes, most often when the particle size distribution revealed a maximum phytoplankton concentration close to the smallest cell size range measured.

Selection and ingestion of cells of a given size were not always tied directly to the concentration of that size cell in the water column, however. In situations where the maximum concentration of particles occurred in the smallest size ranges, accompanied by a secondary peak in a slightly larger size range, particles in the smallest size range were occasionally rejected in favor of the slightly larger cells.

Poulet (1973) found particles in the 1.6-3.6 μm size range to be relatively rare in Bedford Basin; substantial ingestion was found in this size range only when particles in the 1.6-9.0 μm range comprised greater than half of the total cell volume present.

Larger cells were ingested preferentially by the oceanic calanoids, *Centropages* sp. and *Temora longicornis*, at our shelf station in February and April; on both of these occasions, most of the phytoplankton biomass was present in the larger part of the size range.

The particle size distribution at station 854G in August 1973 was the only one encountered inside the bay in which the maximum in phytoplankton concentration occurred in the largest size range. *Acartia* responded to this situation by showing moderate positive preference toward the larger cells. In addition,

at many stations in February and April, *Acartia* showed moderate positive preference for larger cells even though these cells were not present in high concentrations compared to smaller cells. At all of these latter stations, the particle size spectra were either relatively flat, or showed an upturn in the concentrations of the larger particles.

This preference for larger cells regardless of their relative abundance is a response typical of many oceanic copepods, and has been well documented for *Calanus* (Harvey, 1937; Raymont and Gross, 1942; Mullin, 1963; Mullin and Brooks, 1967; Parsons et al., 1969; Richman and Rogers, 1969). *Pseudocalanus minutus*, a small neritic copepod, has also been shown to ingest larger cells in preference to small. Parsons et al. (1969) demonstrated that on two cruises, *P. minutus* ingested *Skeletonema costatum* (14 μ m equivalent spherical diameter) in preference to smaller μ -flagellates when their respective cell volume concentrations were similar; some ingestion of μ -flagellates did, however, take place. On another cruise, when μ -flagellates alone were present, no measurable ingestion took place.

P. minutus feeding on natural phytoplankton in Bedford Basin has been shown by Poulet (1973) to be able to ingest particles in sizes ranging from 1.6-114 μ m. When particle concentrations in all size ranges are about equal, *P. minutus* preferentially ingests the largest available size, although substantial ingestion in smaller size classes persists.

Very few studies on selective feeding by *Acartia* have been published. Conover (1956) examined microscopically the gut contents of preserved *Acartia* from Long Island Sound and found that the copepod fed primarily on two species of *Thalassiosira* and on *Thalassionema nitzschioides* in winter, and on *S. costatum* during the spring bloom, but the guts "always contained a considerable quantity of greenish material of unknown origin." In summer the most common recognizable form was *Coscinodiscus radiatus*; a higher percentage of unrecognizable remains was found in summer. Grazing experiments performed in an attempt to quantify any selectivity in feeding disclosed no differences in choice of food when a natural population of *S. costatum* and *Thalassiosira nordenskioldii* was used. However, *Acartia* did prefer lab cultures of *S. costatum* to *Nitzschia closterium*.

Curl and McLeod (1961) noted that *A. tonsa* and *Pseudocalanus* sp. grazed *S. costatum* preferentially to *Rhizosolenia* sp. and other diatoms, in continental shelf waters south of Long Island.

Martin (1970) observed a similar grazing pattern in mixed zooplankton dominated by *A. clausi* in Narragansett Bay in early winter. *S. costatum*, the dominant diatom in the bay, was grazed in preference to *Rhizosolenia delicatula* until *S. costatum* cell numbers were reduced by a factor of 10, after which both species were grazed. It was also observed that longer chains of *S. costatum* were ingested first by the mixed zooplankton. The original concentration of *S. costatum* in terms of cell numbers

was about twice as high as *R. delicatula*, but since cell sizes were not given, it is not possible to compare concentrations in terms of total cell volumes.

It is difficult to compare the results of our experiments with those mentioned above, as little data is offered in the earlier papers concerning cell sizes or chain lengths of the diatoms involved. Martin (1970) suggests that *Acartia* selected *S. costatum* on the basis of cell size "rather than the larger *Rhizosolenia*" among other factors including cell morphology and chemical composition. After selecting for smaller cell size, *Acartia* then preferentially grazes longer chains of *S. costatum*, which may still be smaller than *Rhizosolenia*.

In addition, and perhaps of great significance, these earlier papers did not investigate the role of smaller nanoplankton or μ -flagellates in the feeding patterns of *Acartia*, even though in Chesapeake Bay, and perhaps other coastal waters as well, these small cells may comprise a larger portion of the phytoplankton biomass.

Wilson (1973) was the first to attempt to quantify selective feeding by *Acartia*, by using a modification of Ivlev's (1961) electivity index E. By allowing *A. tonsa* to feed on various sizes of plastic beads, it was established that this copepod selectively ingested particles slightly larger than those particles present in the greatest abundance. Thus selection was in some way related to particle abundance rather than particle

size. The size frequency distributions of plastic beads in Wilson's experiments were usually relatively simple, with one major peak in abundance. It is particularly interesting that the maximum in selective feeding always occurred to the right of this peak, in a larger size range.

As pointed out in Sheldon and Parsons (1967b), a simple size frequency diagram giving numbers of particles vs. particle diameter (as found in Wilson, 1973) does not convey as much information as a size distribution diagram giving particle concentration in terms of volume vs. particle diameter. Thus many of Wilson's plots showing flat size frequency distributions in the larger sizes may have revealed peaks in particle concentration had they been plotted in terms of cell volume. These new increases in cell volume concentration would always occur in the larger sizes, because of the increasing volume per cell in the larger size ranges; thus they might coincide with the peaks in electivity values noted by Wilson. It would be difficult to convert Wilson's data as shown in his figures, however, without access to his original data, because of the large changes in cell volume concentration which would result from relatively small changes in cell numbers in the larger size ranges.

It is possible, therefore, that *Acartia*'s selectivity in feeding may be more directly related to particle volumetric concentration than to particle frequency. This would be suggested by my data, in which increases in selectivity often coincided

with concentration peaks. Unfortunately, in the natural environment, particle concentration plots were usually more complicated than those generated with plastic beads in the laboratory, and the responses of *Acartia* were also more complicated than those found by Wilson. My data indicates, however, that *Acartia* does respond to increases in particle concentration with increases in selective ingestion of that size range. In addition, when particle concentration is relatively constant over a given size range, the largest cells in that size range may be preferentially ingested.

