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THE ASSIMILATION OF PARTICULATE ORGANIC CARBON BY ESTUARINE AND COASTAL COPEPODS

by

MIRA B. CHERVIN

A dissertation submitted to the Graduate faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, City University of New York

1977

Mira Chervin

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

THE ASSIMILATION OF PARTICULATE ORGANIC CARBON BY ESTUARINE AND COASTAL COPEPODS

by

MIRA B. CHERVIN

This study was done to assess the relative roles of phytoplankton and detritus as carbon sources for copepods. A series of shipboard experiments were conducted from April 1975 to March 1976, in which natural assemblages of copepods were incubated with natural suspensions of particulates obtained from the Hudson River Estuary and apex of the New York Bight. Concentrations of total particulate organic carbon (POC) were high, ranging from 0.45 - 1.80 mgC l^{-1} in the estuary and 0.25 - 0.85 mgC l^{-1} in the apex. The POC was composed largely of detritus (55% - 90%) except during periods of phytoplankton blooms when detritus decreased to 20% - 30%. Phytoplankton blooms occurred in May - June and February - March and were dominated by nanoplankton and netplankton, respectively.

Seasonal patterns of copepod abundance in both the estuary and the apex were characterized by peaks in late spring-summer and fall. Abundances were extremely low during the winter. Variations in copepod abundance were attributed to both breeding and growth patterns of copepods as well as seasonal variations in predation and advection.

Peaks in copepod biomass were inversely related to peaks in netplankton biomass. Copepod abundances were highest following the spring-summer nanoplankton blooms, and lowest during the winter netplankton blooms.

Assimilation rates in both areas fluctuated between 2.7% and 156% of body weight daily and were generally independent of food concentrations. Partial correlation coefficients showed variability in assimilation rates to be related to temperature and body weight. At both stations, assimilation of phytoplankton was maximal in the spring when up to 19% of the standing crop of phytoplankton was ingested daily by copepods. At this time, copepods preferentially removed netplankton cells but nanoplankton formed the major component of the total diet. During the winter, low temperatures resulted in a decrease in grazing so that less than 0.1% of the phytoplankton standing crop was removed daily and netplankton was selected against. Winter netplankton blooms were due, at least in part, to the reduction of copepod grazing pressure.

Detritus formed between 26% and 44% of the diet in the estuary, and 31% - 83% in the apex. The greater utilization of detritus in the apex, in spite of generally lower concentrations, was probably related to the quality of the material. Detritus in the estuary was probably derived primarily from sewage sludge, while detritus in the

apex was probably derived from phytoplankton. Net growth efficiencies (K_2) ranged from 9% to 76% and were found to be inversely related to the proportion of detritus in the diet. This suggests that detritus was metabolically more costly to utilize than phytoplankton. While assimilation of detritus in areas of low phytoplankton availability would result in increases in secondary productivity, its assimilation in place of "high quality" available phytoplankton would result in decreases in secondary productivity and food chain efficiencies. Thus, the incorporation of detritus in both the Hudson River Estuary, and especially the Apex of the New York Bight, as a major dietary component serves to decrease copepod growth efficiencies and buffer interactions between copepods and phytoplankton.

1.0 INTRODUCTION

Copepods constitute a major pathway in the flow of energy between primary producers and larger carniverous zooplankton and nekton in many marine environments. Estimates of the incorporation of food material by copepods into animal tissue have been made both in the laboratory and in the field. However, most of these nutritional studies involved feeding copepods unialgal or multi-algal diets, and were often done at artificially high cell densities. Few attempts have been made to provide a diet that resembled the varied composition of natural sea water, including both live phytoplankton and organic detritus.

In previous feeding experiments (cf. Fuller, 1937; Gauld, 1951; Haq, 1967; Parsons and Lebrasseur, 1970) copepods were shown to have metabolic requirements far in excess of carbon available in natural concentrations of phytoplankton. Such observations were based on mean rates of ingestion applied to concentrations of chlorophyll _a_, averaged over the water column. Two non-mutually exclusive hypotheses are possible. Since phytoplankton distributions in the water column are known to be patchy, (Platt, 1975) the average concentration of chlorophyll _a_ may not be a biologically meaningful estimate of food availability. That is, copepods will never

encounter the "average concentration", but areas of very high or very low concentrations. If they are able to locate patches, they could obtain sufficient carbon to meet their metabolic demands (Mullin and Brooks, 1976; Dagg, 1976).

Copepods might also be capable of utilizing other sources of carbon. Field studies have shown that phytoplankton usually account for less than 25% of the total particulate organic matter in both oceanic and coastal regions, the remainder being composed of detritus (Jorgensen, 1966). This vast pool of particulate organic carbon has been postulated as an additional source of nutrition (Krey, 1966).

Work on the nature and utilization of detritus is hampered by the fact that in situ detritus and phytoplankton can not be separated for analysis or experimental feeding. This has led to a general paucity of information on the chemical composition and nutritional quality of natural detritus. Assuming most particulate matter in the deep ocean to be detritus, Strickland and Parsons (1963) concluded that it contains a large enough number of compounds to serve as a potential food source.

Studies attempting to define the nutritional role of detritus have involved the use of either artificially produced detritus (Smirnov, 1959; Darnell, 1961; Paffenhopper and Strickland, 1973; Richman, 1958; Bell and Ward, 1970;

Saunders, 1966 and Roman, 1976) or natural detritus that settled out of the euphotic zone in oceanic (Paffenhoffer and Strickland, 1973) or estuarine areas (Quasim and Sankarayananan, 1972). Detritus has been shown to be either not assimilated or assimilated at a very low efficiency. The question of whether or not copepods can actively select for phytoplankton cells remains unanswered. Many workers have concluded that since this material is largely derived from phytoplankton, and as such constitutes material that has been "reworked", it must be of poor nutritive quality. Indeed, Menzel and Goering (1968) reported on the refractory nature of deep water detritus and dismissed it as of minor importance in food chain dynamics.

More recently, Heinle (1974) found artificially produced detritus to be a suitable substrate for egg production in Eurytemora affinis, but found such production to be significantly lower than in algal controls. In field studies by Gerber and Marshall (1974) in coral reefs, and Poulet (1976) in coastal Canadian waters, detritus was found to be ingested, and composed a major fraction of the diet of copepods.

Little attention has been paid to the significance of detritus in coastal areas where the source of this material may include autochthonous production by phytoplankton and zooplankton, and also allochthanous inputs from land and river

runoff, and, in highly populated areas, vast quantities of industrial and domestic sewage sludge. The effect of water column depth may also be important. Particulate matter will be resuspended more frequently in a relatively short water column, while deep sea detritus may be much older and subject to bacterial action longer. The composition, age, concentration, and nutritional suitability of this material may thus be quite different from that encountered in deep oceanic regions, or produced artificially from dead phytoplankton cultures.

In addition to the nature of the food (phytoplankton or detritus) that copepods assimilate, another important qualitative aspect of feeding is the size of food particles. Roman (1976) concluded that while copepods fed artificially produced detritus utilized it at the same rate as phytoplankton, it was the size of the detrital particle rather than its nutritional quality that was most likely to determine its rate of utilization. Experimental evidence indicates that herbiverous copepods actively select for larger phytoplankton cells when offered a choice (Harvey, 1937; Mullin, 1963; Conover, 1966c; Mullin and Brooks, 1967; Richman and Rogers, 1969; Frost, 1972 and Gaudy, 1974), and are able to obtain their daily ration on lower concentrations of larger cells than smaller ones (Frost, 1972). The conclusion of these experi-

ments are often confounded by the fact that the biomass of the larger species of phytoplankton (with respect to total biomass) was greater than that of the smaller species, even though the smaller species was more numerous (Frost, 1972; Mullin, 1963). Most recently Poulet (1974) concluded that the grazing patterns of Pseudocalanus minutus, when fed natural suspensions of particulates in low concentrations, were related more to particle concentration (total biomass concentration) than particle size or number. P. minutus showed greater selectivity as food concentration increased.

Quantification of rates of assimilation, respiration and growth of copepods fed a variety of food particles have been made by a number of investigators. Copepods are incubated in a relatively small volume of water (20 - 2000 ml) which contains a known quantity of phytoplankton cells (Gauld, 1951; Adams and Steele, 1966; Gaudy, 1974; Poulet, 1973; 1974). Assimilation of food material is then estimated via incorporation of radioactive tracers or disappearance of cells from the media; and respiration as the disappearance of oxygen.

Under the above conditions rates of assimilation and respiration were shown to be affected by food concentration, size and quality (Conover, 1961; 1966, a, b, c; Mullin, 1963; Frost, 1972) as well as temperature, body size and physiological state of the organism (Conover, 1966 b). Respiration has also been shown to be related to rates of food assimilation (Conover, 1962). While filtering rates have been calculated

from removal of phytoplankton cells, little attention has been paid to the removal of detrital particles, or the effects of the presence of such particles on phytoplankton ingestion and assimilation.

The objectives of this work were to observe the ability of adult copepods to assimilate natural suspensions of detritus and phytoplankton and to evaluate changes in copepod abundance and biomass in terms of temperature, salinity, and the concentrations of particulate organic matter assimilated. The relative importance of phytoplankton size classes, the effects of detritus on phytoplankton assimilation, and the importance of copepods as particle grazers in the apex of the New York Bight and Hudson River Estuary were evaluated.

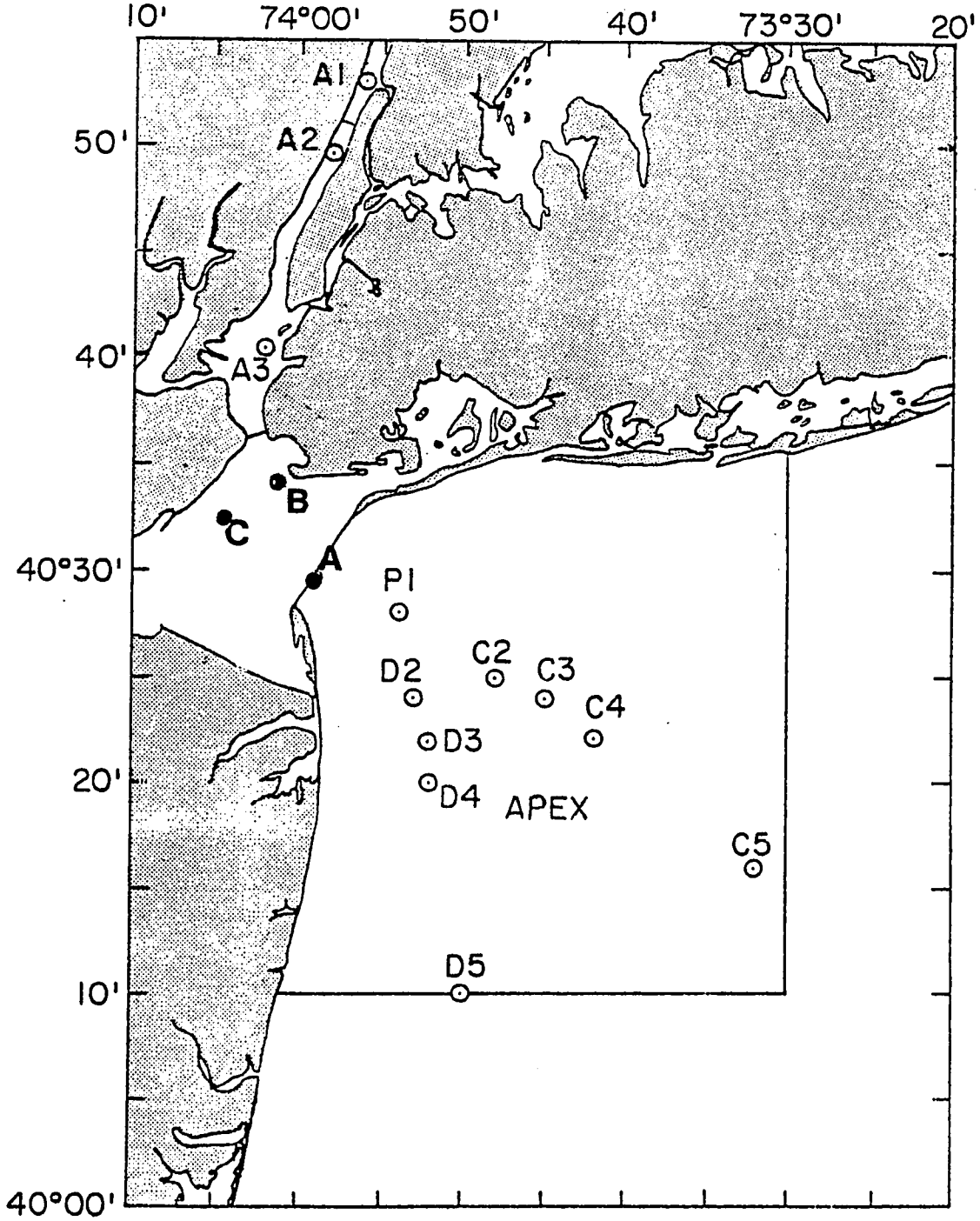
1.1 Hudson River Estuary and New York Bight

1.1.1 Hydrography and Particulates

Stations were occupied in the Upper Bay of the Lower Hudson Estuary and apex of the New York Bight (Fig. 1). The Upper Bay is a transition zone between the fresh water sources of the Hudson River and the marine waters of the New York Bight. As such, the Upper Bay and the apex offer a sharp contrast in both hydrographic conditions and the quantity and quality of particulates available for grazers.

The lower Hudson Estuary has a two-layered, non-tidal circulation pattern, with periods of maximum and minimum

Figure 1. Station locations in the Hudson River Estuary and apex of the New York Bight and station locations (A, B, C) of Jeffries, 1962a.


10'
74°00'
50'
40'
73°30'
20'
A1
A2
A3
50'
40'
B
C
A
40°30'
P1
C2
D2
C3
C4
D3
20'
D4
APEX
C5
D5
10'
40°00'

fresh water transport during the spring and summer respectively (Abood, 1974; Busby and Darmer, 1970). Flushing is rapid, a matter of days during high fresh water flow, and a week or more during low fresh water flow (Simpson, et al., 1975). The near shore non-tidal drift of estuarine water spreading into the Bight is predominantly southerly, tending to remain along the New Jersey coast. As a consequence the area nearest the coast of New Jersey receives a greater proportion of estuarine water than the central portions of the Bight (Ketchum, et al., 1951).

Hydrographic conditions in both the Bight and the Upper Bay are characterized by four seasonal states (Malone, 1976a, b); the spring, during which fresh water runoff is high and temperatures are rapidly increasing; the summer, during which temperatures are uniformly high and fresh water flow is minimal; the fall, during which temperatures are rapidly decreasing and intrusions of offshore oceanic waters are most frequent; the winter, during which temperatures are uniformly low and periods of high fresh water flow occur.

Variations in temperature and salinity in the Upper Bay reflect both its proximity to fresh water sources and the shallow depth of the water column (10 meters). Surface salinities are highly variable and range from 12% - 26%,

indicating the seasonal influence of both river and coastal waters. The water column is nearly always stratified due to a halocline, with most intense stratification occurring during the winter and spring when surface salinities are lowest, and least intense during the fall when surface salinities are highest. Thermal differences are less pronounced, with nearly isothermal conditions in the spring and winter and a maximum of less than $5^{o}C$ between surface and bottom waters in the fall (Table 1).

Surface salinities in the apex are higher and much less variable than in the Upper Bay, ranging from 25-34%. Increases in fresh water flow of the Hudson River are usually reflected in lowered surface salinities, especially along the New Jersey shore, after a 1 - 2 week lag (resolution of 1 week). Periods of highest surface salinity occur in the fall. Vertical differences in salinity are much less pronounced than in the Upper Bay (Table 1) and density stratification is largely due to the presence of a thermocline during the spring and summer. During the remainder of the year the water column is relatively well mixed.

Concentrations of particulate organic carbon (POC) and detritus are greatest and most variable in the region of the Upper Bay (Table 1). High levels of particulates are due

Table 1. Seasonal variability of temperature (°C), salinity (°/oo), chlorophyll a ($\mu g\ l^{-1}$) and POC ($mg\ l^{-1}$) in the Hudson Estuary and apex of the New York Bight, September, 1973 to August, 1974.

	FALL		WINTER		SPRING		SUMMER	
ESTUARY[a]	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
Temperature (°C)								
Surface	15.2	2.84	4.6	1.87	13.1	2.82	21.7	1.02
Near bottom	14.9	2.62	5.3	1.66	12.4	2.71	20.7	1.26
Salinity (%)								
Surface	24.2	1.31	16.7	0.62	15.2	1.79	21.7	0.80
Near Bottom	26.3	1.14	24.9	1.31	22.9	0.74	25.6	0.53
Chlorophyll ($\mu g\ l^{-1}$) Mean water column	1.7	0.11	0.89	0.14	2.6	0.48	3.15	0.48
Particulate Organic Carbon ($mg\ l^{-1}$) Mean water column	1.0	0.10	1.2	0.16	1.2	0.07	1.05	0.11
% Detrital-Carbon	96.1	1.46	97.4	0.19	94.6	1.23	92.2	2.03
APEX[b]								
Temperature (°C)								
Surface	13.9	1.72	6.2	0.73	12.0	1.60	21.9	0.31
Near Bottom	15.0	0.77	7.2	0.60	7.3	0.99	12.2	0.45
Salinity (%)								
Surface	31.2	0.32	31.5	0.22	30.6	0.38	30.4	0.36
Near Bottom	31.6	0.18	32.5	0.12	32.4	0.17	32.3	0.10
Chlorophyll ($\mu g\ l^{-1}$) Mean water column	1.9	0.40	2.67	0.20	1.2	0.12	1.53	0.29
Particulate Organic Carbon ($mg\ l^{-1}$) Mean water column	0.48	0.03	0.39	0.02	0.38	0.02	0.48	0.05
% Detrital-Carbon	89.3	1.41	80.1	1.50	87.3	1.20	92.9	1.20

a. Represents conditions at Station A3 (n=3)
b. Represents mean of conditions at Stations C3, C5, D3 and D5 (n=12)

largely to dumping of domestic sewage wastes. Sewage is discharged directly into the estuary at the rate of approximately 8 x $10^6 m^3$ day^{-1}. While such dumping is relatively constant, seasonal changes in river runoff cause variations in particulate concentrations within the estuary and in the quantities of particulates transported to adjacent coastal waters.

The second major source of carbon input into the estuarine-apex region is in situ primary productivity. Primary productivity is highly variable and characterized by peak periods in February to March and June to July, with lowest production occurring in the lower estuary, especially during February to March. In the estuary the input of primary production to carbon loads is most significant during periods of low summer flow. For example, in 1974, 185 metric tons C day^{-1} were produced as opposed to 425 metric tons C day^{-1} of sewage dumped into the estuary (Garside et al., 1976). On an annual basis, primary production accounts for only 33% (range 6% - 74%) of the total carbon produced (Malone, 1976a).

In the apex, primary productivity accounted for 70%-80% of the total annual input of carbon. The doubling time of POC in the photic zone, as a consequence of phytoplankton production, was less than 15 days and usually

between 2 - 8 days (Malone, 1976a), reflecting the rapid turnover of carbon. The remaining 20% - 30% of POC standing crop is related to sewage wastes originating in the rivers, and to a minor extent ocean dumping. The influence of estuarine discharge on concentration of POC in the apex occurs for greater than 250 km along the New Jersey coast (Rhyther and Dunstan, 1974).