The advantage for a copepod of obtaining its necessary ration of food in the form of large cells is obvious, as long as those large cells are relatively abundant in the environment. Poulet (1973) has pointed out that *Pseudocalanus minutus* may compensate to some extent for a decrease in total particle concentration by ingesting larger size particles. However, the tendency to ingest large cells preferentially would be of limited use to copepods in environments where total particle concentration is relatively high and large cells are not common. Total particle concentrations in Chesapeake Bay during our cruises (Table 1) were two or more times higher than those encountered by Poulet in Bedford Basin, despite the fact that he included particles as large as 114 μm , whereas our measurements were usually limited to particles smaller than 36 μm . *Acartia* in Chesapeake Bay has however retained

Table 1. Total phytoplankton concentrations for stations in Chesapeake Bay and adjacent shelf waters, February through December, 1973. Units are ppm by volume, or $10^6 \mu\text{m}^3 \text{ml}^{-1}$.

Station	Feb	Apr	Jun	Aug	Oct	Dec
904N	6.38	-	8.12	3.80	-	5.25
854G	7.61	14.56	6.44	18.21	10.04	5.74
834G	6.06	19.38	3.56	5.42	4.74	6.72
818P	11.71	5.64	1.95	6.80	3.44	5.07
804C	6.94	7.41	-	4.65	4.75	-
744	9.06	9.13	10.66	3.60	5.76	-
724R	-	6.42	5.85	1.63	4.28	3.32
707Ø	13.78	-	5.31	2.86	4.09	-
Ø707V	8.18	2.83	2.45	-	-	-

the ability to ingest these large particles, and it does so selectively when they form a substantial proportion of the phytoplankton biomass.

In general, due to the overall trend of decreasing phytoplankton concentration with increasing cell size encountered in Chesapeake Bay, the pattern of particle ingestion by *Acartia* is characterized by rejection of those cells too small to be retained efficiently and rejection of those larger cells whose concentrations are so low that hunting for them would be wasteful energy. The range of cell sizes which are ingested tends to depend to some extent therefore on the slope of the particle concentration vs. particle size plot.

Imposed upon this general trend of size selection can be other factors such as cell morphology or chemical composition which might make some species more or less attractive to copepods. These factors may account for some of the otherwise unexplained rejections of certain size ranges of cells in some of these experiments. We have no data from these experiments which could be brought to bear on this subject; however, isolated deviations from the general trend of particle ingestion were relatively rare and are thought to be unimportant in comparison to selection on the basis of cell size or concentration.

The primary factor which results in changes in the selective feeding patterns of *Acartia* is phytoplankton concentration.

Acartia is not limited in its selectivity to a particular size of

particles, but rather is able to respond to increases in concentration of any size particle within its filterable range by increasing selective ingestion of that size range. Poulet (1974) has suggested that if a copepod were fixed in its ability to ingest a particular cell size range, that algal species would soon be eliminated, while other species would go ungrazed. If, however, as in the case of *Acartia* in Chesapeake Bay, the copepod grazes primarily or selectively on the most numerous cells at any given moment, the grazing pressure over a longer period of time is equalized among a greater number of species or size ranges as their concentrations are sequentially reduced as a result of selective ingestion. A particular size range of cells which may have been heavily grazed on one occasion might be ignored completely after its concentration had been reduced by grazing, thus allowing that portion of the phytoplankton assemblage time to recover.

CHAPTER 4

INGESTION AND ASSIMILATION RATES OF *ACARTIA* AND OTHER HERBIVORES*Introduction*

Much of the significance of planktonic herbivorous copepods in the aquatic environment rests in their role in the transfer of energy in the form of food material from the primary producers to higher trophic levels. The rate of transformation of plant biomass into animal biomass determines the extent to which filter feeding herbivores control primary production through grazing pressure, and may also limit production at higher trophic levels by controlling the amount of herbivore biomass available as food for predators.

The vast majority of early investigations into the feeding of marine copepods were concerned with the oceanic copepod *Calanus finmarchicus*, because of both its numerical prominence in the pelagic environment and its relatively large size which makes it a convenient experimental animal. Early experiments on the feeding of *Calanus* were concerned primarily with establishing the kind of food (diatoms, flagellates, or bacteria) that would support the survival and reproduction of the copepod (Clarke and Gellis, 1935; Fuller and Clark, 1936); these and other studies (Fuller, 1937; Clarke and Zinn, 1937; Clarke, 1939) were also among the first to suggest the importance of nanoplankton in copepod nutrition, while Fuller (1937) attempted to quantify the feeding rate of *Calanus* by calculating the volume of water swept

clear of diatoms. All of these and a number of other experiments on the feeding rates of *Calanus* (Marshall et al., 1935; Harvey, 1937; Raymont and Cross, 1942; Gauld, 1951) were reviewed by Marshall and Orr (1955a) and Jorgensen (1955).

Some of these investigations calculated filtering rates from the change in cell concentrations as measured by optical counting methods; Marshall and Orr (1955b, c) were among the first to employ labeled (^{14}C , ^{32}P) algae in an effort to do away with the tedious manual counting of phytoplankton cells employed by other workers.

Faced with the extreme variability in calculated feeding rates obtained for *Calanus* by earlier workers, Mullin (1963) attempted to quantify the effect of a number of environmental variables on filtering rates of copepods. The effects of animal concentration, algal cell concentration, age of phytoplankton culture, phytoplankton species composition, and experimental duration on the feeding of four species of *Calanus* were investigated by Mullin (1963). Amraku (1964b) continued the study of the effect of experimental conditions on grazing and predation by marine copepods.

Corner (1961), noting the variability of existing estimates of rates of feeding on algal cultures by *Calanus*, and the difficulty of extrapolating these results to feeding in the natural environment, carried out experiments in which *Calanus* grazed on natural mixtures of particulate matter from the ocean. Filtering

rates were calculated from the change with time of the concentration of particulate matter in the seawater. A similar method was used by Cushing and Vucetic (1963). Adams and Steele (1966) estimated filtering rates of *Calanus* feeding on natural particulate matter by measuring changes in chlorophyll *a* concentrations in areas of high phytoplankton concentration, and by a ^{14}C technique in areas of low phytoplankton biomass. Parsons et al. (1967) estimated ingestion rates in two species of marine copepods feeding on a bloom of *Chaetoceros* in the natural environment by direct measurement of the changes in cell concentrations with a Coulter Counter; this was the first application of the Coulter Counter in marine copepod grazing experiments using natural phytoplankton assemblages.

The prominence of *Acartia* among copepods of the Chesapeake Bay has been discussed previously in this dissertation. It was felt that to confirm the importance of *Acartia* in the food chain of the bay, it would be desirable to establish what portion of the phytoplankton production is consumed by *Acartia*. Data on feeding rates of *Acartia* are relatively rare; Conover (1956) performed experiments with *Acartia tonsa* and *A. clausi* feeding on cultures of *Skeletonema costatum* at varying temperatures, while Anraku (1964b) performed experiments with *Acartia* feeding on *Thalassiosira fluviatilis* at four different temperatures. Following the suggestion of Adams and Steele (1966) it was thought unwise to attempt to extrapolate from the results of laboratory

experiments using only two phytoplankton species to the natural estuarine environment with its wide variety of phytoplankton species. In order to most accurately estimate the significance of the role of *Acartia* in the transfer of energy in the food chain of the Chesapeake Bay, it was decided to perform feeding experiments using the natural phytoplankton assemblages in the bay.

Hargrave and Geen (1970), using the natural phytoplankton populations in Bras d'Or Lake and Morrison's Pond, Nova Scotia, established feeding rates for *A. tonsa* and three other species of copepods at one temperature in the summer; however, few data on the available phytoplankton were provided other than a stated concentration of cells per milliliter and the observation that most were smaller than 15 μm in largest dimension. It was felt that direct extrapolation from the environment studied by Hargrave and Geen (1970) to that in the Chesapeake Bay would be unwarranted, even when the temperatures are similar.

Methods

Ingestion Experiments

Feeding experiments were performed at each of seven stations (Figure 1) along the longitudinal axis of the Chesapeake Bay and one station 25 km offshore, at eight week intervals from February through December 1973. Ingestion rates of *Acartia* and other zooplankton were measured by the differential cell count method as adapted for the Coulter Counter (Mullin, 1963; Sheldon and

Parsons, 1967a); the equation for calculation of the ingestion rate from changes in cell concentration with time was that used by Paffenhofer (1971). Details of the experimental procedures used in the ingestion experiments were given in the previous chapter. Total ingestion rates were calculated by summing the ingestion rates for each size class. Ingestion rates in terms of cell volumes were converted to a phytoplankton carbon basis by the regression equation for phytoplankton organisms other than diatoms given by Strathman (1967). Ingestion rate measures the amount of food taken in by an animal per unit time, whereas filtering rate measures the volume of water containing the number of cells ingested. Ingestion rate is a more logical expression of the actual quantity which was measured, namely, the number of cells removed from suspension. As Mullin (1963) has pointed out, if filtration is not 100% efficient, the actual rate at which water is filtered will be greater than the experimentally computed filtering rate. Since I have demonstrated for *Acartia* a varying efficiency in retention of different cell sizes, calculation of an ingested ration from filtering rates would necessitate not only knowledge of the concentration of phytoplankton in each cell size class but also an appropriate correction factor for the filtration efficiency in each cell size class. Ingestion rate is both a more meaningful and accessible parameter in this situation.

No attempt was made to differentiate *Acartia tonsa* and *A. clausi* in these feeding experiments. Conover (1956) compared

grazing rates for both species in two experiments at ambient temperature in January and February of 1954, and they were not significantly different. In another comparison in the summer of 1954, *A. clausi* displayed grazing rates 40-60% higher than *A. tonsa* in the temperature range 5-20 C. However, Rupp (1969) demonstrated that *A. clausi* is not found in the Chesapeake Bay in summer.

When another species of copepod was encountered in significant numbers in addition to or in place of *Acartia*, it was selected for feeding experiments. Rotifers were occasionally found in abundance, and were selected for additional feeding experiments, although the lack of quantitative data for rotifer numerical abundance prevented expression of their ingestion on a per unit volume basis.

Measurements of net primary productivity per unit volume were made at each station at two depths in the water column (J. J. McCarthy, unpublished data); these data were converted to an integrated value for net primary productivity in the euphotic zone by multiplying by a factor of 0.5. This conversion factor was derived from a comparison of the productivity values measured at several depths and the calculated integrated value for net primary productivity obtained at these stations during an earlier series of cruises (code name Aesop) (W. R. Taylor, unpublished data).

Assimilation Experiments

Beginning with the second cruise (April, 1973), assimilation rates of *Acartia* and other zooplankton were measured by an application of ^{15}N tracer techniques. Dugdale and Goering (1967), in a study of the uptake of nitrogen in primary productivity, presented a diagram of the circulation of inorganic nitrogen through the euphotic zone of the marine environment. This diagram illustrated the manner in which the rate of transport of nitrogen from the dissolved fraction into the particulate (phytoplankton) fraction could be calculated by observing the change in concentration of labeled material in various compartments with time. In a similar manner, it is possible to calculate the rate of assimilation of nitrogen by zooplankters by measuring the rate of change of the fraction of ^{15}N in the zooplankton during ingestion of phytoplankton labeled with ^{15}N .

Although the ^{15}N tracer method is becoming more common in studies of nitrogen uptake by phytoplankton, there have been no published reports of its use in zooplankton grazing experiments to date.

Samples of phytoplankton to be used in nitrogen assimilation experiments were taken with a polyethylene bucket from the surface waters at the same time as samples to be used in carbon ingestion experiments, and were similarly filtered through a $35\text{ }\mu\text{m}$ screen to remove larger cells and zooplankton. Subsamples were distributed into a number of one liter pyrex bottles with silicone rubber

stoppers. Additions of ^{15}N -labeled KNO_3 , NH_4^+ , or urea were made to the one liter bottles which were then placed in an incubator cooled with running seawater, in full sunlight on the fantail. Incubations were begun as early as possible in the day, generally around 1000 hrs. During the first cruise, phytoplankton samples were incubated for approximately 24 hours, but in later cruises a shorter incubation period (about 10 hrs) was adopted. After incubation the contents of the one liter bottles were combined in a large bottle and then redistributed in 500 ml portions into clean one liter bottles in which feeding experiments were to be performed. Before feeding commenced, subsamples of phytoplankton were taken by filtering through Reeve-Angel 984H glass fiber filters for later analysis of ^{15}N enrichment and particulate nitrogen content.

Copepods were added to the 500 ml portions of labeled phytoplankton suspension in the manner described previously for the carbon ingestion experiments. One or more bottles, to which no animals were added, were reserved as controls. Experimental conditions were identical to those in the ingestion and selective feeding experiments. Feeding experiments were run for approximately 24 hrs. At the end of the feeding period, the animals were transferred to an unlabeled algal suspension and were allowed to feed for one hr. or more to clear their guts of labeled food. The copepods were then removed from the water by screening with a 160 μm mesh, rinsed with filtered station water, then rinsed again on to glass-fiber filters. Phytoplankton samples were taken from

the control bottle at the end of the experiment for determination of PN content and ^{15}N enrichment. Unlabeled zooplankton were also filtered on to glass-fiber filters for analysis of particulate nitrogen content. All phytoplankton and zooplankton samples were dessicated and stored over silica-gel until analysis.