The quality and quantity of particulates found in these two areas are quite different. The source of detritus in the estuary is probably more related to sewage dumping, while that in the apex is more related to primary productivity, resulting in a qualitative difference in this material. In addition detritus forms a larger proportion of total POC in the estuary (Table 1).

1.1.2 Zooplankton species distribution

Distribution of zooplankton species in the Hudson and Raritan River Estuaries and apex of the New York Bight have been described by Jeffries (1962a, b, c; 1964; 1967), Gibson (1973), Wiebe (1973), Grice and Hart (1962) and reviewed by Malone (1977). Four groups of zooplankton occur in the estuarine-apex region: (1) true estuarine species indigenous to the Raritan River Estuary and lower Hudson Estuary including the copepods Acartia tonsa, A. clausi, Eurytemora americana and E. affinis, (2) species indigenous to higher salinity neretic waters of the bight including the copepods Oithona

similis, Centropages typicus, C. hamatus, Paracalanus parvus and Pseudocalanus minutus, (3) pelagic species associated with high salinity offshore waters including the tunicates Fritillaria borealis and Oikopleura labradoriensis and (4) pelagic species associated with warm, high salinity oceanic waters such as the cladoceran, Penilia avirostris; tunicates, Doliolum nationalis, Oikopleura diocia; chaetognaths, Sagitta serratodentata, S. enflata; and the ctenophores, Beroe ovata and Mnemiopsis leidyi.

The species composition of the Upper Bay of the Hudson is an admixture of estuarine and neritic species. The two dominant species are the copepods Centropages typicus and Acartia tonsa. In the lower bay with increasing distance from shore, C. typicus replaces A. tonsa as the most abundant species (Table 2).

While copepods are present throughout the year and are usually the most abundant taxon, other zooplankton are occasionally more numerous. These include meroplankters such as polycheate larvae (Polydora spp. and Nerinidis spp.) which are found most frequently in May and July (Sage and Herman, 1972; Jeffries, 1962b). Also found are seasonal immigrants including the cladocera, Podon polyphemoides and Evadne normandii

and the ctenophore Beroe ovata, all of which are present during the late summer and early fall (Jeffries, 1962b; Nelson, 1925).

In the apex, four copepods dominate the plankton: Oithona similis, Paracalanus parvus, Pseudocalanus minutus and Centropages typicus in decreasing order of average yearly abundance. Peaks in abundance of these species occur most frequently from May through August and in some cases again in November. Estuarine species of Acartia, Eurytemora and Podon are present through most of the year but never dominate the plankton (Gibson, 1973). An increase in the total number of species occurs during the late summer and early fall with the appearance of oceanic forms including Labidocera aestiva, Candacia spp., Metridia sp., Corycaeus, Penilia avirostris, ctenophores and tunicates (Grice and Hart, 1962; Gibson, 1973). Pulses of meroplankters also occur from January to March and August to November, but are not as abundant as in the estuary.

The seasonal variability of species composition in the Upper Bay and the Bight reflect the dynamic interactions of estuarine, coastal and oceanic water masses. During periods of high fresh water flow in the winter and

Table 2. Relative abundance of copepods in Lower New York Bay indicated as those found most frequently (++++) to least frequently (+) or absent (0).

Species	Station[1]		
	Seaward		Landward
	A	B	C
Centropages typicus	++++	+++	++
Paracalanus spp.	+	++	+
Oithona spp.	+	++	0
Temora longicornis	0	+	0
Acartia tonsa	+++	++++	+++

[1] Station locations are noted on Figure 1.

spring, estuarine species are found to occur in larger numbers throughout the Upper Bay and apex of the Bight. Cold water pelagic species appear in the late winter, marking the intrusion of North Atlantic oceanic waters; while in the late summer and early fall, warm water pelagic species are advected into the Bight as the Gulf Stream attains its northernmost penetration.

2.0 METHODS

2.1 Approach

The role of suspended particulates in the trophic dynamics of copepods was investigated by a combination of field observations of standing crops and experimental studies of rate processes. (1) In the field, relationships between temporal and spatial changes in copepod standing crops and pools of suspended particulates were used to infer the nature and extent of food utilized. Potential food was classified as total live carbon, phytoplankton carbon (both netplankton and nanoplankton) and detrital carbon. Monthly sampling was used to obtain a picture of the gross seasonal and spatial fluctuations of standing crops, while weekly sampling was used to monitor time dependent variations in copepod biomass in relationship to the quantity and quality of suspended particulate organic

matter, temperature and salinity. (2) Concurrently, experimental studies were done to obtain direct estimates of the assimilation of particulates, and to infer the response of copepods, as indicated by the rate processes of assimilation, respiration and growth, to the temporal and spatial changes in food quantity and quality. (3) Estimates of rate processes were used to both interpert inferences based on field data and, when applied to standing crop data, to assess the impact of copepods on standing crops of phytoplankton and detritus. Estimates of "instantaneous" secondary productivity and food chain efficiencies were also made. Since data represented only daily growth, and did not include rates of mortality or reproduction, calculated rates of secondary productivity are not meant to represent long term productivity or efficiency.

2.2 Sampling Program

Stations were occupied in both the Hudson River Estuary and apex of the New York Bight (Fig. 1). Station A3 was located in the Upper Bay of the Estuary, station P1 at the mouth of the estuary, stations C3 and D3 were in the sludge and dredge spoil site, respectively, and stations

C5 and D5 were furthest from the estuary and free from the direct effects of dumping. Stations D3 and D5 were most influenced by estuarine discharge, while stations C3, and especially C5, were much less affected. This work was performed in conjunction with that of Dr. Malone's study of phytoplankton dynamics (Malone, 1976a). He kindly supplied the data used here on phytoplankton biomass and productivity.

All stations were occupied at approximately monthly intervals from September 1973 to August 1974 and April 1975 to March 1976. In addition, selected stations were sampled at weekly intervals from April through July 1975 and February to March 1976.

Samples for temperature, salinity, chlorophyll a, particulate organic carbon (POC) and adenosinetriphosphate (ATP) determinations were collected at three to five depths, depending on water depth and rate of light attenuation as estimated from Secchi disc measurements. Measurements of temperature, salinity, chlorophyll a, and POC were done on all sampling dates, while ATP was only measured in 1975 - 1976.

Zooplankton abundance in 1973 - 1974 was estimated

from tows extending over the euphotic zone at stations A3, P1, D3, D5, C3 and C5, and in 1975 - 1976, from the entire water column at stations A3 and D5 only. Samples were usually collected between two hours after sunrise and two hours before sunset, regardless of the tidal cycle.

Measurements of copepod assimilation and respiration were made at stations A3 and D5 in May, June, July and November of 1975 and in February and March of 1976. These two stations were selected on the basis of the quality and quantity of particulates available as food for copepods. The estuarine station (A3) is characterized by high concentrations of POC, composed largely of sewage derived detritus. The coastal station (D5) has generally lower concentrations of POC and lower proportions of detritus. Detritus in this apex area is probably more a function of phytoplankton productivity than sewage dumping.

2.3 Environmental Factors

2.3.1 Salinity and Temperature

Salinity and temperature were measured with an induction salinometer and reversing thermometer at discrete depths. During 1975 - 1976 continuous vertical profiles were also obtained with an Inter-Ocean CSTD system.

2.3.2 Suspended Particulates

POC was analyzed by high temperature combustion in oxygen in a Coleman Carbon-Hydrogen (CH) Analyzer (Strickland and Parsons, 1968). Samples of 0.5 liter (A3) and 1.0 liter (apex) were filtered through 47 mm combusted glass fiber filter (Gelman Type A and Type AE). The filters were then frozen for subsequent analysis on-shore. After defrosting, filters were dried at 60°C for two hours and introduced into the analyzer.

The analytical determination of particulate ATP was adopted from the method as modified by Holm-Hansen (1972). This method is based on the measurement of light emitted when an aliquot of ATP is added to an extract of firefly lanterns (Dow Chemical Corp.). If all reactants are in excess, the light emitted is proportional to the concentration of ATP present, and is then measured on a JRB-ATP photometer. The ATP provides the energy source for the light emitting oxidation of luciferin under the influence of luciferase.

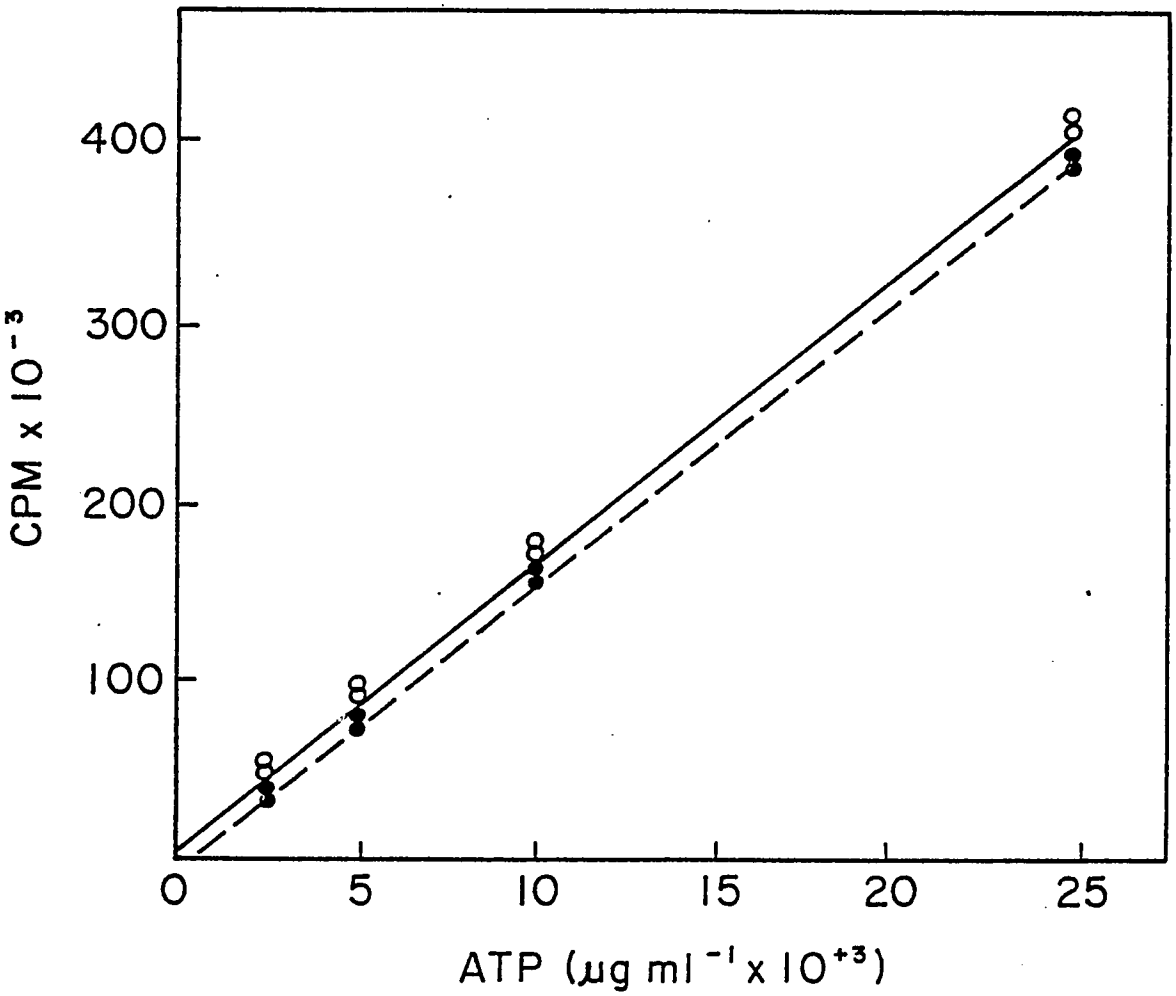
In order to minimize changes in concentrations of ATP due to pressure, temperature and light (Holm-Hansen, 1972), samples were filtered within one half hour of their collection. No more than 0.5 liter of water was filtered

onto glass fiber filters to minimize loss due to absorption (Sutcliffe, 1976). Filters were quickly transferred into scintillation vials containing 10 ml of Tris Buffer (0.2M, ph 7.75) at 100°C. The filter was boiled for five minutes to kill cells and inactivate all enzyme systems, while putting the ATP into homogenous solution. The sample was frozen at -20°C until analysis onshore could be conducted.

In the laboratory, standard curves were run using 1 mg of crystalline ATP dissolved in 1 liter of Tris Buffer. Serial dilutions of this stock were made at the time of analysis to yield a working range of concentrations from 1.0 to 100 μg ATP liter^{-1}. Both ATP and firefly extract decay rapidly at room temperature, and the reaction itself is subject to kinetic changes due to temperature fluctuations, so all chemicals were kept on ice during the analysis. In spite of this precaution, there was some decay of the enzyme, so standard curves were run at the beginning and end of sample analyses (Fig. 2). A mean of these two regressions was then used to calculate ATP concentration. Coefficients of variation between curves were always less than 10%.

ATP extracts were defrosted and further diluted when concentrations of ATP were too high or if there was

Figure 2. Sample standardization curves for JRB-ATP photometer; Y = counts minutes^{-1}, X = µg ATP ml^{-1} x 10^{-3}. Regression equations were calculated before (0); Y = 18.9x + 3.32 (r = 0.99, F = 611.4) and after (●); Y = 16.1x - 10.2 (r = 0.98, F = 211.4) sample analysis.


400
300
200
100
CPM x 10⁻³
0
5
10
15
20
25
ATP (μg ml⁻¹ x 10⁺³)

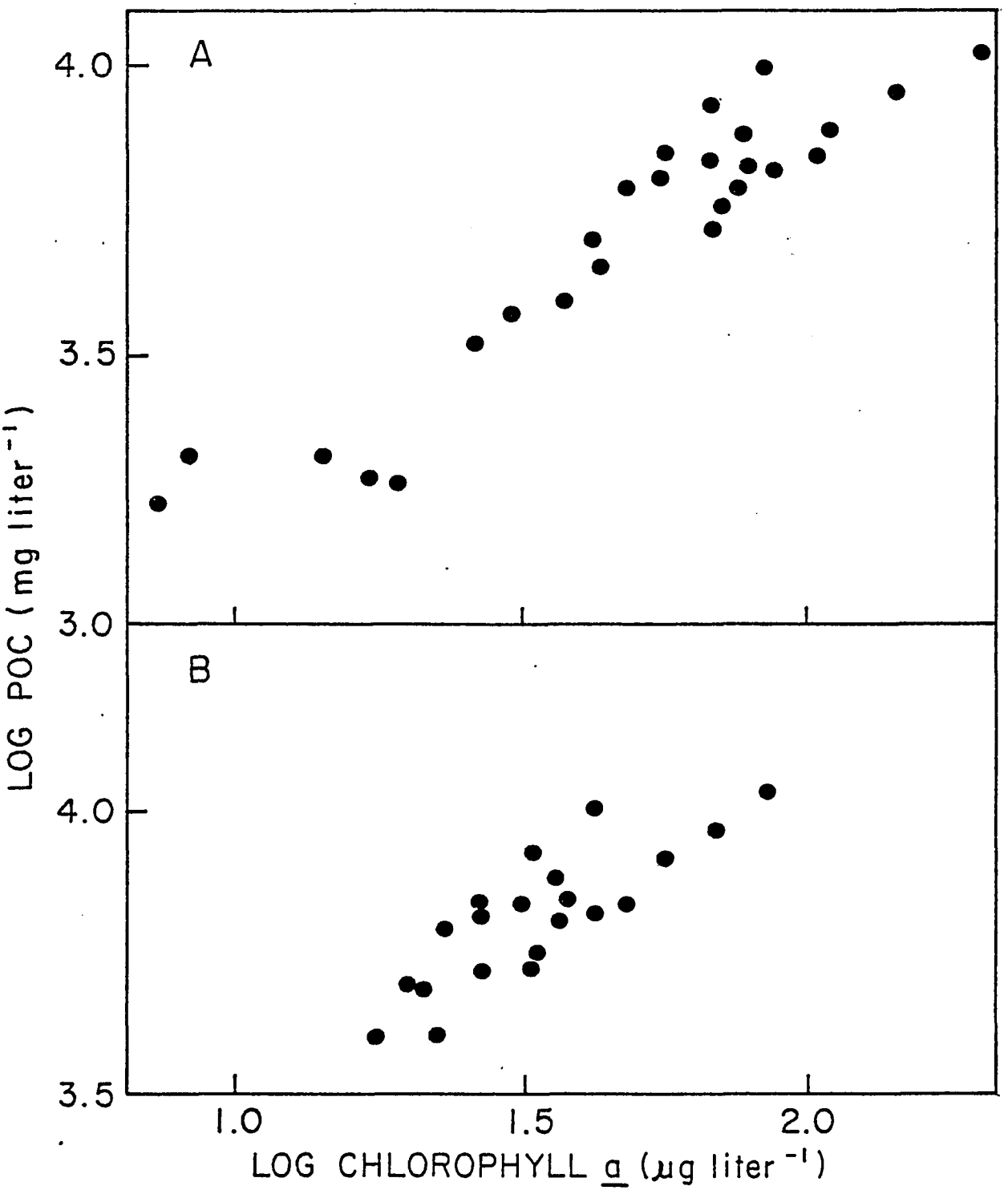
evidence of salt inhibition of the enzyme reaction (Strehler, 1968).

Chlorophyll a was measured by fluorometry (Strickland and Parsons, 1968), following serial fractionation through 22 µm mesh and glass fiber filters (Gelman Type AE). This yielded estimates of net-chlorophyll a and nano-chlorophyll a.

The potential particulate food sources were classified as total live carbon, phytoplankton carbon (both netplankton and nanoplankton) and detrital carbon. Phytoplankton carbon was estimated from the ratio of carbon to chlorophyll a. Ratios were generated from regressions of water column POC and chlorophyll a during periods of phytoplankton blooms (Fig. 3) and were found to be 72 for the periods of May to July and November 1975, and 46 from February to March 1976.

Live carbon was estimated from the ratio of carbon to ATP. Laboratory and field measurements over the past ten years have indicated that the ATP content of microorganisms averaged 0.4% of the cells organic carbon content (Holm-Hansen, 1972). Measurements have been made on algal cultures, bacteria, and zooplankton under varying conditions of temperature, nutrient concentrations and light intensities

Figure 3. Regressions of water column POC (Y) and chlorophyll *a* (X) used to calculate ratios of C:Chl*a*. Regression equations were calculated from measurements made in (A) April to July, 1975 and October to November, 1976 ($Y = 71.8x + 43$, $r = 0.97$, $F = 532$); (B) February to March, 1976 ($Y = 46.3x + 355$, $r = 0.96$, $F = 137$).


A
B
4.0
3.5
3.0
4.0
3.5
1.0
1.5
2.0
LOG POC (mg liter^{-1})
LOG CHLOROPHYLL a (μg liter^{-1})

as well as on natural field assemblages (Table 3). The validity of the use of ATP as an indicator of biomass obviously depends on the constancy of this ratio.

The ratio has been found to vary from less than 100 to greater than 1000 (Table 3). However, in all cases where there was no indication of nutrient limitation, the ratio ranged between 204 and 297 with a mean of 250. Extremely high ratios were seen only when nutrients were known to be limiting, and it has been suggested that the C:ATP ratio be used as an indicator of such limitation (Perry, 1976).