Particulate nitrogen was determined by the method of Holm-Hansen (1968). Enriched samples of phytoplankton and zooplankton were combusted in a Coleman Model 29 nitrogen analyzer and the gaseous product swept into a glass vacuum system similar to that of Barsdate and Dugdale (1965). An AEI MS-10 mass spectrometer was used to determine the $^{15}\text{N}:^{14}\text{N}$ ratio of each sample, which was then compared to a standard for calculation of the rate of uptake of nitrogen, V . Zooplankton nitrogen assimilation rate was obtained from the following computations derived by Dugdale and Goering (1967), in the notation suggested by Sheppard (1962):

$$\rho_{21} = V \times N_2 = \frac{da_2/dt}{a_1 - a_2}$$

where ρ_{21} is the rate of transport of nitrogen from the labeled compartment, 1 (phytoplankton), to the initially unlabeled compartment, 2 (zooplankton). N_2 is the concentration of nitrogen in the zooplankton. a_2 is the atom per cent ^{15}N in compartment 2; a_1 the atom per cent ^{15}N in compartment 1. V is essentially a growth rate in terms of nitrogen and has dimensions of (mass of N assimilated) (mass of N) $^{-1}$ (time) $^{-1}$, or simply (time) $^{-1}$. ρ_{21} , the assimilation

rate in terms of nitrogen, has dimensions of $(\text{mass of N})(\text{time})^{-1}$, and will be expressed in units of ng N day^{-1} .

Results

The results of ingestion experiments performed on the Procon cruises are shown in Tables 2 through 7. Approximately 60% (42) of the ingestion experiments were duplicate or triplicate experiments. An estimate of the precision of these experiments can be made by dividing the range of calculated values of the ingestion rate by the mean calculated ingestion rate, for each replicated experiment; the mean value of this precision estimate for 42 experiments is 14%.

Results of assimilation experiments performed on Procon cruises 9 through 13 are shown in Tables 8 through 12. Approximately 50% (35) of the nitrogen assimilation experiments were duplicate or triplicate experiments. The mean value of the precision estimate as calculated in the previous paragraph is 15%.

The relationship between copepod ingestion rate and the standing stock of phytoplankton is shown in Figure 28. The regression of ingestion rate (y) on phytoplankton standing stock (x) is given by the equation $y = 0.32 + 1.31 x$. The 95% confidence interval for the slope of this line is 1.31 ± 0.73 . The correlation coefficient of the regression of ingestion rate on phytoplankton standing crop is +0.56. The null hypothesis that the correlation coefficient is not different from zero is rejected at the 0.1% level. The 95% confidence interval for the correlation coefficient however is +0.20 to +0.75, indicating that there is little evidence

Table 2. Results of carbon ingestion experiments, February 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}$ animal ⁻¹ day ⁻¹	$\mu\text{g C}$ liter ⁻¹ day ⁻¹		
904N	<i>Acartia</i> & <i>E. affinis</i>	>253 μm	1.99	14.0	1.15	81.9
	<i>E. affinis</i>	"	3.44	15.1	1.24	88.3
854G	<i>E. affinis</i>	"	2.21	8.78	0.66	31.8
834G	<i>Acartia</i>	"	0.79	1.80	0.19	5.00
	<i>Acartia</i> & <i>E. affinis</i>	"	1.78	4.71	0.50	13.1
818P	<i>Acartia</i>	"	2.57	9.78	0.53	26.8
804C	<i>Acartia</i>	"	0.55	2.46	0.23	12.3
744	<i>Acartia</i>	"	1.05	10.5	0.78	55.8
707Ø	<i>Acartia</i>	"	0.71	7.92	0.40	41.5
Ø707V	<i>Centropages</i> sp.	"	1.39	12.9	1.34	43.9

Table 3. Results of carbon ingestion experiments, April 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}$ animal ⁻¹ day ⁻¹	$\mu\text{g C}$ liter ⁻¹ day ⁻¹		
854G	Rotifer	>160	0.257	2.14	0.093	0.62
834G	Rotifer	>160	0.271	-	-	-
818P	<i>E. affinis</i>	253-405	1.92	3.03	0.344	4.97
	<i>E. affinis</i>	>405	2.25	0.034	0.0038	0.056
	Rotifer	>160	0.209	-	-	-
804C	<i>Acartia</i>	>253	0.814	3.03	0.275	5.05
	Rotifer	>160	0.170	-	-	-
744	<i>Acartia</i>	>253	1.34	9.85	0.800	16.8
724R	<i>Acartia</i>	253-405	1.47	14.1	1.54	43.2
	<i>Acartia</i>	>405	1.15	2.63	0.287	8.07
Ø707V	<i>T. longicornis</i>	253-405	0.991	1.76	0.410	18.0
	<i>T. longicornis</i>	>405	2.03	1.74	0.404	17.8

Table 4. Results of carbon ingestion experiments, June 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}_{\text{animal}}^{-1}$ day^{-1}	$\mu\text{g C}_{\text{liter}}^{-1}$ day^{-1}		
904N	<i>Acartia</i>	>253	2.49	2.24	0.168	0.470
	<i>Acartia</i>	>405	3.63	0.127	0.0095	0.027
854G	<i>Acartia</i>	>253	1.27	5.00	0.472	2.94
	<i>Acartia</i>	>405	1.26	0.976	0.092	0.57
834G	<i>Acartia</i>	>253	0.151	0.935	0.151	0.71
	<i>Acartia</i>	>253 male	0.240	0.018	0.0029	0.014
818P	<i>Acartia</i>	>253	0.434	0.262	0.072	0.30
	<i>Acartia</i>	>253 male	0.427	0.017	0.0047	0.019
	<i>Acartia</i>	>405	0.408	0.037	0.010	0.042
744	<i>Acartia</i>	253-405	4.67	8.71	0.525	5.92
	<i>Acartia</i>	>405	8.08	7.88	0.475	5.36
724R	<i>Acartia</i>	>253	1.53	12.2	1.25	13.4
707Ø	<i>Acartia</i>	>253	1.32	28.2	3.70	37.6
Ø707V	<i>T. longicornis</i> & <i>Centropages</i> sp.	>253	0.80	20.3	5.85	106