In both the Hudson River Estuary and apex of the Bight it has been found that spatial gradients in nutrient concentrations have little effect on phytoplankton growth, and nutrients were generally not limiting (Malone, 1976a, b). This observation combined with the constancy of the ratio of C:ATP (250) under conditions of abundant nutrients, indicates that reasonable estimates of total live carbon cab be obtained from ATP measurements in the estuary and apex of the New York Bight.

Estimates of detrital carbon are difficult to obtain due to the inability of workers to separate live from dead carbon in the field. Estimates have been made from either

Table 3. A comparison of literature values of the ratios of Carbon (C) to ATP and Carbon to Chlorophyll a (Chla).

	Sample Type and Conditions	C:ATP	C:Chl a	Reference[a]
I.	Laboratory cultures (unialgal)			
	Thalassiosira			
	Increasing P-limitation	780-2088	28-67	1
	N-limitation	139-309	28-91	1
	Ditylum brightwelli			
	No nutrient limitation	204	22	2
	Peridinium			
	P-limited	2374		3
	P-unlimited	297		
	Various species of algae and bacteria, no nutrient limitation	210-260		4
II.	Shipboard culture of Natural assemblages of phytoplankton			
	Coastal Phytoplankton			
	No nutrient limitation	263	60	5
	Phytoplankton from the North Pacific, nutrient limited			
	1-70 meters	337	448	1
	80-120 meters	77	166	
	Coastal phytoplankton from S. California			
	No nutrient limitation			6
	Phytoplankton of Lake Kinneret			3
	Fall-Winter	210-270		
	P-unlimited			
	Spring-Summer	349-2700		
	P-limited			

[a] References

1. Perry, 1976
2. Strickland et al., 1969
3. Cavari, 1976
4. Holm-Hansen, 1972
5. Eppley et al., 1971
6. Holm-Hansen, 1969

direct microscopic examination, or indirectly as the difference between phytoplankton carbon (estimated from assumed rates of C:Chl a) and total POC. Microscopic analysis, while affording information on the nature and size of detrital particles, is very time consuming and can not distinguish between organic or inorganic material nor yield estimates of carbon content. The chlorophyll method has two sources of error: (1) the assumption that all organic carbon not contained in phytoplankton is detrital, and (2) the error associated with the C:Chl a ratio.

The use of ATP as an indicator of live biomass seems to be a more valid approach since it includes all living organisms and, as long as nutrients are unlimiting, composes a relatively constant fraction of the cell's weight. Detrital carbon is then estimated as the difference between total POC and total live carbon. This approach was utilized by Poulet (1976) in his study of detritus.

2.4 Zooplankton abundance and biomass

Zooplankton samples were obtained with a half-meter 202 μm mesh net equipped with both inner and outer TSK flowmeters. At each station two replicate oblique tows were made for periods

of five to thirty minutes depending on the density of organisms. During 1973 - 1974 tows extended over the top half of the water column only. In 1975 - 1976 tows extended from 2 - 3 meters above the bottom to the surface. Volumes of water filtered ranged from 1 - 20 m^{-3}. Half of each catch was preserved in 4% buffered formalin for enumeration and identification. The remaining half was briefly rinsed in distilled water and frozen for dry weight analysis.

Samples for dry weight analysis were thawed and then split in half with a Folsom plankton splitter. An aliquot of 10 ml was taken from one half of the sample, homogenized in a blender and dried to constant weight at 60°C. The sample was then cooled in a dessicator and weighed on a semi-micro balance. To obtain an estimate of the proportion of total dry weight attributable to copepods, 200 - 300 organisms were picked from the remaining sample, and dried and weighed as described above.

2.5 Copepod Feeding Experiments

Feeding experiments were conducted on board ship using incubation bottles strapped to a wheel rotating at approximately 3 - 5 rev/minute which was immersed in flowing sea water. The movement kept particulates in suspension while the flowing sea water maintained the bottles at ambient sea surface temperature. At each station, one control and three replicate experimental bottles were incubated. Each bottle contained 2500 ml of water collected at a depth of 1 - 2 meters and

filtered through 202 μm mesh to remove macrozooplankton. To each of the experimental bottles, 20 - 100 copepods were added which had been obtained on station from a short tow from 1 - 2 meters below the surface. Highest densities were of the order of 1 animal/25 ml, with most between 1 animal/75 ml and 1 animal/125 ml. There was no indication that container size affected rates of respiration or assimilation, as had been noted by Mullin (1963). To insure minimal mechanical damage, only copepods captured in the codend were removed and examined microscopically for selection of the most active organisms. Copepods were transferred to experimental bottles with a large bore pipette.

Initial concentrations of oxygen were measured with a YSI Oxygen Probe, and samples were drawn for analysis of POC, ATP and chlorophyll *a*. Bottles were then sealed with fitted glass stoppers and incubated in the dark for 24 hours. At the completion of the experiment, bottles were visually inspected for dead copepods. Mortality was never greater than 15% and usually less than 2 - 5 individuals/bottle. If any dead organisms were found, they were not included in estimates of grazing, as it was assumed that they had been injured in handling and so did not actively feed. After final oxygen measurements were taken, copepods were removed, rinsed, and frozen for dry weight analysis. Aliquots were again drawn for all particulate analyses.

Rates of assimilation (A) of live, detrital and phytoplankton (net and nanoplankton) carbon were estimated from the disappearance of each particulate fraction from incubation bottles. This method gives accurate estimates of total particulate organic carbon assimilation but potentially yields overestimates of live-carbon and phytoplankton-carbon and underestimates of detrital-carbon assimilation. Some quantity of ATP and chlorophyll-a may pass through the gut of the animal, be degraded but not assimilated, and pass out of the animal as detritus. The disappearance of ATP and chlorophyll-a thus corresponds to something between assimilation and ingestion.

Respiration (R) was calculated from the change in oxygen over the incubation period. A respiratory quotient of 1 was used to convert oxygen respired to carbon assimilated. Growth (G) was calculated as the difference between assimilation and respiration:

$$G = A - R$$

The net efficiency of growth (K_2) was calculated as the ratio of growth to assimilation (Kozolovsky, 1968):

$$K_2 = G/A$$

Application of rate measurements to field standing crops yielded estimates of instantaneous productivity. Gross secondary productivity (GSP) was calculated as the product of assimilation per copepod and total copepod abundance. Net secondary productivity was calculated as the product of growth per copepod and total copepod abundance.

An estimate of the efficiency of conversion of plant material to copepod biomass (assuming all growth is due to assimilation of phytoplankton) is termed trophic level production efficiency (Kozolovsky, 1968), and was calculated as the ratio of copepod GSP to phytoplankton net production (NP). Estimates of phytoplankton particulate production (assumed to approximate net primary production) were made by Dr. T. Malone in conjunction with this work.

I. FIELD OBSERVATIONS

3.0 RESULTS

3.1 Hydrography

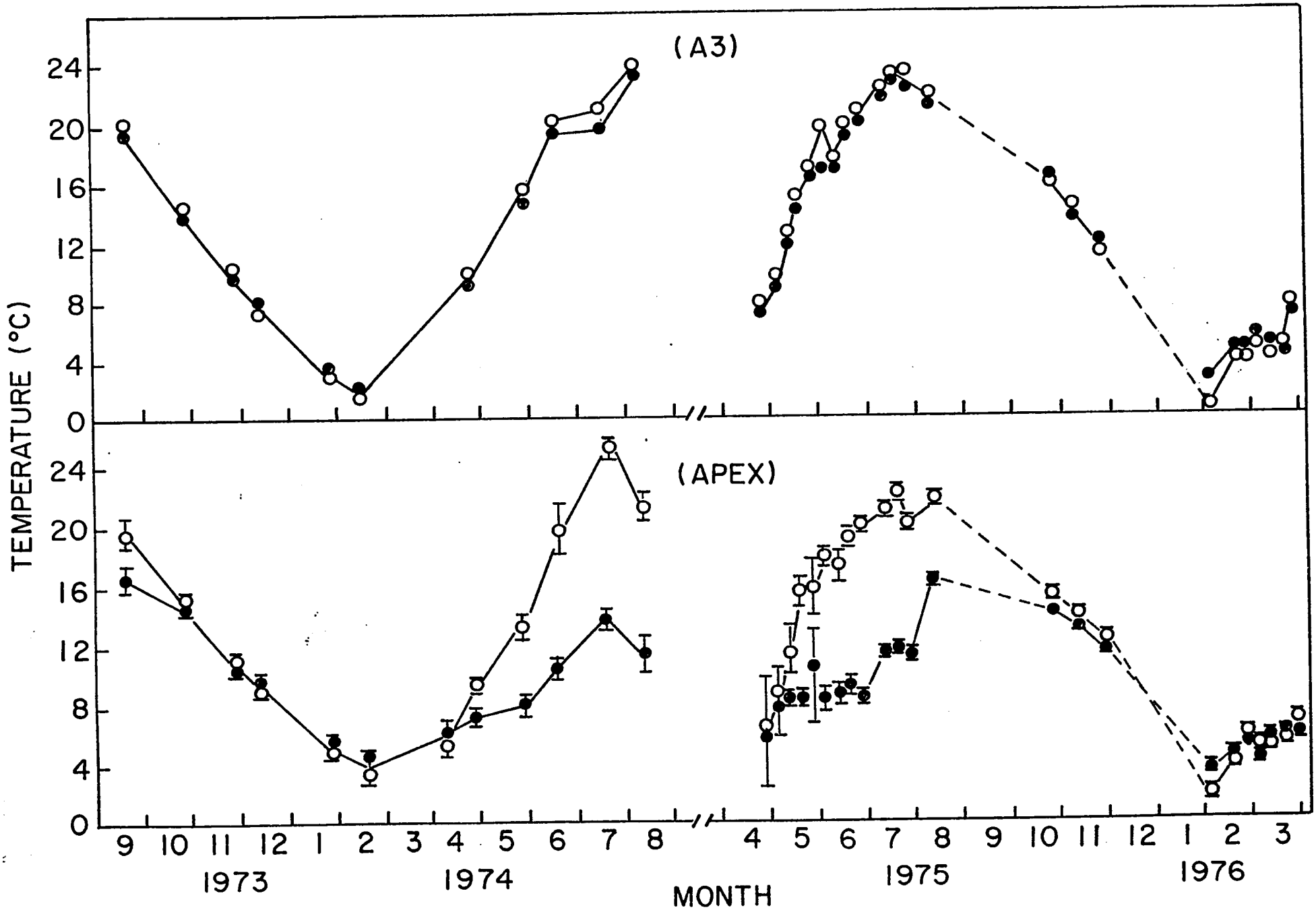
The seasonal cycle of surface temperatures at station A3 was characterized by a winter minimum of 1° - 2°C in February rising through the spring to a maximum of 24°C

in July and August (Fig. 4). The water column was almost always isothermal, with maximal vertical differences of 2 - 4°C occurring in June and July.

Patterns of surface temperature in the apex (average of values at stations C3, C5, D3 and D5) roughly paralleled those at station A3. There was usually less than a 2°C geographic range in temperature in the apex, with the greatest horizontal differences occurring in May and June. During the period of October to March the water column was nearly isothermal, but as surface temperatures began to rise in April a thermocline developed which remained until September.

Surface salinity at station A3, in 1973 - 1974, fluctuated between 6 and 26°/oo, with highest salinities in September and October, declining to a minimum in March and then rising to a peak in August. While the general temporal pattern was similar in 1975 - 1976, surface salinities tended to be lower during October through March of 1975 - 1976.

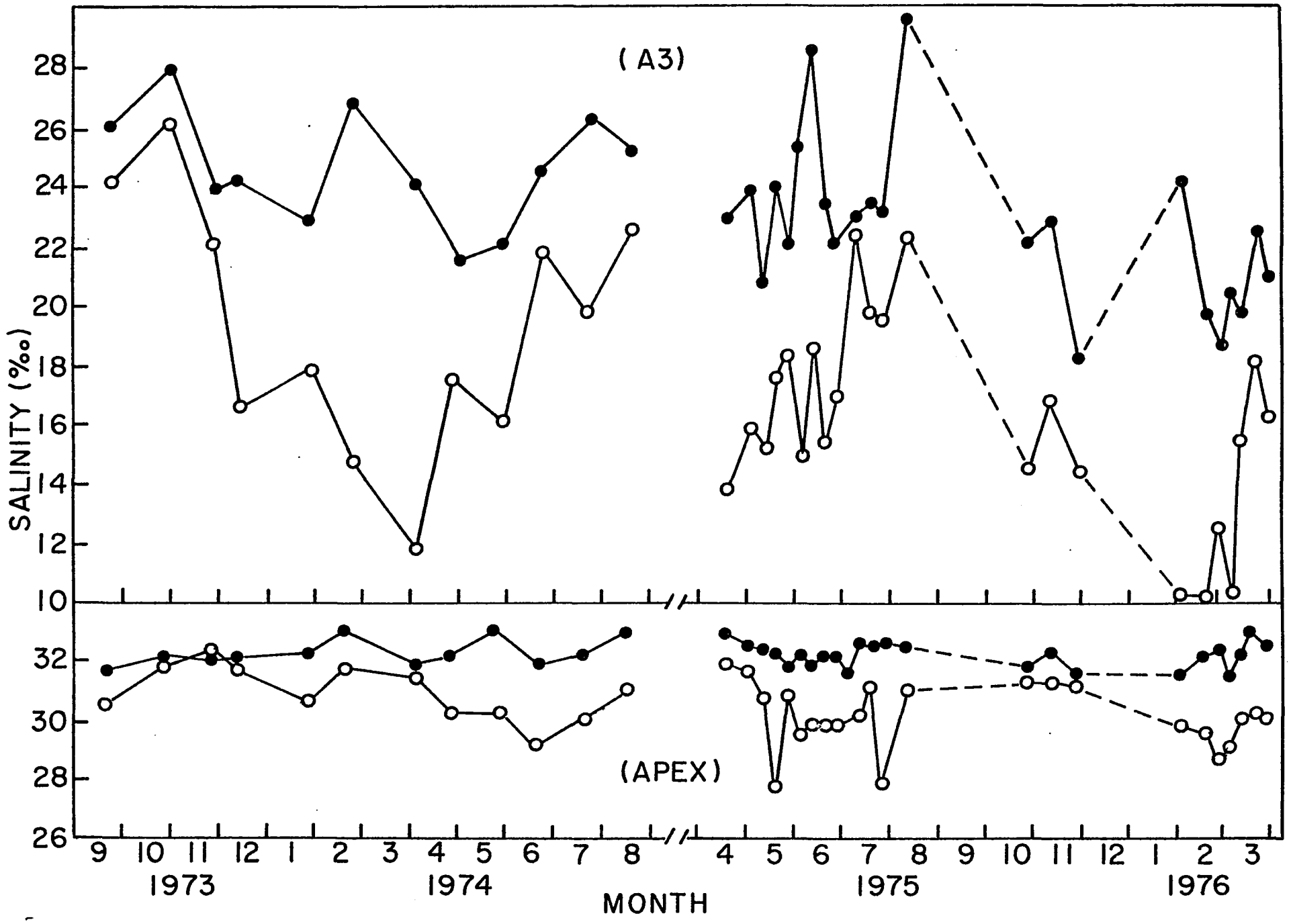
Figure 4. Annual variations in surface (0) and near bottom (●) temperature (°C) from 1973 - 1974 and 1975 - 1976 at station A3 and the apex (mean of stations C3, C5, D3 and D5); vertical bars represent ± 1 S.D.


(A3)
(APEX)
TEMPERATURE (°C)
0
4
8
12
16
20
24
9 10 11 12 1 2 3 4 5 6 7 8
4 5 6 7 8 9 10 11 12 1 2 3
1973
1974
1975
1976
MONTH

The water column was always stratified at station A3 due to salinity differences. Stratification was most poorly defined during July and August when the surface salinities were at a yearly maximum and river flow at a minimum, and most intense during February through April due to increased river runoff. Pulses of high river flow were seen as spikes of depressed surface salinity in December through March of 1973 - 1974 and April to June 1975 and February to March 1976.

Surface salinities in the apex increased with increasing distance from the mouth of the estuary and tended to be lowest along the coast of New Jersey. Salinities were highest and least variable at station C5, which was furthest from the estuary and in the central bight. Highest salinities occurred in October through November and April, and lowest in late April through July 1974, and May, July and February of 1975 - 1976 (Fig. 5). The observed decreases in salinity and the continued presence of low salinity surface water in May through August were due to periods of increased estuarine discharge and the presence

Figure 5. Annual variations in surface (0) and near bottom(●) salinities (%) from 1973 - 1974 and 1975 - 1976 at station A3 and the apex (mean of stations C3, C5, D3 and D5).


(A3)
(APEX)
SALINITY (‰)
28
26
24
22
20
18
16
14
12
10
32
30
28
26
9 10 11 12 1 2 3 4 5 6 7 8
1973
1974
4 5 6 7 8 9 10 11 12 1 2 3
1975
1976
MONTH

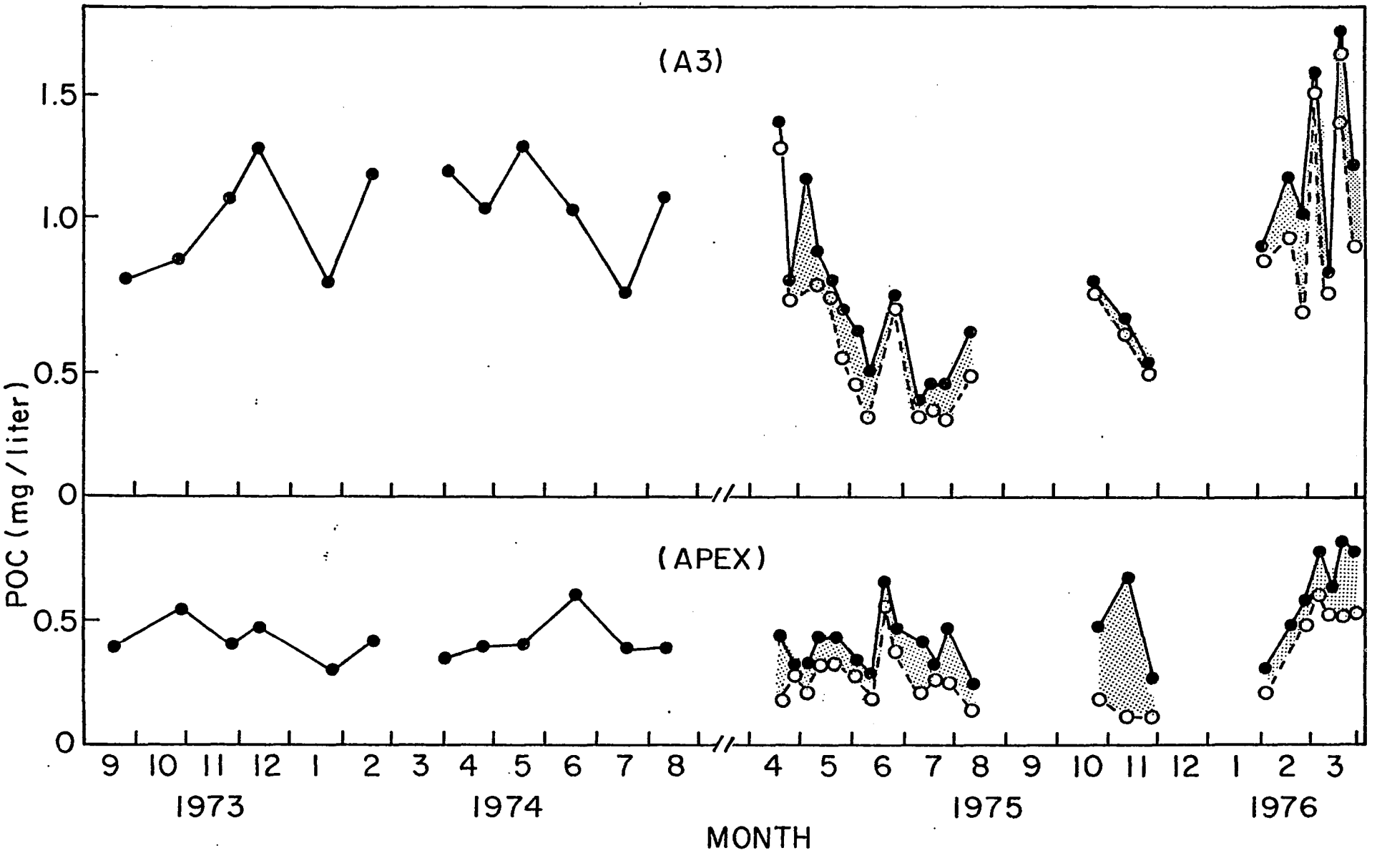
of a thermocline in April through August which tended to confine estuarine waters to the surface. Periods of high surface salinity, especially in October and November of 1973, indicate the increased proportion of offshore oceanic waters at this time.

Stratification in the apex was present all year, except October through December and April of both years, but was much less intense than that occurring in the estuary. Maximal vertical densities differences were due to temperature and not salinity.

3.2 Suspended particulates

In 1973 - 1974, concentrations of mean water column POC at station A3 ranged between 0.65 and 1.4 mgC l^{-1} (Fig. 6) and were greater than 1.2 mgC l^{-1} except in September, October, June and July. In 1975 - 1976, the amplitude of the variation of POC concentrations was greater, with a range of 0.4 to 1.8 mgC l^{-1}. Peaks occurred in April and May 1975, February and March, 1976.

Figure 6. Annual variations in mean photic zone concentrations of POC (mg l^{-1}) (0) from 1973 - 1974 and 1975 - 1976, and detrital carbon (●) (mg l^{-1}) for stations C3, C5, D3 and D5).


(A3)
(APEX)
1.5
1.0
0.5
0
0.5
0
POC (mg / liter)
9 10 11 12 1 2 3 4 5 6 7 8
4 5 6 7 8 9 10 11 12 1 2 3
1973
1974
1975
1976
MONTH

In the apex, mean water column POC concentrations fluctuated between 0.30 and 0.65 mgC l^{-1}, in 1973 - 1974, and between 0.25 and 0.85 mgC l^{-1} in 1975 - 1976. In 1973 - 1974, concentrations greater than 0.5 mgC l^{-1} occurred only in October, 1973 and June, 1974 and concentrations remained relatively constant, between 0.3 and 0.5 mgC l^{-1}, for the remainder of the year. In 1975, values greater than 0.5 mgC l^{-1} occurred again in June, October and November. Maximal yearly concentrations exceeding 0.85 mgC l^{-1} occurred in February and March, 1976. Generally, highest concentrations occurred at stations D3 and lowest at station D5. During April - May and June - July, concentrations were similar to the previous year and fluctuated between 0.35 and 0.50 mgC l^{-1}. Temporal changes at station D5 paralleled those for the apex in general, and were usually 2 - 10% lower than average apex values.

Both the amplitude of variability and absolute concentrations of POC in the apex were lower than those in the estuary. Except for the period of February to March 1976, concentrations in the apex were relatively low and constant.

During the 1975 - 1976 sampling period, when measurements of ATP and carbon to chlorophyll ratios were made, it was possible to partion the total pool of POC into detritus, total living and phytoplankton carbon. From April through August, 1975, the majority of POC at station A3 was composed of detritus (55% - 90%), except for one date in late June when live carbon accounted for 70% of total carbon (Fig. 6). Concentrations of detritus during this time varied from 0.35 to 1.40 mgC l^{-1}, and were responsible for increases in total POC that occurred during April and June. Increases of POC in early May and August were due largely to live carbon which accounted for 70% of the total carbon. In October and November high concentrations of detritus (0.6 - 0.83 mgC l^{-1}) were again responsible for increases in total carbon. At this time detritus accounted for greater than 85% of total carbon.

During February and March peaks in detritus alternated with increases of live carbon. Live carbon also reached a yearly maximum during this period.

During April to August 1975, the first peak of POC in the apex occurred 1 - 2 weeks later than the peak at station A3. The increase in the apex was due to increases in detrital carbon. Concentrations of detritus were at a yearly maximum of 0.60 mgC l^{-1} in June and composed 90% of the total POC. During late June through August, secondary peaks in POC were due to increases in live carbon (up to 60% of total POC) while detritus was present in concentrations of less than 0.3 mgC l^{-1}. Similarly, increases in POC in October and November were due to live carbon with concentrations of detritus reaching a yearly minimum of less than 0.20 mgC l^{-1} (20% of total POC). During February and March, while concentrations of detritus remained constant, increases in live carbon resulted in highest concentrations of POC observed in both years.

The absolute concentration of detritus and its proportion of total POC were greatest at station A3. While both areas had two peaks in POC concentration, increases at station A3 occurred in April and March, while those in the apex occurred in June and February (1975 - 1976). Peaks in live carbon occurred in both areas from May through August and again in February to March, and were present in approximately equal concentrations in both areas.

Temporal variations in ATP were significantly correlated with concurrent variations in chlorophyll a (Fig. 7) in both the estuary and the apex. This indicated that variations in ATP were primarily a consequence of changes in phytoplankton standing crops. The greatest deviations from this relationship occurred during May. Both ATP and chlorophyll a measurements indicated two major bloom periods, one from May to June and a second from February to March, with depressed concentrations from July to August and October through December. Similar trends were seen in the apex, where highest concentrations of ATP and chlorophyll a were found during April through July and February to March. The amplitude of these peaks during both periods was approximately equal with respect to chlorophyll a, but the February - March peaks in ATP were twice those of June - July.

In order to compare absolute living biomass as estimated by ATP and chlorophyll a, values of both were converted to carbon using appropriate ratios (Fig. 8). In both areas, peaks in ATP carbon (live carbon) generally corresponded with peaks in chlorophyll carbon (phytoplankton carbon). The greatest discrepencies between these two estimators were found at station A3 from April to June, when estimates of chlorophyll-carbon exceeded those of live-carbon.

Figure 7. Correlation between mean water column chlorophyll a ($\mu g\ l^{-1}$) and ATP ($\mu g\ l^{-1}$) at stations A3 ($r = 0.87$, $p < 0.01$) and D5 ($r = 0.82$, $p < 0.01$).

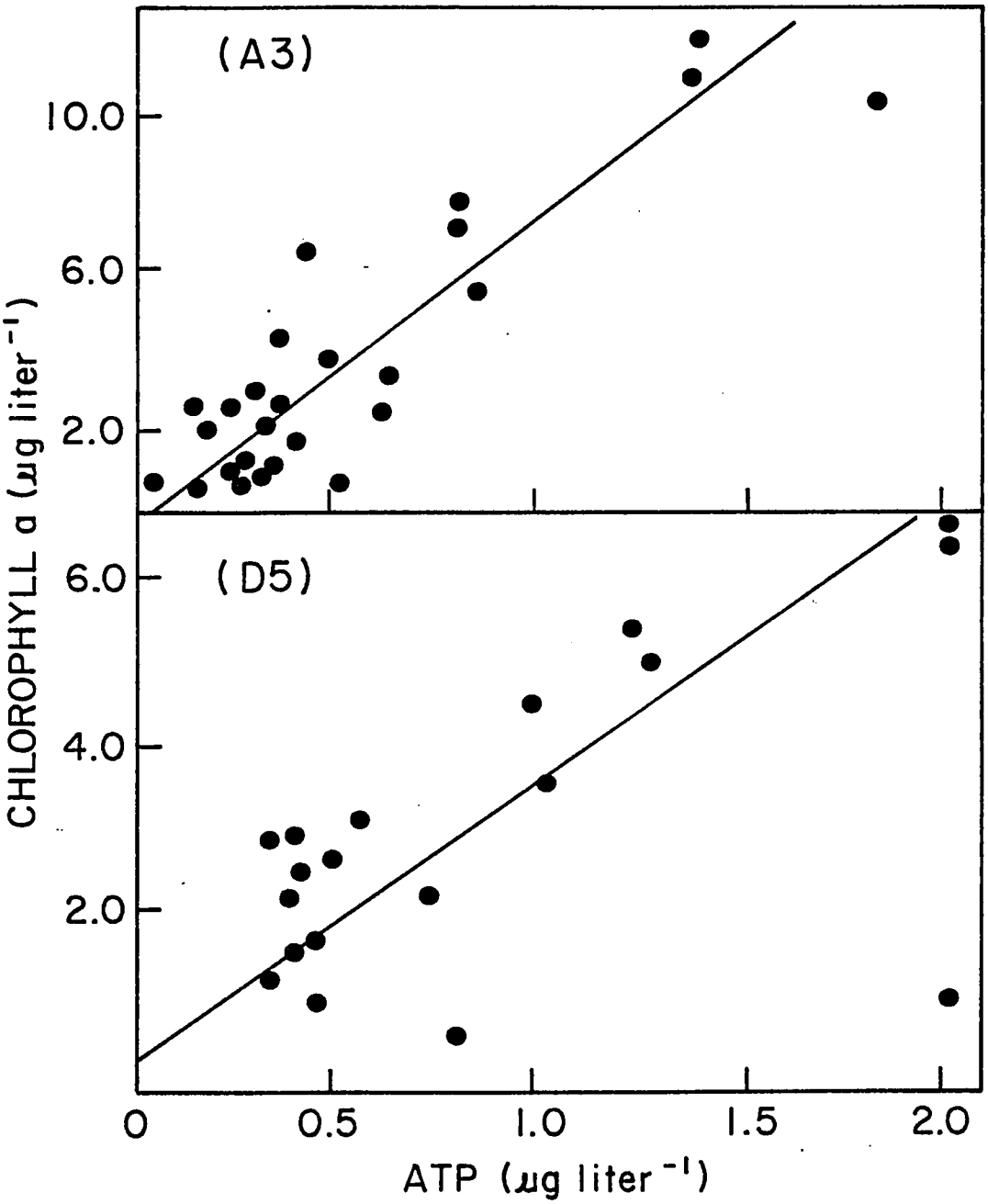
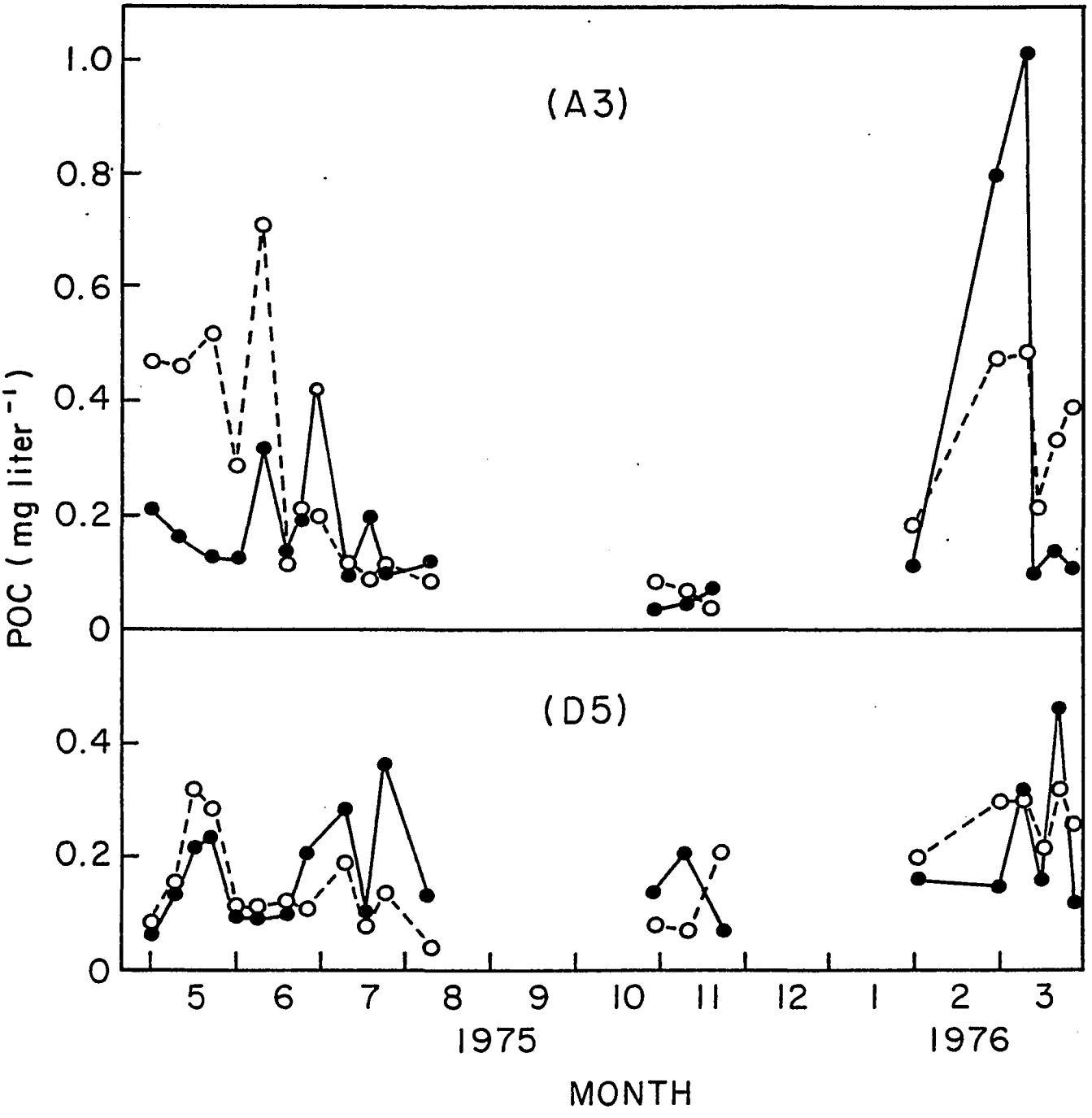

(A3)
10.0
6.0
2.0
(D5)
6.0
4.0
2.0
0
0.5
1.0
1.5
2.0
CHLOROPHYLL a (μg liter⁻¹)
ATP (μg liter⁻¹)

Figure 8. Annual variations in estimates of total live-carbon (mg l^{-1}) obtained from the ratio of C:ATP (0) and total live phytoplankton carbon (mg l^{-1}) obtained from the ratio of C:Chl*a* (●) at stations A3 and D5.


(A3)
(D5)
POC (mg liter⁻¹)
1.0
0.8
0.6
0.4
0.2
0
0.4
0.2
0
5
6
7
8
9
10
11
12
1
2
3
1975
1976
MONTH

Peaks in spatial distributions of mean water column chlorophyll a were shown by Malone (1976a) to occur further offshore in the apex (stations C3, C5, D3 and D5) during September to January, and at stations in the inner apex (P1, C2 and C3) during late winter and spring (Fig. 9). Maximum phytoplankton biomass generally occurred between stations P1 and D4 along the coast of New Jersey (Fig. 1).

Temporal patterns at all stations showed two major periods of increased phytoplankton biomass during April to July and February to March. The amplitude of these peaks at both stations A3 and D5 were somewhat lower in 1973 - 1974 than in 1975 - 1976 (Fig. 10).

At station A3, peaks occurring from April to May and June to July of both years, were dominated by nanoplankton. Netplankton decreased steadily from April to extremely low concentrations (less than 0.05 mg m^{-3}) during June through August when they composed less than 15% of the total population. Nanoplankton continued to dominate through October, and was replaced by netplankton in January. Net-

Figure 9. Annual variations in mean photic zone chlorophyll *a* ($\mu g\ l^{-1}$) during 1973 - 1974 at stations A3, P1, C2, C3, C4, C5, D2, D4 and D5 (after Malone, 1975).