Table 5. Results of carbon ingestion experiments, August 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}_{-1}$ animal $_{-1}$ day	$\mu\text{g C}_{-1}$ liter $_{-1}$ day		
904N	<i>Acartia</i>	>253	1.74	29.9	5.54	5.98
854G	"	>253	5.13	13.1	0.648	2.85
	"	>405	5.14	1.88	0.093	0.41
834G	"	>253	1.47	2.76	0.287	1.19
	"	>405	2.41	1.57	0.163	0.68
818P	"	>253	1.64	1.34	0.113	0.38
	"	160-253	2.60	1.21	0.102	0.34
	"	>405	2.07	0.36	0.307	0.10
804C	"	>253	2.10	36.1	4.50	20.6
	"	>405	1.92	14.6	1.82	8.34
744	"	>253	1.65	2.65	0.467	1.25
	"	>405	2.02	0.84	0.148	0.40
724R	"	>253	0.86	2.27	0.794	1.50
	"	>405	0.80	0.24	0.085	0.16
707Ø	"	>253	1.19	4.54	0.849	4.05
	"	>405	0.89	0.089	0.017	0.08

Table 6. Results of carbon ingestion experiments, October 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}$ animal ⁻¹ day ⁻¹	$\mu\text{g C}$ liter ⁻¹ day ⁻¹		
854G	<i>Acartia</i>	>405	5.35	15.9	1.01	10.4
	"	160-405	6.43	10.8	0.684	7.06
834G	"	>253	1.26	7.59	0.943	7.23
	"	160-253	0.78	1.10	0.137	1.05
818P	"	>253	1.84	11.8	2.04	14.8
	"	>405	1.89	1.67	0.289	2.08
804C	"	>253	1.55	3.40	0.423	2.58
	"	160-253	1.97	3.31	0.411	2.51
744	"	>253	2.06	2.76	0.276	2.89
724R	"	>253	1.09	3.10	0.421	3.60
	"	>405	1.03	0.47	0.064	0.55
707Ø	"	>253	1.50	4.68	0.730	4.93
	"	>405	1.30	0.25	0.038	0.26

Table 7. Results of carbon ingestion experiments, December 1973.

Station	Organism	Size (μm)	INGESTION RATE		Portion of phyto. stock ingested daily (%)	Portion of prim. prod. ingested daily (%)
			$\mu\text{g C}_{-1}$ animal $_{-1}$ day $_{-1}$	$\mu\text{g C}_{-1}$ liter $_{-1}$ day $_{-1}$		
904N	<i>Acartia</i>	>405	1.37	1.64	0.198	7.19
	"	160-405	0.65	2.34	0.282	10.3
854G	"	>405	1.51	1.93	0.180	1.69
	"	>253	1.51*	6.58*	0.615*	5.77*
834G	"	>405	1.44	0.295	0.030	0.34
	"	>253	1.44*	3.87*	0.401*	4.45*
818P	"	>253	1.51	0.673	0.090	2.30
724R	"	>253	1.21	0.392	0.076	0.52

(*Estimated from *Acartia* >405 μm data)

Table 8. Results of nitrogen assimilation experiments, April 1973.

Station	Organism	Size (μm)	ASSIMILATION RATE		Portion of phyto. stock assimilated daily (%)
			ng N ⁻¹ animal ⁻¹ day ⁻¹	ng N ⁻¹ liter ⁻¹ day ⁻¹	
854G	<i>Acartia</i>	>253	94.1	3.76	0.00077
	Rotifer	>160	9.72	81.1	0.016
834G	<i>Acartia</i> & <i>E. affinis</i>	>405	33.7	16.2	0.0077
	<i>Acartia</i> & <i>E. affinis</i>	>253	33.7	107	0.051
804C	<i>Acartia</i>	>253	26.7	99.4	0.065
	Rotifer	>160	4.24	-	-
744	<i>Acartia</i>	>253	52.8	388	0.132
	Rotifer	>160	4.15	-	-
724R	<i>Acartia</i>	253-405	45.7	545	0.462
	<i>Acartia</i>	>405	2.42	-	-

Table 9. Results of nitrogen assimilation experiments, June 1973.

Station	Organism	Size (μm)	ASSIMILATION RATE		Portion of phyto. stock assimilated daily (%)
			ng N ⁻¹ animal ⁻¹ day ⁻¹	ng N ⁻¹ liter ⁻¹ day ⁻¹	
904N	<i>Acartia</i>	>253	171	154	0.039
	"	>405	273	9.56	0.0024
854G	"	>253	142	560	0.182
	"	>405	146	113	0.036
834G	"	>253	96.0	631	0.410
	"	>253 male	104	7.80	0.005
	"	>405	64.1	24.0	0.016
	"				
818P	"	>253	60.6	42.4	0.028
	"	>253 male	47.8	1.91	0.0012
	"	>405	52.0	4.68	0.0030
804C	"	253-405	157	20.4	0.017
744	"	253-405	187	531	0.271
724R	"	>253	77.7	622	0.444
707Ø	"	>253	118	2570	2.22

Table 10. Results of nitrogen assimilation experiments, August 1973.

Station	Organism	Size (μm)	ASSIMILATION RATE		Portion of phyto. stock assimilated daily (%)
			ng N ⁻¹ animal ⁻¹ day ⁻¹	ng N ⁻¹ liter ⁻¹ day ⁻¹	
904N	<i>Acartia</i>	>253	246	4230	0.540
	"	>405	220	1870	0.239
854G	"	>253	157	402	0.125
	"	>405	159	58.0	0.018
834G	"	>253	176	333	0.108
	"	>405	149	97.3	0.032
818P	"	>253	67.4	54.9	0.020
	"	>405	51.8	9.06	0.003
804C	"	>253	87.8	1510	0.600
	"	>405	69.9	532	0.211
744	"	>253	114	184	0.069
	"	>405	167	69.3	0.026
724R	"	>253	32.3	85.3	0.041
	"	>405	18.8	5.73	0.003
707Ø	"	>253	88.2	336	0.171
	"	>405	58.2	5.82	0.003

Table 11. Results of nitrogen assimilation experiments, October 1973.

Station	Organism	Size (μ m)	ASSIMILATION RATE		Portion of phyto. stock assimilated daily (%)
			ng N ₋₁ animal ₋₁ day ₋₁	ng N ₋₁ liter ₋₁ day ₋₁	
854G	<i>Acartia</i>	>405	371	1100	0.462
	"	160-405	372	625	0.263
834G	"	>253	187	1127	0.575
	"	160-253	123	174	0.089
	"	>405	35.4	12.2	0.006
818P	"	>253	78.9	506	0.329
	"	>405	56.6	50.1	0.032
804C	"	>253	120	263	0.156
	"	160-253	48.5	81.7	0.049
744	"	>253	213	286	0.102
724R	"	>253	73.4	208	0.124
	"	>405	52.2	24.0	0.014
707Ø	"	>253	133	415	0.247
	"	>405	75.8	14.4	0.009

Table 12. Results of nitrogen assimilation experiments, December 1973.