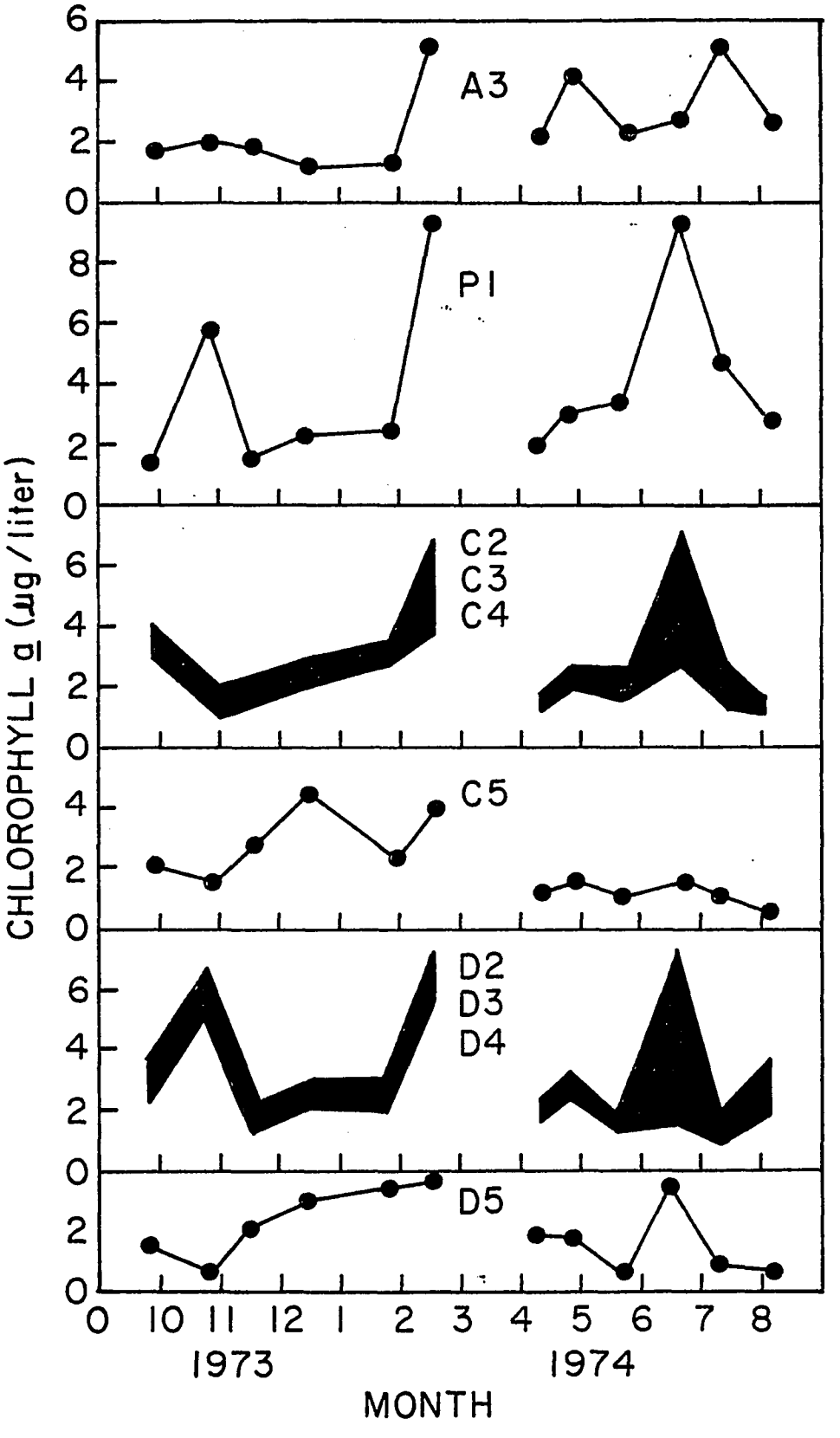
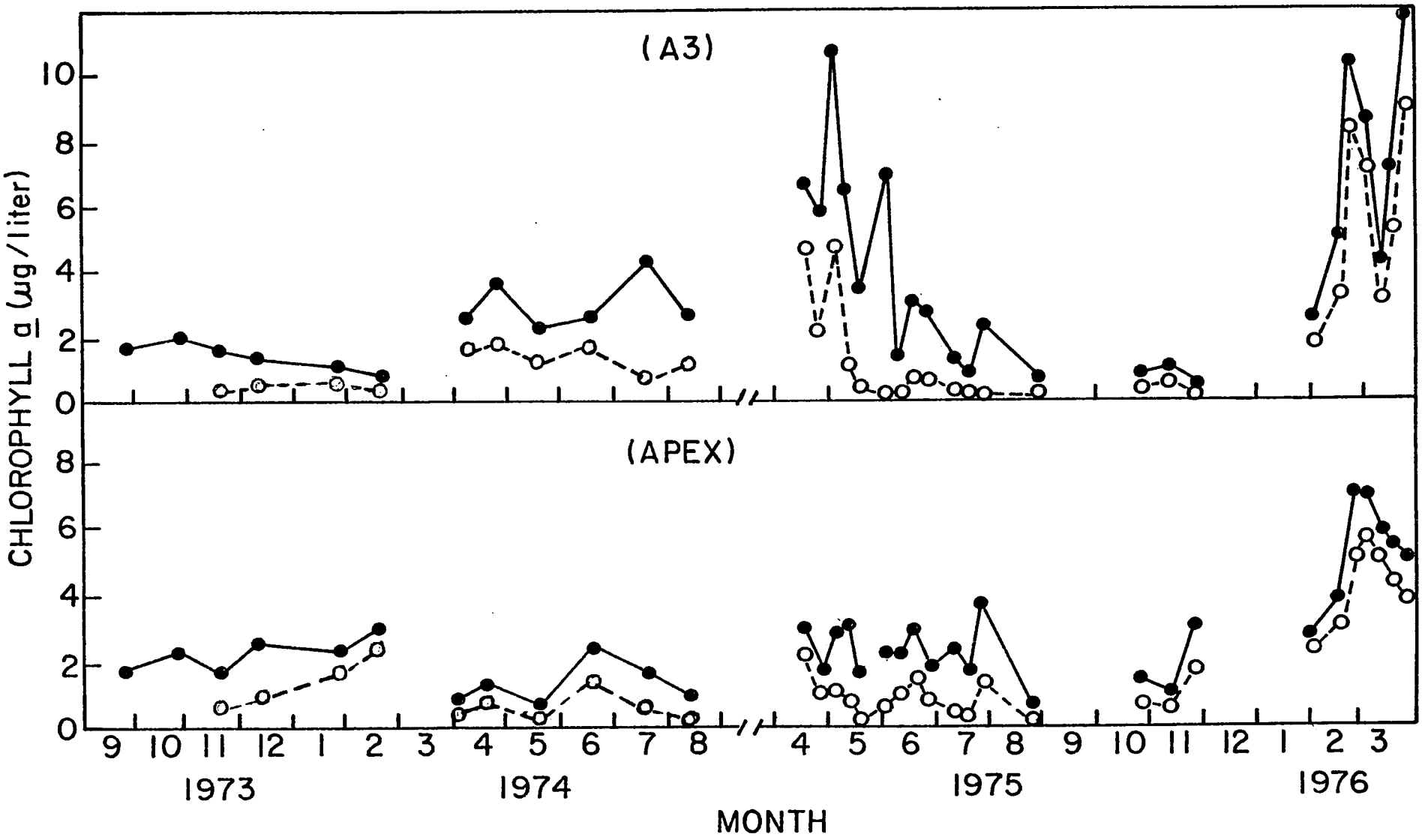

A3
P1
C2
C3
C4
C5
D2
D3
D4
D5
CHLOROPHYLL a (µg / liter)
0 10 11 12 1 2 3 4 5 6 7 8
1973
1974
MONTH

Figure 10. Annual variations in mean photic zone chlorophyll *a* ($\mu g\ l^{-1}$) (●) and net-chlorophyll *a* ($\mu g\ l^{-1}$) (O) during 1973 - 1974 and 1975 - 1976 at stations A3 and the apex (mean of stations C3, C5, D3 and D5).


(A3)
(APEX)
CHLOROPHYLL a (µg/liter)
0
2
4
6
8
10
9 10 11 12 1 2 3 4 5 6 7 8
4 5 6 7 8 9 10 11 12 1 2 3
1973
1974
1975
1976
MONTH

plankton populations then increased in biomass through February and March, when they composed between 60 - 75% of the population.

In the apex, the April to July peaks were similarly dominated by nanoplankton, with concentrations of netplankton fluctuating between 5 and 60% of the total population. Netplankton replaced nanoplankton during January to March, reducing it to less than 20%.

During April to July in 1973 and 1975, and February to March 1976, concentrations of chlorophyll *a* were significantly lower at station A3 than in the apex (Wilcoxin Signed Rank Test, $p < 0.01$) while the reverse was true for the remainder of the years. The decrease of netplankton biomass during May through August was never as pronounced in the apex as at station A3, where extremely low concentrations were found, and absolute concentrations were significantly lower (Wilcoxin Signed Rank Test, $p < 0.01$). During February to March, netplankton continued to form a larger proportion of the total in the apex, but the concentrations of netplankton were greater at station A3.

3.3 Zooplankton Abundance and Biomass

3.3.1 Total abundance

Temporal variability of zooplankton at both stations

A3 and D5 showed a bimodal cycle with maximum abundances in June through August and again in September to October. Between these periods, abundance was uniformly low (Figs. 11, 12).

Rapid increases in abundance at station A3 occurred between May and June of 1973 and 1975. With the increased frequency of sampling in 1975, densities were found to begin rising in the first week of May, and within two weeks reached 11,000 organisms m^{-3}. This was followed by depressed abundances in early June and then another rapid rise to a second peak in July or early August with maximum densities of 5,000 and 20,000 organisms m^{-3} in 1974 and 1976 respectivly. The first increase was due to populations of benthic larvae while the second increase was due almost entirely to copepods.

High abundances at station A3 in September through November of 1973, if they did occur, were not observed in 1975 due to an interruption of sampling. The bloom in 1973 was composed largely of copepods (92%) which reached concentrations of 9,000 organisms m^{-3}. During the period of December to March, in both 1973 - 1974 and 1975 - 1976, zooplankton densities were uniformly low and dominated by copepods (greater than 85%).

Figure 11. Annual variations in major taxonomic groups of zooplankton (number m^{-3}) and copepod dry weight (mg dry wt m^{-3}) (0) at station A3 during 1973 - 1974 and 1975 - 1976.

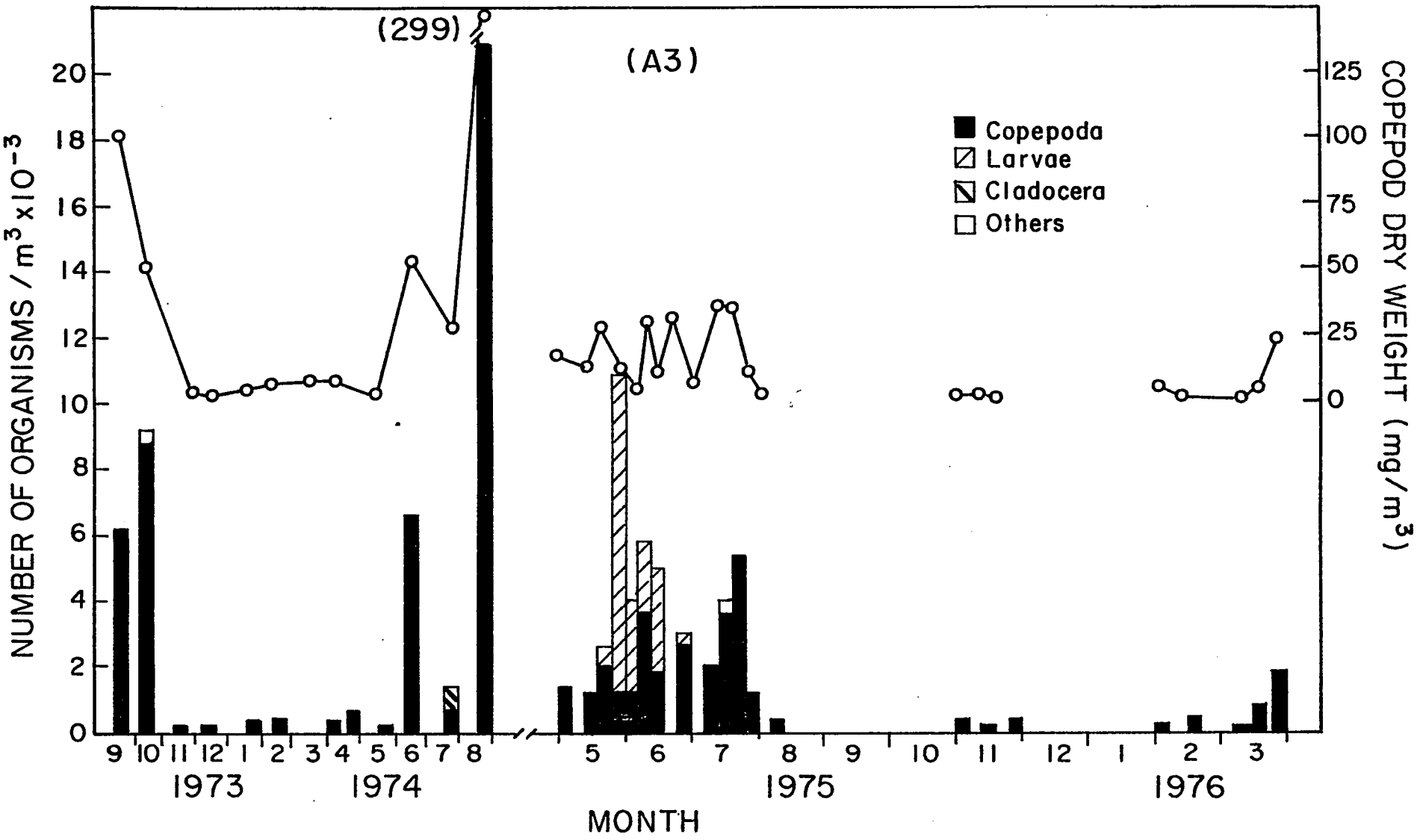
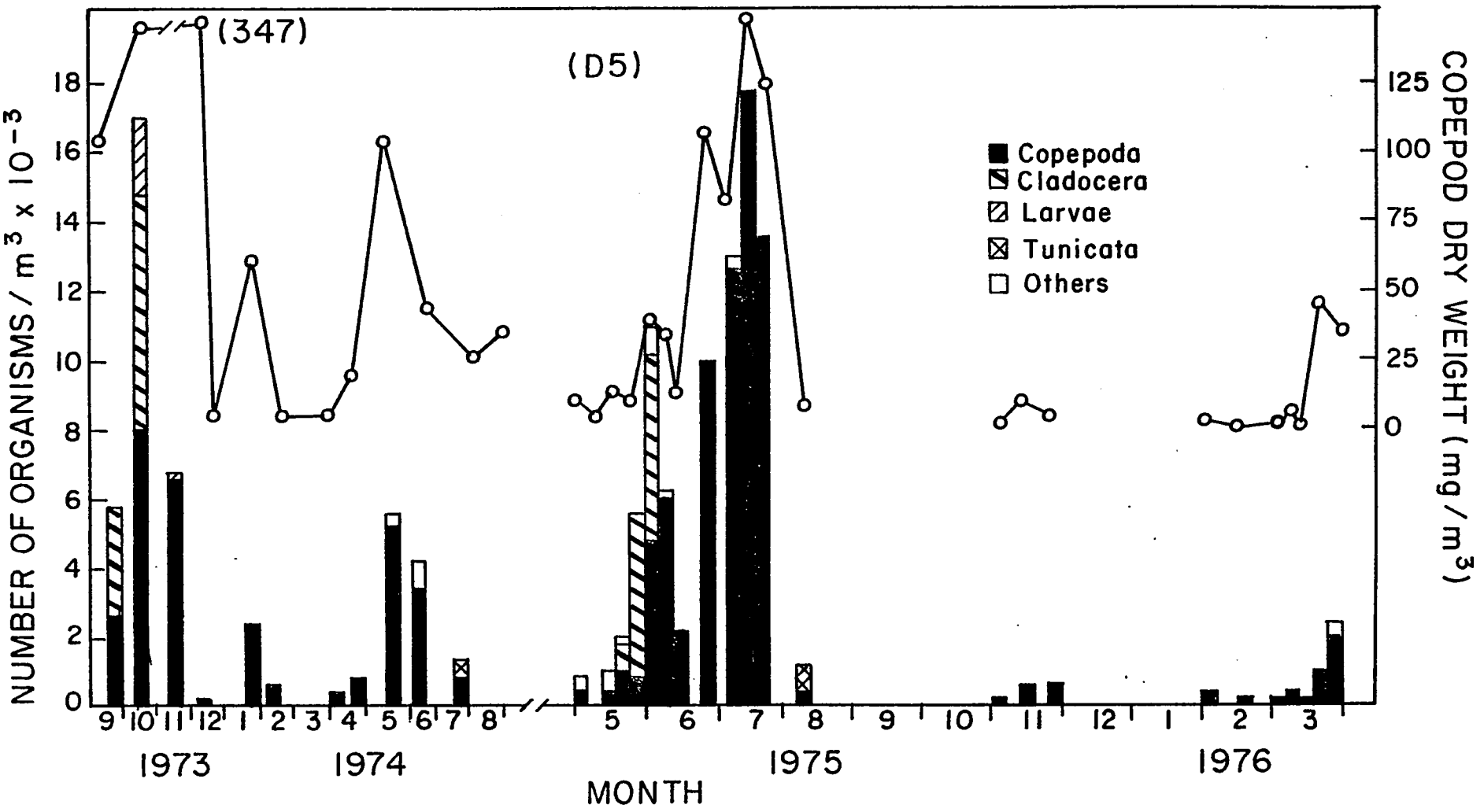

(299)
(A3)
Copepoda
Larvae
Cladocera
Others
NUMBER OF ORGANISMS / m³ x10⁻³
COPEPOD DRY WEIGHT (mg/m³)
0
2
4
6
8
10
12
14
16
18
20
0
25
50
75
100
125
9 10 11 12 1 2 3 4 5 6 7 8
5 6 7 8 9 10 11 12 1 2 3
1973
1974
1975
1976
MONTH

Figure 12. Annual variations in major taxonomic groups of zooplankton (number m^{-3}) and copepod dry weight (mg dry wt m^{-3}) (O) at station D5 during 1973 - 1974 and 1975 - 1976.


(347)
(D5)
Copepoda
Cladocera
Larvae
Tunicata
Others
NUMBER OF ORGANISMS / m³ x 10⁻³
COPEPOD DRY WEIGHT (mg / m³)
0
2
4
6
8
10
12
14
16
18
0
25
50
75
100
125
9 10 11 12 1 2 3 4 5 6 7 8
5 6 7 8 9 10 11 12 1 2 3
1973
1974
1975
1976
MONTH

At station D5, the high abundances in May through early June of 1975 were largely composed of a cladoceron (Evadne), which reached densities of greater than 10,000 organisms m^{-3}. Zooplankton abundances rapidly decreased to a minimum in early June and then rose to a second peak in July - August composed almost entirely of copepods. In 1973, while abundances increased during May and June, densities never exceeded 6,000 organisms m^{-3}, and there was a complete absence of cladocera. The difference between the two years may have been real or just a function of the longer sampling interval (1 month) in 1973 - 1974. Zooplankton peaks in September and October of 1973 were composed of both copepods and cladocera, with densities as high as 20,000 organisms m^{-3}.

In 1973 - 1974, average densities from April to June were greater at station A3, while the reverse was true in September - February (Table 4). In 1975 - 1976, average densities during all periods was approximately twice as great at station D5 than A3.

3.3.2 Taxonomic Composition

Spatial variability of copepods along the "C" and "D" transects was examined only during 1973 - 1974. Peaks in copepod density and biomass during September - July increased with increasing distance from the estuary and were

Table 4. Taxonomic composition of zooplankton at stations A3 and D5 from September 1973 to August 1974 and April 1975 to March 1976. Values are averages for spring-summer, fall and winter periods and are reported as the mean ($\bar{X}$) ± Standard Error (S.E.) and as a per cent of the total zooplankton.