Station	Organism	Size (μm)	ASSIMILATION RATE		Portion of phyto. stock assimilated daily (%)
			ng N^{-1} animal $^{-1}$ day $^{-1}$	ng N^{-1} liter $^{-1}$ day $^{-1}$	
904N	<i>Acartia</i>	>405	154	185	0.150
	<i>Acartia</i>	160-405	112	402	0.327
	Rotifer	>160	4.74	8.62	0.007
854G	<i>Acartia</i>	>405	113	144	0.105
	<i>Acartia</i>	>253	89.7*	430*	0.314*
834G	<i>Acartia</i>	>405	144	29.5	0.015
	<i>Acartia</i>	>253	125*	336*	0.171*
818P	<i>Acartia</i>	>253	92.0	41.0	0.030
	Rotifer	>160	4.26	1.18	0.0009
804C	Rotifer	>160	8.37	0.33	0.0002
744	Rotifer	>160	32.4	3.89	0.0037
724R	<i>Acartia</i>	>253	108	35.0	0.028

(*Estimate from *Acartia* >405 μm data)

Figure 28. Copepod ingestion rate versus phytoplankton standing crop, from *Acartia* feeding experiments.

Figure 29. Copepod ingestion rate versus ambient water temperature, from *Acartia* feeding experiments.

of a linear relationship between ingestion rate and phytoplankton standing crop.

Ingestion rates on a per animal basis for *Acartia* varied by about two orders of magnitude during the six cruises; both the maximum and minimum values were found in June. The regression of ingestion rate (y) on ambient water temperature (t) is given by the equation, $y = 1.12 + 0.021 t$ (Figure 29); the 95% confidence interval for the slope of this line is 0.021 ± 0.031 . The correlation coefficient and 95% confidence interval for these two sets of variables is $+0.32 \pm 0.30$, suggesting the lack of a significant linear relationship between ingestion rate and temperature. Ambient water temperature was less than 13 C in December, February, and April, and greater than 21 C in June, August, and October. Unfortunately, since feeding experiments were run at ambient water temperatures, no data were collected in the 13-21 C range. It appears that the range of observed ingestion rates is smaller in the colder months than in the three warmer months, but this may result from fewer experiments having been performed at the lower ambient water temperatures.

Calculations of the total ingestion rate by the population of *Acartia* retained on a 253 μ m mesh at each station (Tables 2 through 7) indicate that these copepods ingest only a small portion of the phytoplankton standing crop daily. No seasonal or spatial pattern was observed in the proportion of phytoplankton standing crop utilized by the population of *Acartia* in the bay.

Comparison of the total phytoplankton carbon ingested by the *Acartia* population with the daily net primary production at each station revealed a seasonal trend. A far greater part of the net primary production was utilized by the copepod populations in February and April than in subsequent months; this may be related to the longer phytoplankton doubling time in these colder months. Mean copepod utilization of net phytoplankton production at all bay stations was 38% and 20% in February and April, respectively, then declined to a minimum of 5% in August; the overall mean for six cruises was 14%.

Results of nitrogen assimilation experiments performed during Procon cruises 9 through 13 (Tables 8 through 12) indicate that *Acartia* assimilates only a small portion of the standing crop of phytoplankton nitrogen; these results are similar to those derived from carbon ingestion experiments.

Discussion

A number of comparisons can be drawn between this study and earlier investigations into the production of *Acartia* in marine ecosystems.

Conover (1956) measured respiratory rates and grazing rates of *Acartia tonsa* and *A. clausi* feeding on *Skeletonema costatum*, at a variety of temperatures in the laboratory. Using these data, and the total biomass of zooplankton derived from 160 μ m plankton net tow displacement volumes, Conover calculated a mean gross efficiency of growth (secondary production / ingestion) of approximately 30%

for zooplankton over the entire year in Long Island Sound. Conover estimated that the zooplankton ingested virtually all of the net phytoplankton production, using Riley's (1956) estimate of primary production for this area. Conover did admit, however, that since grazing rates vary with food sources and concentrations, extrapolation of laboratory grazing rates based on one species of phytoplankton to grazing rates in the natural environment may not be justified.

In contrast to Conover's (1956) study, Riley (1956), using different respiratory rates for *Acartia*, estimated that the zooplankton retained on a #10 net (153 μ m) utilized about 26% of the net primary production in Long Island Sound, averaged over the entire year.

Smayda (1966) used Conover's (1956) data on grazing rates of *Acartia* to estimate the proportion of phytoplankton standing stock and net production utilized by zooplankton in the relatively shallow Gulf of Panama. Mean ingestion of the phytoplankton standing stock at 30 stations sampled throughout the year was about 2% per day; the maximum value encountered was 11%. At only one station did the daily ingestion of phytoplankton exceed the daily net phytoplankton production as measured by ^{14}C assimilation; generally the daily zooplankton utilization of net primary production was less than 10%. Smayda (1966) also presented similar calculations using Anraku's (1964b) values for grazing rates of *Acartia*; this resulted in a maximum grazing intensity of about 35% of the phytoplankton

standing stock per day and a mean value of 4.5%. Smayda concluded that in the Gulf of Panama, grazing was insignificant in regulating phytoplankton abundance; unless grazing rates were grossly underestimated, there would still be a considerable excess of phytoplankton production over that grazing by zooplankton in the Gulf of Panama.

Smayda (1973) also investigated the effects of grazing on a bloom of *Skeletonema costatum* in Narragansett Bay. From February until mid-March, *A. clausi* consumed about 5% of the *S. costatum* standing stock daily; after mid-March, daily grazing pressure was reduced to about 2%, which, combined with increased phytoplankton growth rates, resulted in a pulse of *S. costatum* in May. The decline of the *S. costatum* bloom in June came about both as a result of increased grazing pressure (about 20% daily), natural phytoplankton mortality, and reduced zooplankton nitrogen excretion, which restricted the daily supply of dissolved nitrogen to less than 7% of *S. costatum* requirements.

Qasim (1970) reported net primary production far in excess of herbivorous zooplankton consumption in Cochin Backwater, a shallow tropical estuary in India. About 24% of the daily net phytoplankton production was consumed by the herbivorous copepods which dominated the zooplankton in this estuary; the remainder of the net primary production, according to Qasim (1970), was available to herbivorous fish, omnivorous prawns and shrimp, and benthic animals. Tranter and Abraham (1970) have noted that the zooplankton of Cochin Back-

water is comprised primarily of nine copepod species of the family Acartiidae; seven of these species belong to the genus *Acartia* and are herbivorous, while the two remaining species belong to the genus *Acartiella* and are thought, from examinations of the morphology of their mouthparts, to be carnivorous. The two species of *Acartiella* may play an important role in limiting the size of the population of *Acartia* in this estuary through predation, thus restricting the utilization of primary production by the herbivores.

A number of production studies from the Russian literature have been reviewed by Mullin (1969); the original papers were not available to me, but the results reported in Mullin (1969) are adequate for comparison.

Greze and Baldina (1964; cited in Mullin, 1969) constructed growth curves of *A. clausi* in the Black Sea over the period of one year. The summer rates of production of this copepod were then compared to estimates of summer production of phytoplankton from Sorokin (1964). Production of *Acartia* was found to be about 0.1% of net primary production. Gross efficiency of growth for *Acartia* in the Black Sea was found to be 15% (Petipa, 1966; cited in Mullin, 1969), so that ingestion by *Acartia* removed approximately 0.7% of the daily net phytoplankton production.

Petipa (1966; cited in Mullin, 1969) calculated the production of *Acartia* in the Black Sea in summer from data on growth rates and respiratory rates measured in the laboratory, combined with field observations of copepod biomass. Using a growth efficiency of

growth of 15% as measured by Petipa, *Acartia* feeding in the upper water layers only ingested about 56% of the net primary production of the upper 20 meters daily. At least part of the discrepancy between the estimates of Petipa, and Greze and Baldina, arises from the fact that the former study restricts its net phytoplankton production estimate to the upper 20 meters; net primary production in the entire water column was five times greater than in the shallow depths alone. Additionally, Sorokin's (1964) estimate of primary production in the Black Sea in summer is more than twice as high as that provided by Petipa (1966; cited in Mullin, 1969); this would further exaggerate the differences between the two studies.

Zaika and Malovitskaya (1967; cited in Mullin, 1969) calculated the production of *A. clausi* in the Azov Sea, an arm of the Black Sea, following the methods of Greze and Baldina. The production per unit biomass for *Acartia* was calculated to be 4% per day, which agrees closely with the estimates of Greze and Baldina, but is lower than Petipa's estimate by a factor of five.

Heinle (1966) conducted an extensive study of the production of *A. tonsa* in the Patuxent River estuary of the Chesapeake Bay. Instantaneous death rates, which were used to estimate population turnover times, were calculated from population age structures observed in the field, and development times measured in the laboratory; production was then obtained from the observed population biomass in the estuary and the calculated turnover times. Copepod production estimates were given only for a two

month period in late summer, when the average total secondary production was $2.7 \text{ mg m}^{-3} \text{ hr}^{-1}$, or $77 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the 3 m water column; this is equivalent to about 5% of the net primary production. Invoking a 30% gross growth efficiency, as calculated by Conover (1956), to relate secondary production to ingestion, it can be calculated that the *A. tonsa* population ingested about 17% of the net primary production. Petipa's (1966; cited in Mullin, 1969) estimate of 15% gross growth efficiency would yield a 33% utilization of primary production by the *Acartia* population.

My data on the per cent utilization of net phytoplankton production by *Acartia* in the Chesapeake Bay in summer are generally lower than that estimated by Heinle (1966). In August, values from my study ranged from a maximum of 21% at mid-bay (station 804C) to a minimum of 0.4% at a station near the mouth of the Patuxent River (station 818P); the mean for eight stations was 4.7%.

A major factor in the discrepancy between my results and those of Heinle (1966) in calculating the relative magnitudes of copepod ingestion and net primary production in the Chesapeake Bay is undoubtedly the inclusion in Heinle's data of naupliar stages of *Acartia*. Rupp (1969) has shown that *Acartia* nauplii were more numerous than later stages in the Chesapeake Bay in summer; Heinle (1966) demonstrated that at one station in the Patuxent River in August, nauplii outnumbered copepodites by an order of magnitude and outnumbered adults by more than two orders of magnitude. In terms of biomass, nauplii outweighed copepodites and adults combined

by a factor of two during the summer months studied by Heinle (1966); naupliar production was almost three times greater than production of copepodites and adults. Although Heinle does not provide data on ingestion rates, as these were unnecessary for his calculations, Paffenhofer (1971) demonstrated that, on a body weight basis, ingestion rates of naupliar stages of *Calanus* were three to five times higher than those of copepodites and adults; similar results could be expected for *Acartia* and other copepods.

The combined effect of the greater total biomass and higher weight-specific ingestion rates of *Acartia* nauplii probably result in a substantial contribution by these stages to utilization of net primary production during the summer months in the Chesapeake Bay. Since nauplii were not sampled during my study, an underestimation of the total ingestion by the *Acartia* population during times of naupliar abundance would have resulted. The magnitude of the underestimation would be reduced at other times of the year when the older stages of *Acartia* predominate (Heinle, 1966).

The increased importance of the later development stages which were used in this study may partially explain the increased consumption of net phytoplankton production in the winter months, along with the general decline in primary production resulting from decreased light levels and water temperatures. Results from the colder months are in closer agreement with results of other studies, with the exception of Conover's (1956) estimate in Long Island Sound. Conover's (1956) results, however, are significantly

higher than those of Riley (1956) for the same area and those of the Russian workers in the Black Sea reviewed by Mullin (1969).

Hargrave and Geen (1970) estimated the portion of net primary production ingested by all developmental stages of *Acartia tonsa* in Morrison's Pond, Nova Scotia, and originally found a high rate of utilization (approximately 100%), similar to that of Conover (1956). Estimates of primary production on which these results were based were calculated from long (20 hr) ^{14}C incubations (Geen and Hargrave, 1966) for which Hargrave and Geen (1970) suggest a 50% correction factor, reducing zooplankton utilization of primary production to about 66%. Estimates of mean primary production for Morrison's Pond (Geen and Hargrave, 1966) were approximately one-third the estimates of mean primary productivity for the entire Chesapeake Bay in summer used in this study, and less than one-fifth the maximum values encountered in the upper bay (Taylor and McCarthy, unpublished data). The overall higher phytoplankton productivity in the Chesapeake Bay as compared to Morrison's Pond, combined with the higher densities of *Acartia* encountered in Morrison's Pond by Hargrave and Geen (1970), may to some extent explain the differences between the two studies.

In considering the apparent variability in published estimates of the utilization of phytoplankton production by zooplankton, it can be noted that those studies which included the microzooplankton generally revealed the most complete utilization of net primary production. Riley's (1956) study of Long Island Sound determined

the utilization of phytoplankton productivity by microzooplankton by difference, after calculation of the utilization by the larger net zooplankton and by benthic organisms; he estimated that a substantial part of the primary production was utilized by benthic organisms, although theirs was a smaller contribution than the remainder which he attributed to nauplii and bacterioplankton.