STATION A3

1973-1974	SPRING-SUMMER[a]			FALL[b]			WINTER[c]		
	$\bar{X}$	S.E.	%	$\bar{X}$	S.E.	%	$\bar{X}$	S.E.	%
HOLOPLANKTON	6326	3940	98.4	5272	2751	90.6	160	74.0	96.4
Copepods	6160	3981	95.8	5135	2769	88.2	140	57.0	84.3
Cladocera	205	159	3.2	94	86	1.6	1	1.0	0.1
MEROPLANKTON	49	44	0.8	9	5	0.2	7	7.0	3.9
Balanus	45	44	0.7	0	0	0.0	7	7.0	3.9
Lamellibranch	0	0	0.0	6	6	0.1	0	0.0	0.0
CARNIVORES	2	1	0.1	6	6	0.1	1	0.1	0.1
TOTAL	6430	3916	100.0	5822	2756	100.0	166	64.0	100.0
1975-1976	SPRING-SUMMER[d]			FALL[e]			WINTER[f]		
HOLOPLANKTON	2527	502	66.0	127	9	99.8	295	162	99.8
Copepods	2364	405	62.0	125	9	99.0	289	158	98.0
Cladocera	157	79	4.1	0	0	0.0	0	0	0.0
MEROPLANKTON	1518	692	44.0	1	1	0.2	4	3	0.2
Balanus	595	256	16.0	1	1	0.2	4	3	0.2
Lamellibranch	0	0	0.0	0	0	0.0	0	0	0.0
CARNIVORES	4	1	2.0	1	1	0.3	2	2	0.3
TOTAL	3795	706	100.0	130	9	100.0	297	163	100.0

STATION D5

1973-1974	SPRING-SUMMER[a]			FALL[b]			WINTER[c]		
HOLOPLANKTON	2859	883	96.6	9466	2727	90.4	833	504	96.4
Copepods	2306	973	77.9	6025	1673	57.5	819	502	94.8
Cladocera	39	38	1.3	3334	1968	31.8	1	1	0.1
MEROPLANKTON	50	35	1.7	949	738	9.1	39	24	4.5
Balanus	40	37	1.4	0	0	0.0	30	23	3.5
Lamellibranch	0	0	0.0	907	710	8.9	1	1	0.1
CARNIVORES	21	18	0.7	23	11	0.2	6	2	0.7
TOTAL	2960	861	100.0	10475	3379	100.0	864	527	100.0
1975-1976	SPRING-SUMMER[d]			FALL[e]			WINTER[f]		
HOLOPLANKTON	7449	1752	98.6	600	425	99.9	736	401	94.6
Copepods	6337	797	84.0	355	117	59.0	405	288	52.0
Cladocera	909	572	12.0	89	69	14.8	0	0	0.0
MEROPLANKTON	106	57	1.4	1	1	0.1	42	31	5.4
Balanus	52	46	0.8	0	0	0.0	13	11	1.7
Lamellibranch	0	0	0.0	0	0	0.0	27	19	3.5
CARNIVORES	52	22	0.7	1	1	0.1	11	8	1.4
TOTAL	7555	1706	100.0	601	425	100.0	779	416	100.0

a. April-August, n=5 b. September-November, n=3 c. December-February n=13 e. October-November, n=3, f. February-March, n=10

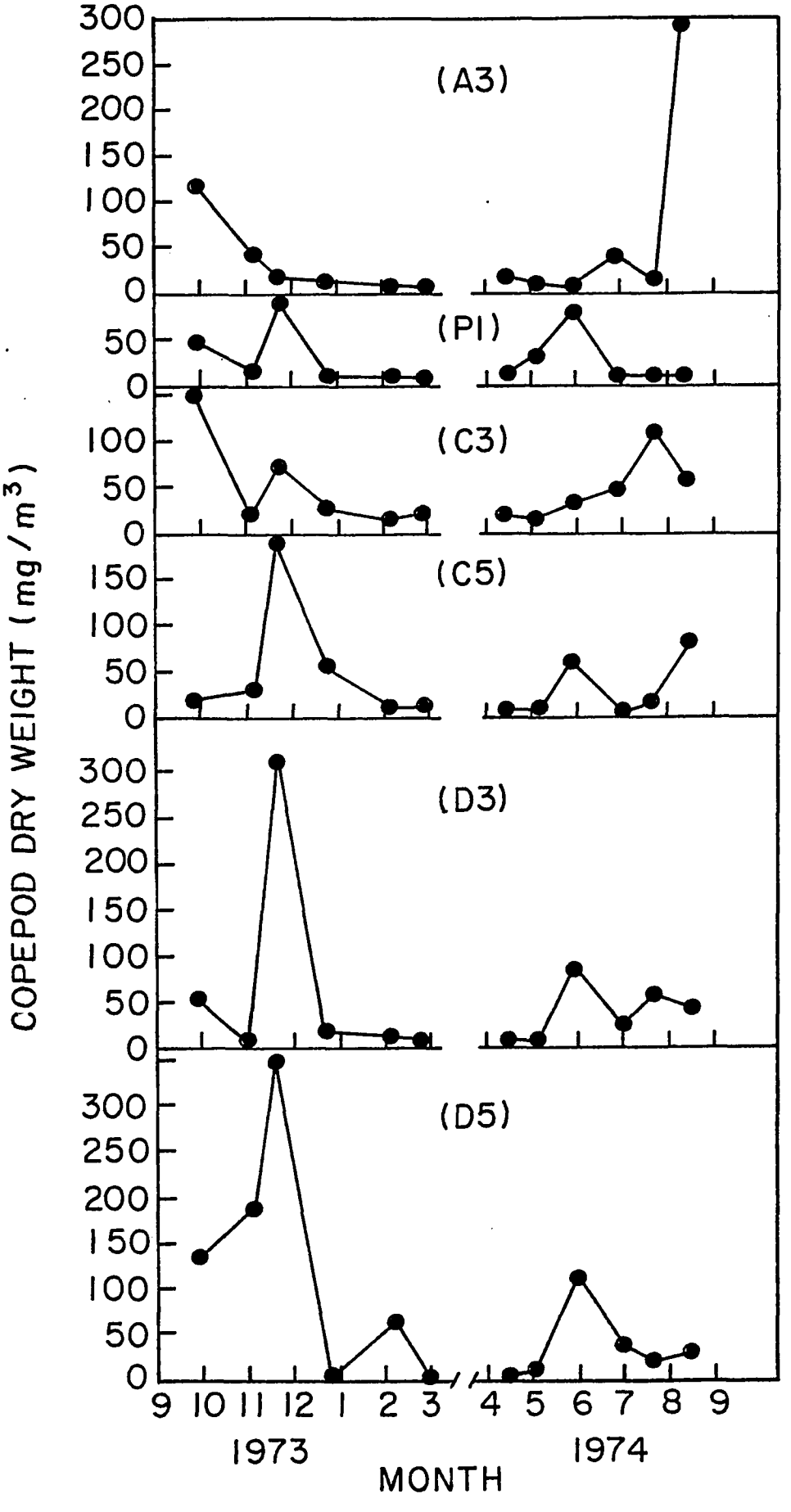
most pronounced along the New Jersey coast (Fig. 13). Only during August, 1974, did copepod biomass and abundance show a sharp peak in the estuary (station A3) while remaining low at all other stations.

At station A3, copepods generally comprised greater than 90% of total organisms except during April to June of 1975 when they comprised 20%. Maximum abundances occurred during April to June reaching concentrations of greater than 20,000 organisms m^{-3}. A second peak in September and October of 1973 had an average density of 5135 and maximum concentrations of greater than 8,000 organisms m^{-3}. During both years, abundances were lowest from December to March, with average densities of less than 300 organisms m^{-3}.

At station D5, copepods were also the most abundant group, with average densities from April to June (1974 - 1975) of 2306 to 6337 organisms; and maximum densities of up to 17,000 organisms m^{-3} in June, 1976. In September and October of 1973 densities averaged 5135 organisms m^{-3}, but only comprised 57% of the total zooplankton. Copepod densities were lowest during December through March in both 1973 - 1974 and 1975 - 1976, with average concentrations of less than 900 organisms m^{-3}.

Patterns of temporal variations of copepods at both stations were similar, with higher abundances at station D5

Figure 13. Annual variations in copepod dry weight (mg dry wt m^{-3}) during 1973 - 1974 at stations A3, P1, C3, C5, D3 and D5.


COPEPOD DRY WEIGHT (mg/m³)
(A3)
(P1)
(C3)
(C5)
(D3)
(D5)
300
250
200
150
100
50
0
9 10 11 12 1 2 3 4 5 6 7 8 9
1973
1974
MONTH

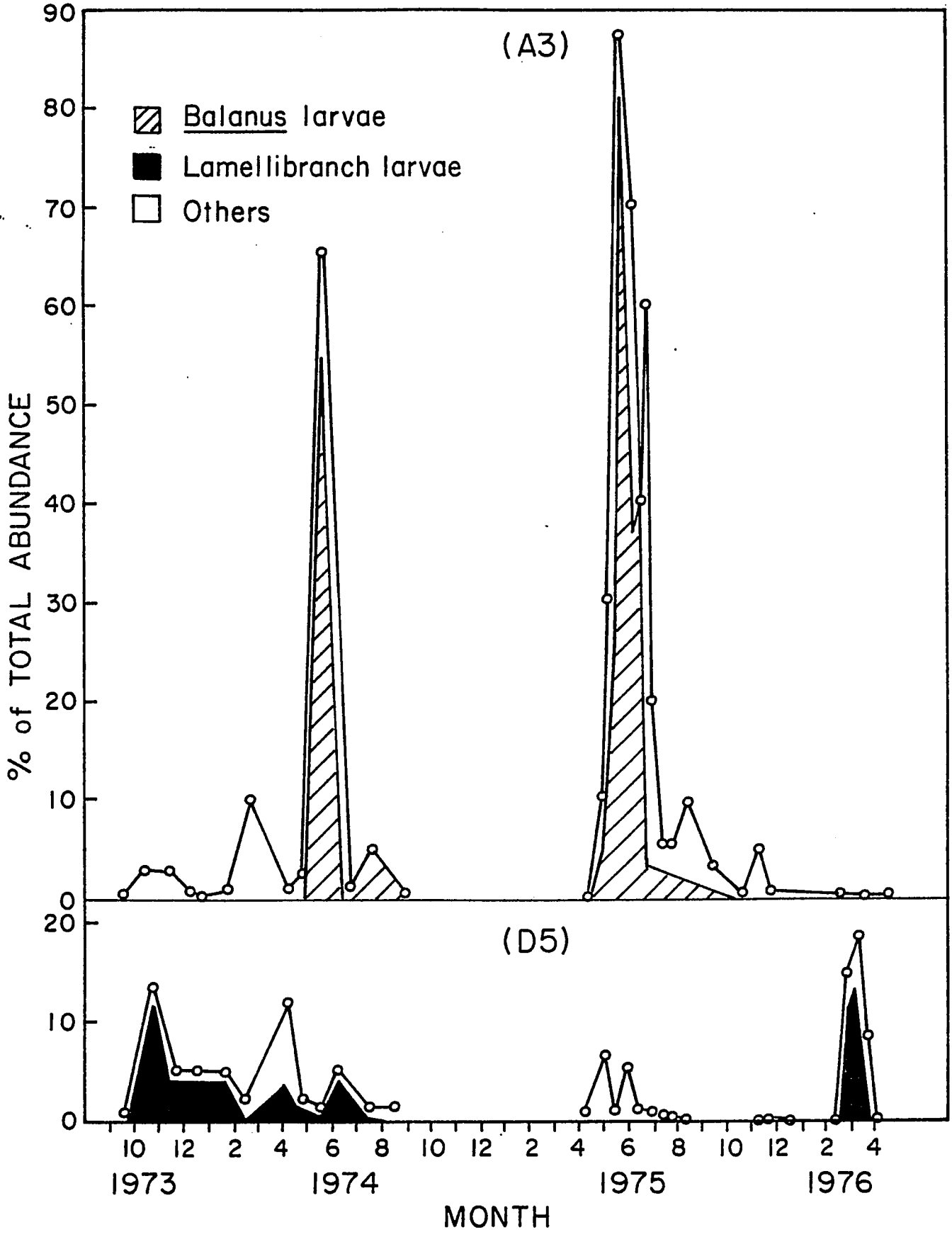
during June to July of 1975, and at A3 during June to August of 1973. Concentrations were approximately equal during the remainder of the year.

Meroplankton were of seasonal importance at station A3, where they comprised up to 86% of the total zooplankton during June of 1975. Primary peaks occurred in May and June of 1974 and again in 1975 (Fig. 14). Peaks were dominated by the larval stages of the barnacle, Balanus spp.

Intensive sampling in 1976 showed that Balanus nauplii appeared in May and increased to a maximum of greater than 8,000 organisms m^{-3} in late May, diminishing to very low levels by July (Appendix I-II). This was followed by the appearance of the cyprid larvae, which peaked in June and disappeared by August, when they presumably settled out of water column. The time elapsed between maximum abundances of these stages indicated a naupliiar developmental stage of 20 days.

At station D5, in both years, meroplankton were most abundant during October to November and again in March to April. While concentrations were occasionally quite high, they never formed greater than 20% of the total population (Fig. 14). The increases were due largely to lamellibranch larvae. These larvae were most abundant in September 1973 and were present in low concentrations for the remainder of

Figure 14. Seasonal importance of meroplankton (% of total zooplankton) from 1973 - 1974 and 1975 - 1976 at stations A3 and D5.


(A3)
Balanus larvae
Lamellibranch larvae
Others
% of TOTAL ABUNDANCE
90
80
70
60
50
40
30
20
10
0
(D5)
20
10
0
10 12 2 4 6 8 10 12 2 4 6 8 10 12 2 4
1973
1974
1975
1976
MONTH

the year. In 1975 lamellibranch larvae were found much less frequently. However, since no samples were taken during September and October, peaks in abundance may have occurred between sampling times.

Nauplii larvae of Balanus were present in much lower concentrations at station D5 than A3, with a maximum of 200 organisms m^{-3} in late May. The cyprid larvae showed a sharp increase in mid-June (2000 organisms m^{-3}) and another slight increase in late June through July. Other larvae found at both stations included fish, zoeae and polycheate (Appendix I-II).

The greater abundances and relative seasonal importance of meroplankton at station A3 reflected both its proximity to fresh water and the shallow depth of the water column. It was numerically the second most important group and comprised 44% of the zooplankton during April to June (Table 4). At station D5, meroplankton never comprised greater than 15% of the population, with maximal abundances occurring in April through June and September to October. While the nauplii of Balanus were never numerous at station D5, peaks of the cyprid larvae did occur. The increases in cyprids followed the appearance of nauplii at station A3 by 1 - 2 weeks, suggesting that they were advected into the apex from the estuary.

Three genera of cladocera were found, Evadne, Podon and Penilia. At station A3, Evadne was present from April to June

of 1974, with maximum concentrations of up to 680 organisms m^{-3}. It occurred again in May to July of 1975, but in densities of less than 150 organisms m^{-3}. Penilia was only seen in September and October of 1973, when it reached densities of up to 250 organisms m^{-3}.

Cladocera were sporadically found at very high densities at station D5, and dominated the peak in zooplankton that occurred in June of 1975. Evadne was present in low numbers in April 1975, and quickly rose to concentrations of 4200 - 4400 organisms m^{-3} in late June. Penilia was present in very high densities in September to October of 1973, reaching concentrations of up to 6800 organisms m^{-3}. Cladocera were rarely found during December through March in 1973 - 74 or 1975 - 76.

At station A3 cladocera never accounted for greater than 15% of the total zooplankton. They composed from 3.2% to 4.1% during April to August of 1974 and 1975, respectively. For the remainder of both years they composed less than 2% of the total zooplankton. They were more abundant and formed

At station D5 the tunicates found included the appendicularian, Doliolum spp. and the larvaceans, Oikopleura spp. a larger percentage of total zooplankton at station D5. Evadne accounted for 1.3% to 12% in April to June, and Penilia for 14.8% to 31.8% in September to November for 1974 and 1975 respectively. The horizontal distribution of the latter

species was related to salinity. Penilia was present in lower concentrations and later in the season at station A3, suggesting that it was an offshore species that was advected into the bay.

Tunicates were rarely found at station A3, except for isolated individuals in December 1973 and January 1974. (Appendices I, II). At station D5 the tunicates found included the appendicularian, Doliolum spp. and the larvaceans, Oikopleura spp. and Frittalaria sp. The two warm water oceanic species (Doliolum and Oikopleura) became abundant during July and August in both 1974 and 1975. At these times they dominated the zooplankton, reaching concentrations of 1600 organisms m^{-3}. During March of 1976, Frittilaria was found in densities of greater than 800 organisms m^{-3}.

The sampling procedure utilized was not designed for quantitative sampling of larger carnivores, but some qualitative statements can be made on those that were captured. Carnivores at both stations included ctenophores, chaetognaths, coelenterates, polycheates, mysids and fish larval (Appendices I, II).

The chaetognath Sagitta sp. was rarely seen at station A3 but was frequently captured at station D5 during most of the year. They were most abundant in May 1973 (95 organisms m^{-3}) and June 1975 (244 organisms m^{-3}), at which

time they comprised up to 3% of the zooplankton (Table 4). At other times they accounted for less than 0.5% of total abundance.

Ctenophores captured included the warm water oceanic species, Beroe ovata and Mnemiopsis sp. These reached extremely high densities from June to August of 1974 and 1975 at both stations, causing the nets to clog and in the process becoming fragmented. It was not possible to quantatively sample these organisms, but populations reached earlier peaks at higher densities at station D5 than A3.

3.3.3 Copepod Biomass

Estimates of total zooplankton and copepod biomass were made by dry weight analyses of unsorted catches and individual copepods, respectively (Table 5). Data for the unsorted catches are difficult to interpert since they included a variety of non-zooplankton organisms and debris. Microscopic observations at station A3 showed that the quantity of debris in the form of papers, twigs and amorphous particles often far outnumbered organisms. At station D5, complications arose during February and March when large quantities of the dinoflagellate Ceratium tripos were captured in the nets, and added greatly to estimates of dry weight. To avoid these problems, the weight of copepods was multiplied by their density to yield estimates of total dry weight (Figs. 11 and 12).

Table 5. Average body weights of copepods at stations A3 and D5 (mg dry weight copepod^{-1}).

	STATION A3		STATION D5	
	Mean	± S.E.	Mean	± S.E.
1975-76				
Spring-Summer (n=13)	0.0086	0.0009	0.010	0.0010
Fall (n=3)	0.0220	0.0090	0.014	0.0028
Winter (n=10)	0.0345	0.0053	0.0274	0.0039
1973-74				
Spring-Summer (n=5)	0.011	0.0013	0.0168	0.0036
Fall (n=3)	0.017	0.0056	0.0280	0.0096
Winter (n=4)	0.0192	0.0009	0.0280	0.0030

Spring-Summer: April to August

Fall: September to November

Winter: December to March

Dry weights of individual copepods at both stations ranged between 0.004 and 0.05 mg. Analysis of variance showed no significant differences between the two stations ($F = 1.46$), however there were significant seasonal variations (Table 5). During April to July, dry weights were lowest and ranged between 0.0086 ± 0.001 and 0.168 ± 0.004. Weights increased slightly in September and November, and were greatest during December to March. Weights during the latter period ranged between 0.019 ± 0.001 to 0.035 ± 0.005 mg.

3.4 Factors affecting copepod abundance and biomass

The effect of temperature was examined with respect to both individual body weights and total abundance of organisms. There was an inverse relationship between temperature and body size (Fig. 15) which was not significantly different between stations. Total abundance of copepods was positively related to temperature in the range of 5° - 23°C (Fig. 16). When temperatures were below 5°C, abundance at both stations was uniformly low, but increased logarithmically as temperature began to rise in the spring. When data were pooled for all months in both 1973 - 1974 and 1975 - 1976, correlation coefficients at stations A3 and D5 are not significantly different during each year. The combined correlations for both stations during 1973 - 1974 and 1975 - 1976 respectively were +0.82 and +0.87.

Figure 15. Correlation between log copepod dry weight (mg copepod^{-1}) and temperature (°C). Data pooled for stations A3 and D5 ($r = 0.71$, $p < 0.01$).