Williams, Murdoch, and Thomas (1968) have suggested that in shallow estuaries zooplankton are relatively unimportant in regulating the standing crop of phytoplankton. In the extreme case of North Carolina estuaries with an average depth of 1.2 meters, zooplankton retained on a 160 μ m mesh net consumed an average of 6% of the daily net primary production; Williams et al. (1968) suggest that benthic animals dominate the herbivore trophic level in that ecosystem. According to Williams et al. (1968), in an estuarine system of moderate (10 m) mean depth such as the Chesapeake Bay, zooplankton would be expected to be somewhat less important in the utilization of phytoplankton than in deeper bodies of water such as Long Island Sound.

Heinle (1974) has recently re-examined the data of Herman et al. (1968) in light of his own unpublished work, in an attempt to balance the phytoplankton-zooplankton energy budget in the Patuxent River estuary. It is apparent from the results of both this study and that of Heinle (1974) that *Acartia* is not food-limited in the Chesapeake Bay or its estuaries; this study has demonstrated that *Acartia* is able to ingest phytoplankton cells

in a wide range of sizes at rates comparable to those found in recent literature. The difficulty arises in establishing the factors which limit the size of the population of *Acartia* to a level too small to utilize most of the primary production available in the estuary.

Heinle (1974) reports that Herman et al. (1968) overestimated the abundance of ctenophores and jellyfish by three orders of magnitude, leading Miller and Williams (1972) to conclude that the phytoplankton and zooplankton standing crops in the Patuxent River were too small to support the populations of ctenophores and jellyfish. A recalculation of the displacement volumes by Heinle (1974) indicates that, while the zooplankton population may at times be insufficient to support the ctenophores and jellyfish, the phytoplankton population is always more than adequate to support the metabolic requirements of copepods, ctenophores, and jellyfish. Heinle (1974) presents the hypothesis, based on observations by Nelson (1925) and the energy budget of the Patuxent River, that *Mnemiopsis leidyi*, a common Chesapeake Bay ctenophore, may not be strictly carnivorous, but rather may also be able to utilize nanoplankton and detritus as food material. Although not cited by Heinle (1974), Lebour (1922, 1923) has also noted the presence of phytoplankton, primarily diatoms, in the guts of *Beroe*, another ctenophore found in the bay, but later authors (e.g. Swanberg, 1974) have considered these algal cells to have been ingested incidental to carnivorous feeding on other ctenophores

or crustaceans. If Heinle's (1974) suggestion is correct, ctenophores in Chesapeake Bay may be instrumental in limiting the size of the copepod population not only by preying on *Acartia*, but by competing with *Acartia* for food material in the form of nanoplankton.

Other organisms in the Chesapeake Bay may also compete with *Acartia* to some degree for food resources. A herbivorous fish, the menhaden, is common in these waters, but the effect of its feeding on phytoplankton crops is not known. Smayda (1973) noted the abundance of tintinnids and other protozoans during his study of the effect of *Acartia* grazing in Narragansett Bay, but he was unable to assess the extent of their grazing due to lack of feeding rate data. Loftus et al. (1972) found tintinnids in considerable numbers at some stations in Chesapeake Bay. Small (1972) has noted that although protozoa are known to ingest phytoplankton, no studies have been made on their role in estuarine energy flows. Another group whose significance in the estuarine system has not been investigated is the tunicates; members of the class Thaliacea (e.g., *Salpa*) have been shown (Madin, 1974) to ingest particles as small as 1 μm , while *Oikopleura* (class Larvacea) has been mentioned as an important epiplanktonic herbivore in the Black Sea (Petipa, Pavlova, and Mironov, 1970). In view of the importance of nanoplankton in the primary production of the Chesapeake Bay in summer, the role of organisms such as these, which are specialized in the capture of small particles, should be investigated further.

The results of this study have emphasized the possible importance of rotifers in the Chesapeake Bay, as suggested by Loftus et al. (1972). While quantitative data on rotifer abundance were not collected, it was apparent that at times rotifers vastly outnumber all other metazoa in the Bay; during these periodic increases in abundance, their lower ingestion rates per animal as compared to copepods may be more than compensated by their increase in numbers. Loftus et al. (1972) have demonstrated the marked effect of rotifer predation on a bloom of *Oxytoxum* sp. in Chesapeake Bay.

The herbivorous copepod *Eurytemora affinis* was also shown in this study to be a potential competitor with *Acartia* for food resources; *E. affinis* replaced *Acartia* at low salinity stations on two cruises in this series, where it displayed ingestion rates comparable to those of *Acartia*.

Other species of copepods may control the size of the population of *Acartia* through predation. Although the biology of *Oithona brevicornis* in Chesapeake Bay is not well known (Heinle, 1972), Petipa et al. (1970) have noted that while immature *Oithona* are mixed food consumers, adult *Oithona* are carnivores, feeding on small crustaceans. No estimate can be made from the data of this study of the significance of predation of *Oithona* on *Acartia* in the Chesapeake Bay.

The distribution and abundance of the predaceous cladoceran *Podon polyphemoides* have been documented by Bosch and Taylor (1973a). *Podon* was apparently less abundant during this study than in

previous years; numbers did not approach those found by Bosch and Taylor (1973a), and were therefore not included in our quantitative counts of zooplankton. The effect of predation by *Podon* on the *Acartia* population cannot be assessed at this time.

Similarly, little data on the impact of predation on *Acartia* by higher carnivores such as the planktivorous anchovies and silversides are available for the Chesapeake Bay.

Summary

The estuarine ecosystem of the Chesapeake Bay and its tributaries is especially diverse and complex; the study of energy flow in this ecosystem is still in its infancy. It is evident from the results of this final chapter that much remains to be learned of the pathways of energy flow beyond the first trophic level.

Data of this study suggest that in the Chesapeake Bay in summer, the larger zooplankton are relatively unimportant in the utilization of net phytoplankton production, although they play an increasingly significant role as water temperatures drop in the colder months. Considering the results of Heinle's (1966) study in the Patuxent River, it is possible that nauplii and younger copepodite stages of *Acartia* may utilize a greater portion of the daily net primary production than the more mature stages in the summer months. In addition, preliminary data on feeding rates of rotifers from this study, combined with measurements of

rotifer abundance from Loftus et al. (1972), suggest that rotifers, and possibly protozoans such as tintinnids, may consume large amounts of phytoplankton during their periodic increases in abundance.

In short, the questions of what factors prevent *Acartia* from consuming the bulk of the primary production, and what organisms actually do consume the excess algal production, remain essentially open. It appears that until the ecology of the smaller, less conspicuous zooplankton is better known, these questions will remain unanswered.

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