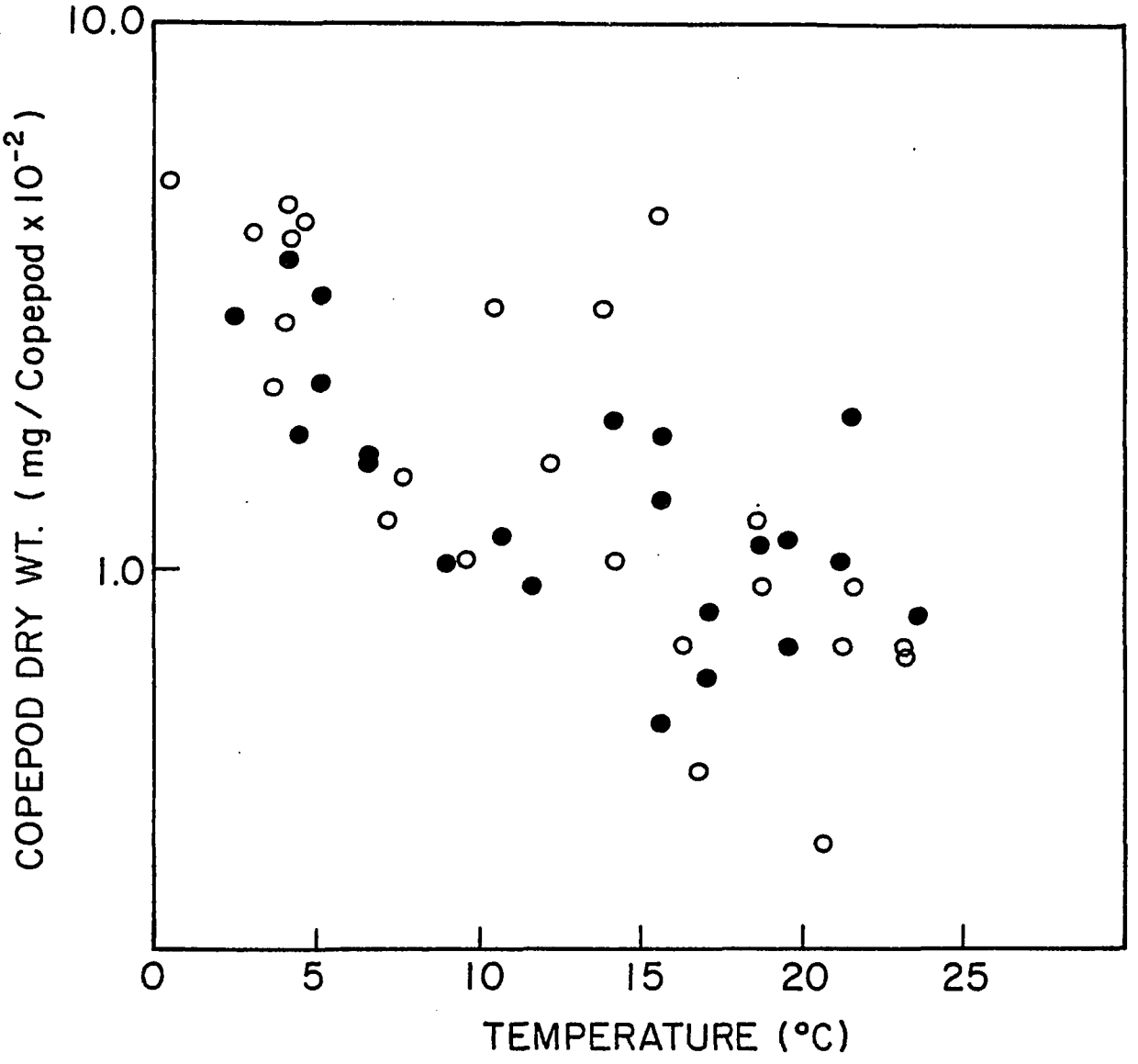
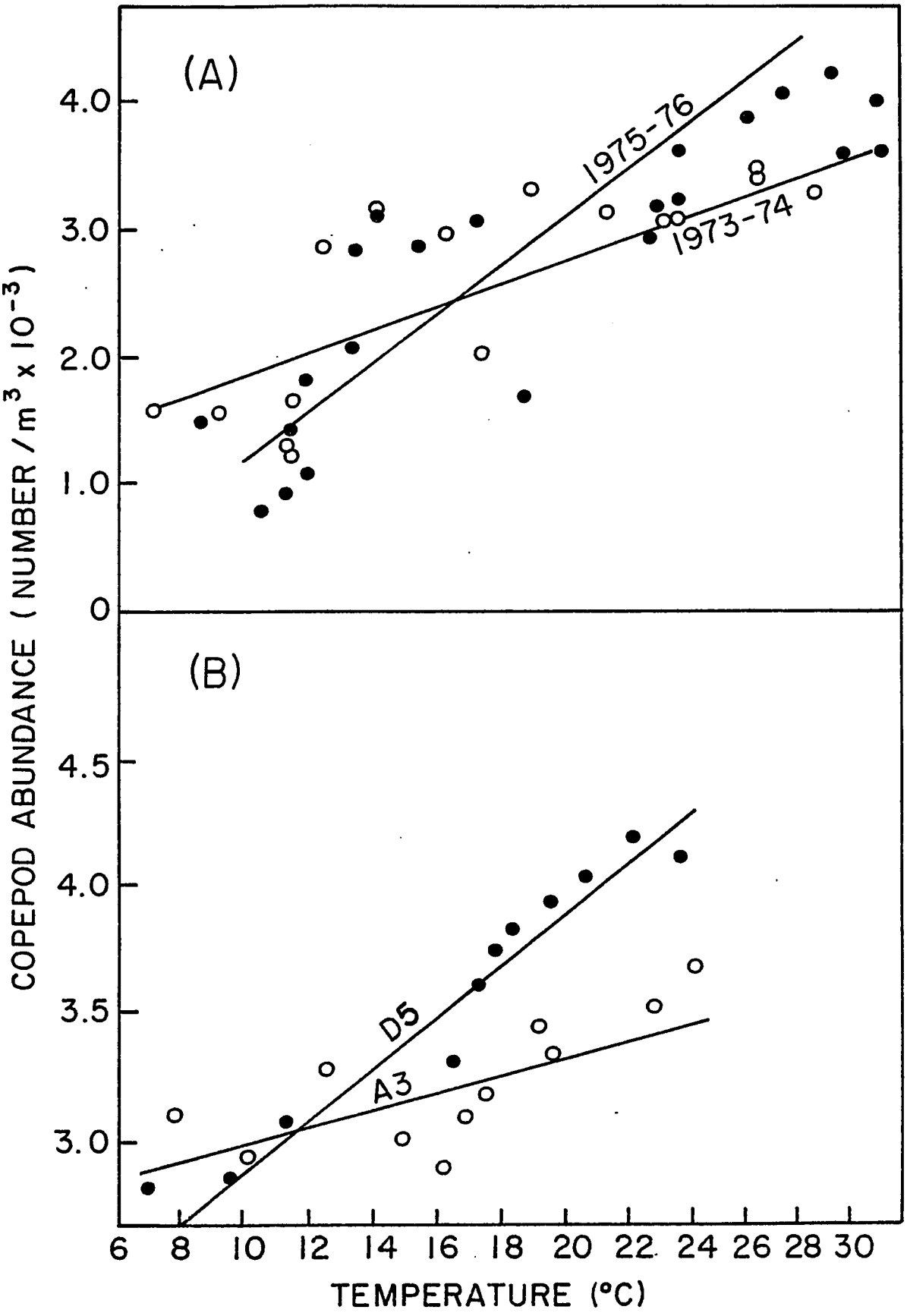

10.0
1.0
COPEPOD DRY WT. (mg / Copepod x 10^{-2})
0
5
10
15
20
25
TEMPERATURE (°C)

Figure 16. Correlations between copepod abundance (number m^{-3}) and temperature (°C) in the range of 5° - 23°C, at station A3 (0) and D5 (●). (A) Data pooled for station A3 and D5 for 1973 - 1974 ($r = 0.82$, $p < 0.01$) and station A3 and D5 for 1975 - 1976 ($r = 0.87$, $p < 0.01$); (B) Data include only spring-summer period pooled for 1973 - 1974 and 1975 - 1976 at station A3 ($r = 0.73$, $p < 0.01$) and D5 ($r = 0.89$, $p < 0.01$).


(A)
1975-76
8
1973-74
8
(B)
D5
A3
COPEPOD ABUNDANCE (NUMBER / m³ x 10⁻³)
TEMPERATURE (°C)
0
1.0
2.0
3.0
4.0
3.0
3.5
4.0
4.5
6
8
10
12
14
16
18
20
22
24
26
28
30

If data for only the period of rapidly increasing temperatures in the spring are considered, there is a significantly smaller slope in the line defining the relationship between temperature and abundance at station A3 ($r = 0.73$, $p < 0.01$) than D5 ($r = 0.89$, $p < 0.01$). At temperatures greater than 23°C, standing crops decreased and were unrelated to temperature.

The extent to which temporal changes in copepod abundance correlates with concurrent changes in pools of suspended particulate food can be used to infer information on the nature and extent of food utilized, and the interactions between phytoplankton and zooplankton. It was assumed that conditions at station A3 were representative of the estuarine area, but since copepod densities at station D5 probably reflect interactions over the larger area of the apex, and such information on concentrations of particulates is available, copepod densities at station D5 were compared to values of particulates averaged from stations C3, C5, D3 and D5.

In both the estuary and the apex, peaks in phytoplankton chlorophyll a decreased in amplitude during the spring and summer, while both growth rates of phytoplankton and copepod abundance increased (Figs. 17 and 18) (Malone, 1976a). The absence of a correlation between phytoplankton biomass and chlorophyll a specific carbon production increases, coupled with

Figure 17. Annual variations in mean photic zone chlorophyll *a* (mg m^{-3}) and copepods (number m^{-3}) at station A3. (*) indicates sampling dates in 1973 - 1974, all other dates are 1975 - 1976.

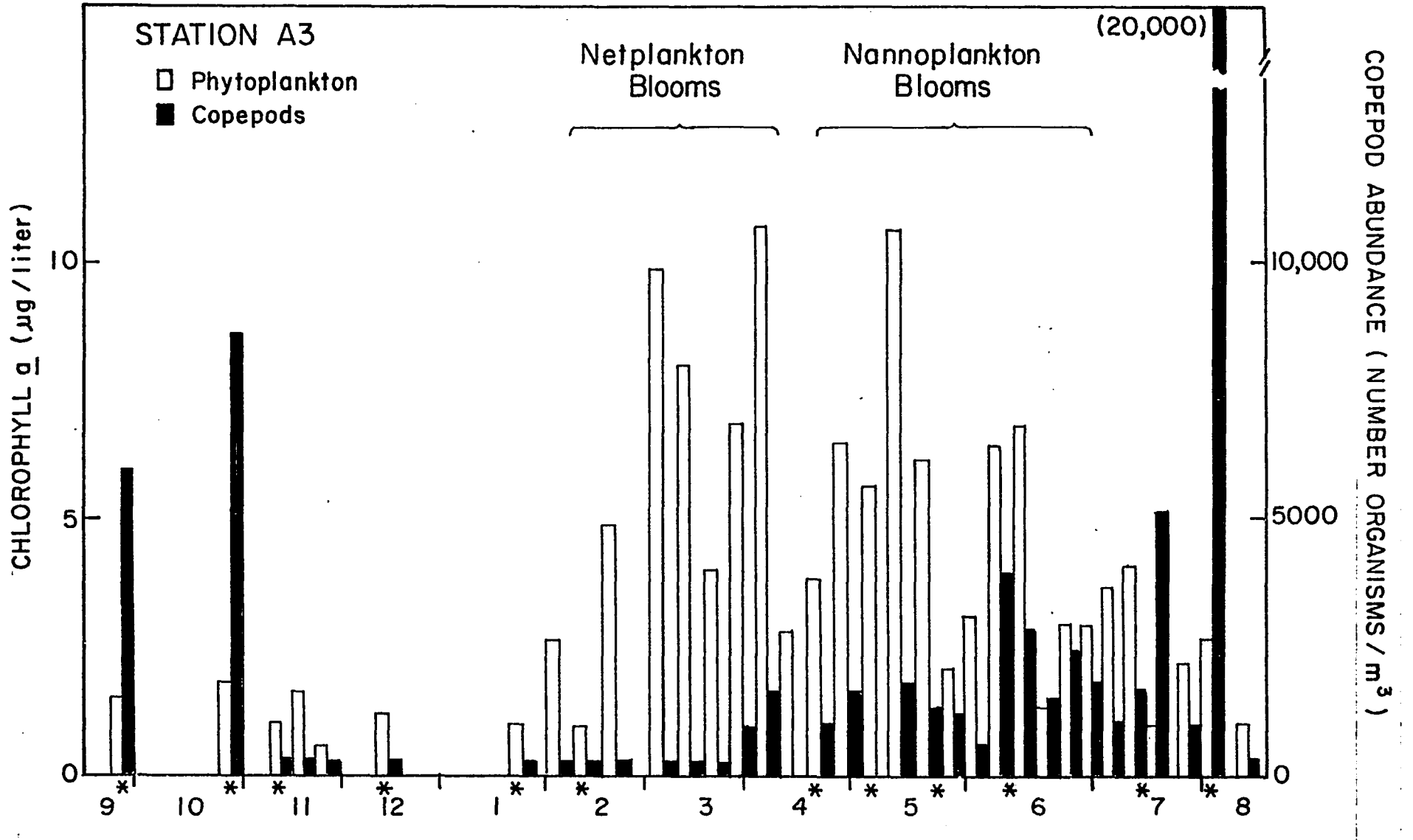
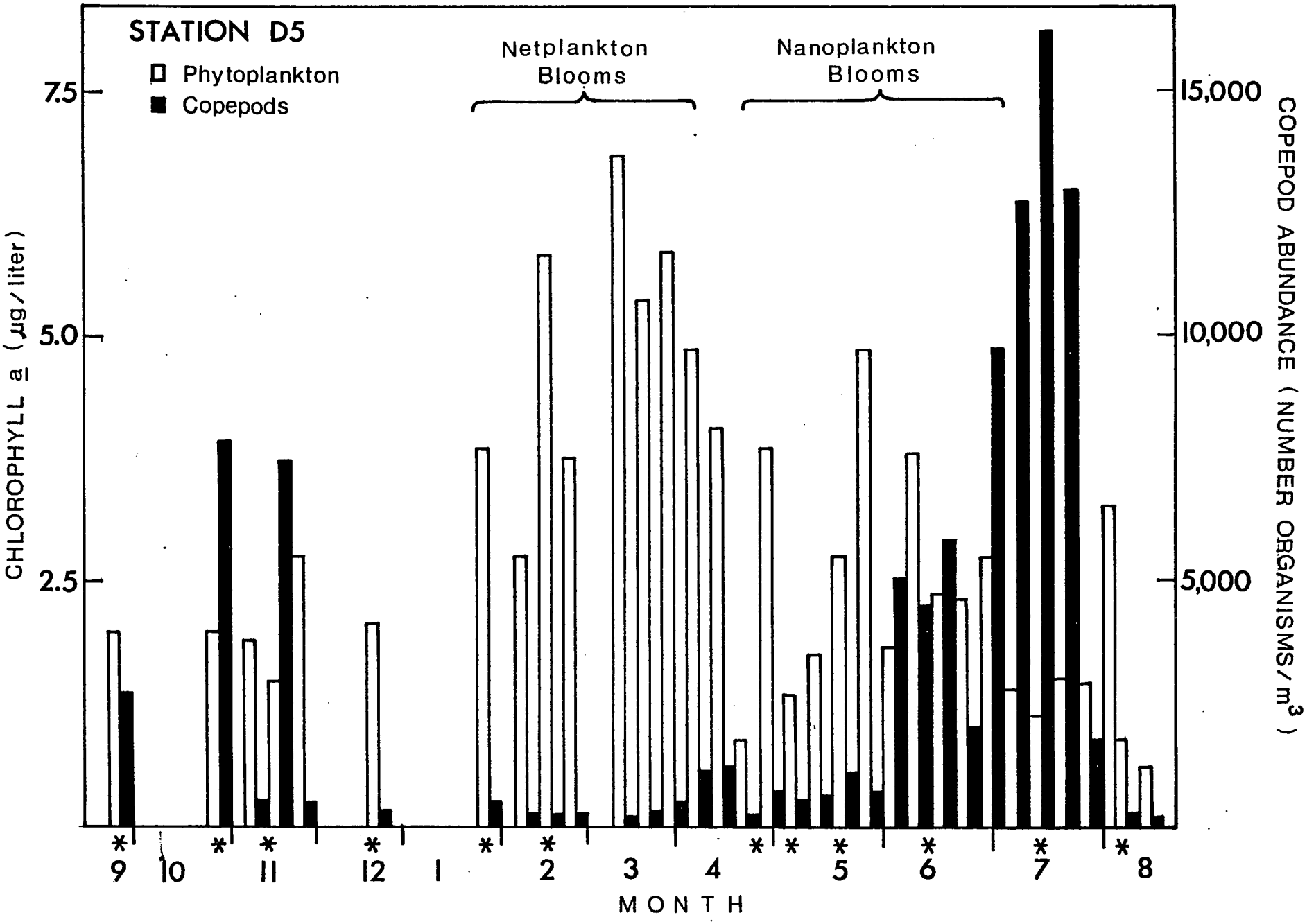

STATION A3
Phytoplankton
Copepods
Netplankton Blooms
Nannoplankton Blooms
(20,000)
CHLOROPHYLL a (µg / liter)
COPEPOD ABUNDANCE (NUMBER ORGANISMS / m³)
10
5
0
10,000
5000
0
9
10
11
12
1
2
3
4
5
6
7
8

Figure 18. Annual variations in mean photic zone chlorophyll a (mg m^{-3}) and copepods (number m^{-3}) at station D5. (*) indicates sampling dates in 1973 - 1974, all other dates are 1975 - 1976.


STATION D5
Phytoplankton
Copepods
Netplankton Blooms
Nanoplankton Blooms
7.5
5.0
2.5
15,000
10,000
5,000
CHLOROPHYLL a (µg/liter)
COPEPOD ABUNDANCE (NUMBER ORGANISMS/m3)
9
10
11
12
1
2
3
4
5
6
7
8
MONTH

increases in copepod abundances, suggest grazing pressure as an important factor in limiting phytoplankton standing crop during the late spring and summer.

Increases in the amplitude of peaks in phytoplankton occurring during the winter, even though of greater magnitude than spring-summer blooms, were not followed by a corresponding increase in copepod abundance. Densities of copepods did increase slightly in late May and April, but increases were less than one tenth the magnitude of those occurring in the spring-summer period. The fall copepod increases (1973) did not correspond to any observed increases in phytoplankton.

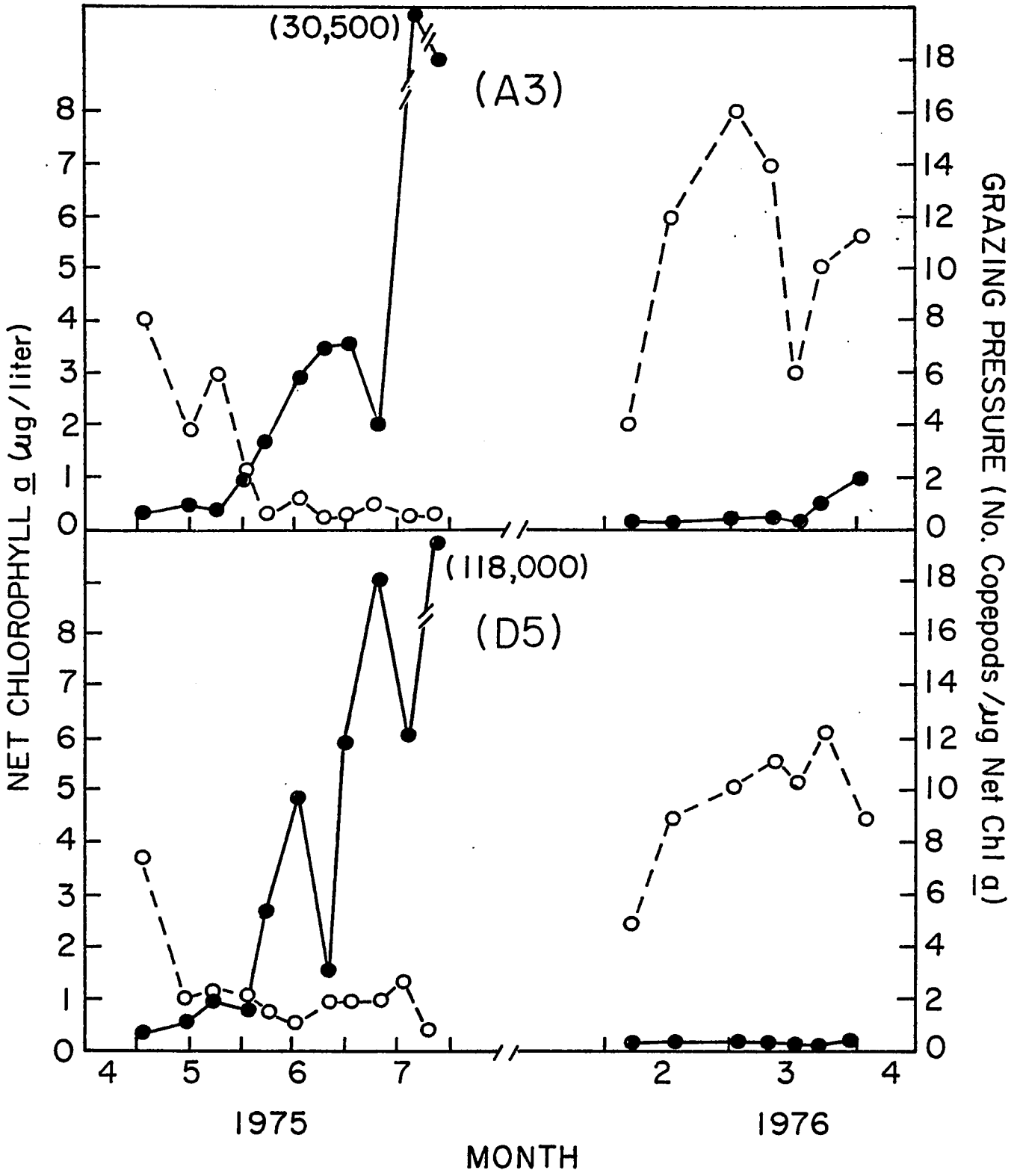
Temporal changes in phytoplankton-zooplankton peaks were similar in both the estuary and the apex, however the magnitude of phytoplankton peaks were greatest in the estuary and inner apex (stations C2, C3, C4, D2, D3 and D4), while peaks of copepods were greatest in the apex (stations C5 and D5) (Malone, 1976a). This spatial pattern might represent a "downstream effect" such as seen in upwelling areas by Strickland (1969). The longer developmental time of copepods coupled with the net seaward flow of water, results in the spatial separation of centers of maximum density of copepods and phytoplankton.

The coupling between zooplankton and phytoplankton appeared to be different for the two size classes of phytoplankton. There was an inverse relationship between temporal changes in grazing pressure, as estimated by the ratio of copepods to chlorophyll a, and the proportion of total chlorophyll a composed of net-chlorophyll a (Fig. 19). During times when copepods were most abundant, and presumably exerted the greatest grazing pressure, nanoplankton dominated the phytoplankton. When copepod populations were severely reduced in the winter, netplankton dominated the phytoplankton.

The interactions of copepods and food in the form of total POC or detritus was more difficult to define from field data. There were no obvious correlations between either of these pools of particulates and standing crops of copepods at either station. Only when concentrations of POC fell below 0.6 mgC l^{-1} was there a positive correlation between log copepod abundance and POC ($r = 0.70$, $p < 0.01$). Concentrations rarely fell this low in the estuary, suggesting that food may have been limiting to copepod growth at times in the apex, but not the estuary.

In both areas, the response of copepods to food in the form of phytoplankton carbon fell into three approximate

Figure 19. Annual variations in mean photic zone net-chlorophyll *a* (mg m^{-3}) (0) and grazing pressure (●), estimated as number of copepods m^{-3}/net chl *a* (mg m^{-3}), at stations A3 and D5.


(30,500)
(A3)
(118,000)
(D5)
NET CHLOROPHYLL a (µg/liter)
GRAZING PRESSURE (No. Copepods/µg Net Chl a)
MONTH
1975
1976
4
5
6
7
2
3
4
0
1
2
3
4
5
6
7
8
0
2
4
6
8
10
12
14
16
18

groups, defined by lines of increasing slope (Fig. 20). During the winter when temperatures were below 7°C and phytoplankton biomass was high (0.1 - 0.65 $\mu gC\ l^{-1}$), the slope was nearly zero, indicating the independence of the two variables. As temperatures increased in the spring over the range of 8° - 19°C with phytoplankton biomass still high (0.1 - 7.5 $\mu gC\ l^{-1}$), the increasing response of copepods is seen in an increase in slope. When temperatures reached greater than 19°C (19° - 23°C) phytoplankton biomass was reduced to less than 0.4 $\mu gC\ l^{-1}$, and there was a sharp increase in slope.

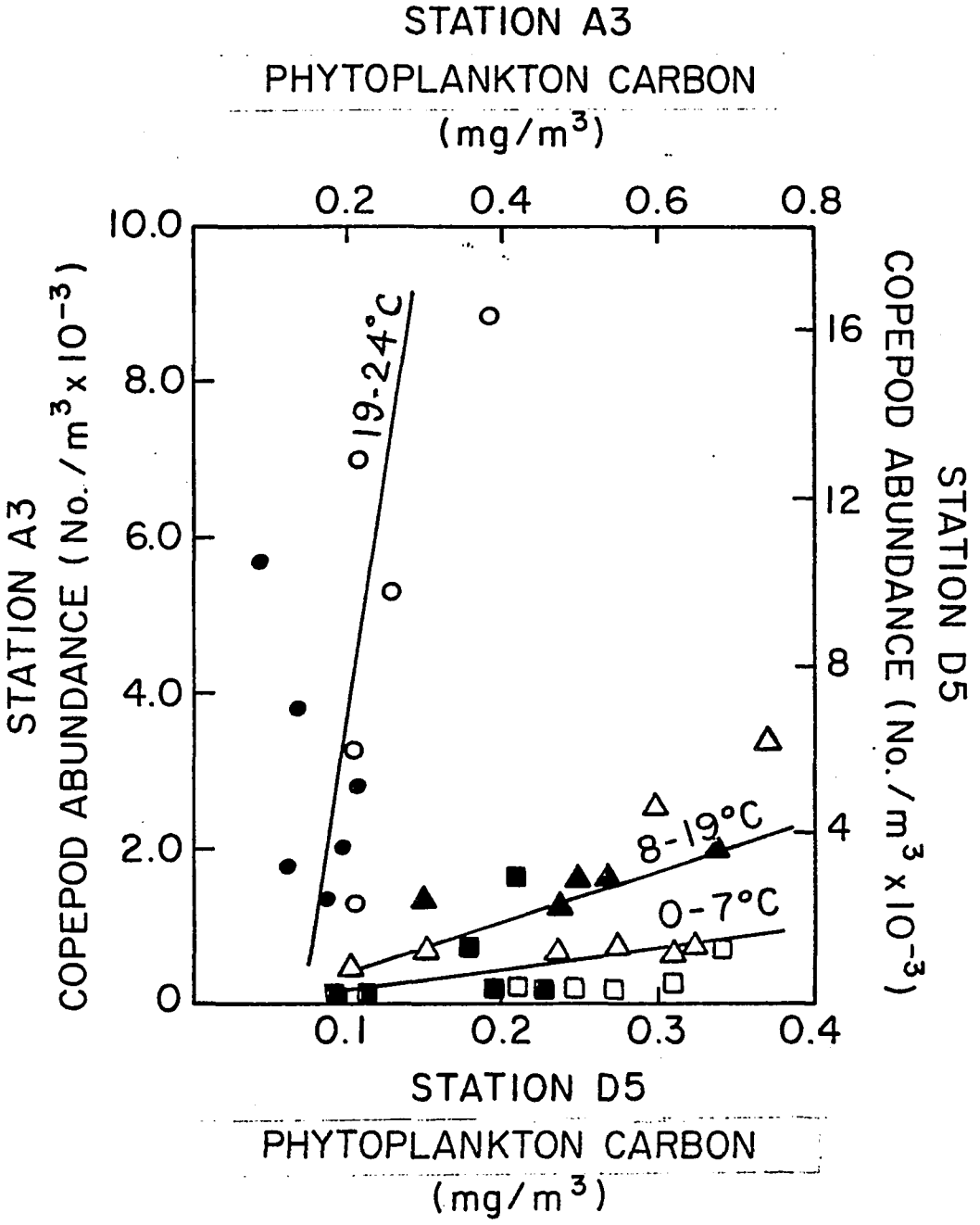
4.0 DISCUSSION AND CONCLUSIONS

4.1 Suspended Particulates

Concentrations of POC were quite variable in the estuary and at times accumulated to extremely high levels as compared to the apex where concentrations were usually at a lower and relatively constant level. The only time POC accumulated in the water column in the apex was during February and March of 1976. The normally rapid dilution and turnover of POC in the apex was related to dilution and advection from the system, sinking from the water column or uptake by grazers.

Peaks in concentrations of POC in both areas occurred

Figure 20. Copepod abundance (number m^{-3}) as a function of phytoplankton carbon (mg l^{-1}) when temperatures were in the range of; 0 - 7°C at station A3 (□) and D5 (■); 8 - 19°C at station A3 (△) and D5 (▲); 19 - 24°C at station A3 (○) and D5 (●).


STATION A3
PHYTOPLANKTON CARBON
(mg/m³)
0.2
0.4
0.6
0.8
10.0
8.0
6.0
4.0
2.0
0
STATION A3
COPEPOD ABUNDANCE (No./m³ x 10⁻³)
19-24°C
8-19°C
0-7°C
16
12
8
4
STATION D5
COPEPOD ABUNDANCE (No./m³ x 10⁻³)
0.1
0.2
0.3
0.4
STATION D5
PHYTOPLANKTON CARBON
(mg/m³)

in the summer and winter with increases in the apex following those in the estuary by 2 - 3 weeks. Two of the major sources of this material were phytoplankton productivity and organic loads transported by estuarine and river runoff. The estuarine source of some of this material is suggested by (1) temporal correlations between peaks in POC in the estuary and high river flow, and a time lag between these peaks and those in the bight. This lag was presumably due to the time necessary to transport patriculates out of the estuary, and (2) the inverse spatial relationship between POC concentrations and surface salinities (Malone, 1976a). These observations can also be interpreted as indicative of the response of phytoplankton to estuarine nutrient enrichment. It has been found that increases in POC were frequently a consequence of increases in phytoplankton biomass.

Water column POC in February and March of 1976 increased to levels not observed prior to 1976. This was due to the bloom of C. tripos which appeared in January and reached maximum concentrations in March (Malone, unpublished). This species was apparently not heavily grazed upon, and so accumulated in the water column. If the contribution of this species to total POC is subtracted, values decline to levels found in the previous year (Malone, 1976b).

4.2 Factors Affecting Copepod Abundance and Biomass

Seasonal patterns of copepod abundance were similar to those

in the summer and winter with increases in the apex following those in the estuary by 2 - 3 weeks. Two of the major sources of this material were phytoplankton productivity and organic loads transported by estuarine and river runoff. The estuarine source of some of this material is suggested by (1) temporal correlations between peaks in POC in the estuary and high river flow, and a time lag between these peaks and those in the bight. This lag was presumably due to the time necessary to transport particulates out of the estuary, and (2) the inverse spatial relationship between POC concentrations and surface salinities (Malone, 1976a). These observations can also be interpreted as indicative of the response of phytoplankton to estuarine nutrient enrichment. It has been found that increases in POC were frequently a consequence of increases in phytoplankton biomass.

Water column POC in February and March of 1976 increased to levels not observed prior to 1976. This was due to the bloom of C. tripos which appeared in January and reached maximum concentrations in March (Malone, unpublished). This species was apparently not heavily grazed upon, and so accumulated in the water column. If the contribution of this species to total POC is subtracted, values decline to levels found in the previous year (Malone, 1976b).

4.2 Factors Affecting Copepod Abundance and Biomass

Seasonal patterns of copepod abundance were similar to those

observed by Deevy (1942), Jeffries (1962) and Raymont (1952) in nearby temperate coastal areas. There were characteristically two peaks in abundance, in late spring-summer and fall, with extremely low abundances during the winter. This cycle can be attributed to breeding and growth patterns of copepods, and seasonal variations in predation and advection of migrants from adjacent coastal and river waters.

While no quantitative estimates of predation on copepods were made in this study, its importance during the late summer has been noted here and in other nearby areas (Deevy, 1952; Martin, 1968). The influx of swarms of warm water oceanic ctenophores at this time is correlated with a sharp decrease in copepod populations. Predation may well cause the demise of spring copepod blooms. At the onset of colder temperatures in September, these warm water predators disappeared and copepods again increased in abundance.

The influx of offshore organisms is most apparent in the fall when surface salinity is highest. The increases in total abundance occurring at this time are due to both copepod breeding and probably to advection. This process has been well documented by Austin and Dickinson (1973), Gibson (1973), Deevy (1952) and Grice and Hart (1962).

Breeding of dominant copepods in this region has been shown to occur in the late spring and early summer (Oithona

similis and Acartia tonsa) and early fall (Paracalanus) (Martin, 1972; Gibson, 1973). These breeding periods correspond to periods of maximum observed abundance in this study. The frequency of breeding, the number of animals per brood and growth rates have been shown to be related to temperature and food (Mullin and Brooks, 1970; Frost, 1972).

Seasonal variability in body size of copepods has been attributed to the effects of both temperature and food supply during growth (Mullin and Brooks, 1970). In this study there was a negative correlation between copepod dry weight and temperature. Similarly, Deevy (1960, 1964) found that the cephalothorax length of adult copepods is nevatively correlated with temperatures during development. This was only true for copepods that were exposed to large annual variations in temperature. McLaren (1965) concluded that while temperature and food are usually not independent in nature, it was temperature that was directly responsible for variations in body weight. He found that at low temperatures, development proceeded more slowly, resulting in a higher final weight for any individual stage. Contrary to these studies, Mullin and Brooks (1970) concluded that temperature had little effect on the body weight of Calanus pacificus.

The observed variations in body weights could be due to the direct effect of temperature on body size, or indirectly, by selecting for smaller copepod species. Other factors affecting body weight could be the seasonal variations in reproductive stages or size selective predation.

The positive relationship between temperature and copepod abundance may reflect the direct effects of temperature on rates of reproduction growth or the indirect effect of temperature on food sources. The effect of temperature on reproduction has been reviewed by Kinne (1976), and has been shown to influence the time of onset of reproduction, the number of broods produced and rates of development. Copepods indigenous to the apex-estuarine area (Oithona similis, Paracalanus parvus and Acartia tonsa) have been shown not to breed during the cold winter months. Conover (1956) suggested that copepods in Long Island Sound may have some sort of resting stage in which they overwinter.

The effects of low temperature have also been found to inhibit the feeding of coastal copepods. Anraku (1964) and Martin (1968) both found that the filtering rates of copepods was severely depressed by temperature below 5°C.

As temperatures warmed in the spring, the onset of reproduction and increased rates of feeding and growth

would result in the observed copepod blooms. The decreases in copepod populations that occurred during the late summer, were probably related to the effects of predation since concentrations of food were still quite high.

Increases in standing crops of copepods during the spring period of rising temperatures were not as rapid in the estuary as they were in the apex. The apparent limitation of copepods in the estuary may have been due to differences in growth or reproductive patterns of indigenous species or a relatively high rate of copepod biomass removal. Given the high salinity tolerances of estuarine species and the high concentrations of POC, it is likely that low copepod biomass in the estuary relative to the apex was due to advection of organisms out of the estuary (Malone, 1976b). This is supported by the observation that high densities of organisms usually occurred at station A3 when river runoff was minimal.

Temperature may have affected abundance of copepods indirectly via its effect on the quantity and quality of food. Seasonal variations in temperature are commonly found to affect both productivity and onset of phytoplankton blooms. In the estuarine-apex region, Malone (1976a) showed that

temperature was a selective factor that differentially influenced the growth of net- and nanoplankton.

The inverse temporal and spatial relationship between peaks in standing crops of phytoplankton and zooplankton during the spring-summer blooms suggests that a good deal of phytoplankton productivity occurring at this time enters copepod food chains. Conversely, during the winter period the demise of the winter phytoplankton bloom in spite of an absence of synoptic increases in grazers, suggests that little of the winter primary productivity enters copepod food chains.

The fall peak in copepods did not seem to be related to increases in phytoplankton and may have been the result of increased copepod production after the demise of predaceous ctenophores, and/or the result of advection of offshore copepods into the area. This latter hypothesis is supported by a number of observations. (1) Increases in copepod density occurred in conjunction with increases in surface salinity. (2) Stenohaline species were present in association with offshore water. (3) During October

and November of 1975, anomalously high river runoff and strong southerly winds were reflected in lowered surface salinities and the absence of offshore species, and increases in copepod abundance.

The relationship between phytoplankton and zooplankton can be further elucidated by examining the impact of copepod grazers on different size classes of phytoplankton cells. The inverse relationship between copepod biomass and net-chlorophyll _a_ indicates that copepods may be selectively removing net-phytoplankton. During periods of highest copepod density (the spring and summer) both the concentration of net chlorophyll _a_ and its proportion of total chlorophyll _a_ were minimal. During the winter, when copepod densities were extremely low, netplankton dominated the phytoplankton and increased sharply in biomass.

Temporal variability in such selective grazing pressures would have a significant effect on the species composition of phytoplankton communities. If grazing pressure by copepods limits netplankton populations, the decrease in grazing that occurred during the winter should result in an increase in netplankton biomass. In fact, netplankton blooms that occurred during the winter have been shown not to be a function of increased phytoplankton growth rates (Malone, 1976a),

but to an accumulation of phytoplankton biomass.

While both absolute concentrations and dominance of netplankton were greater in the apex than the estuary, the differences were not associated with spatial differences in grazing pressure but rather was due to the selective effect of water movements. It has been observed that increased upwelling velocities in Peru upwelling systems (Strickland et al., 1969) or high flushing rates (Dickman, 1961) select for small cell size. Similarly, Malone (1976b) found that larger (netplankton) cells can not maintain themselves in the Hudson River Estuary, in face of prevailing flushing rates, resulting in a predominance of nanoplankton in the bay.

The general lack of a relationship between temporal variability of POC (and detritus) and copepod abundance suggests the following: (1) The rates of removal of particulates by copepods is not sufficient to result in observable decreases in water column concentrations. In the estuarine-apex area, where rates of input of detritus via river runoff, dumping and in situ production are extremely high, it is quite possible that grazing would not significantly affect the biomass of particulates. (2) Food is not limiting to copepods, so that increases in concentrations of carbon would not result in

increases in copepod communities. Observed concentrations of POC are extremely high, especially in the estuary, and approach the maximum feeding threshold of copepods (Adams and Steele, 1966). Biomass of copepods in this region may thus be largely limited by factors other than food.

The differential response of copepods in terms of increased biomass of copepods to winter and spring phytoplankton blooms seems to be mediated by the effects of temperature. During the spring when temperatures are high and phytoplankton populations are increasing, conditions were favorable for the rapid development of large copepod populations.

It is likely that netplankton production during the winter (February - March) had little affect on copepod abundance during February and March. Low copepod abundances at this time were probably due to the effects of low temperature on metabolism, breeding and growth. It is also likely that netplankton blooms during the winter are, at least in part, the consequence of low grazing pressure.

PART II. FEEDING EXPERIMENTS

5.0 RESULTS

5.1 Carbon specific assimilation rates

Feeding experiments were conducted during periods of

netplankton and nanoplankton dominance over a temperature range of 3° - 20°C. During all experiments, concentrations of particulates available in incubation bottles were greater at station A3 than D5 (Table 6).

The species of copepods present at both stations, and subsequently used in feeding experiments, were generally common to both stations A3 and D5 and included Acartia tonsa, A. Clausi, Acartia species unknown, Eurytemora americana, Temora longicornis, Centropages typicus, C. hamatus, Pseudocalanus minutus and Oithona similis (Appendix III and IV). The relative abundances of these species was different at the two stations, with a tendancy for the more oceanic species to be prevalant at station D5, and the estuarine species at station A3 (Appendix III and IV).

At station A3 species of the genera Acartia were the dominant species, composing up to 94.6% of total copepods. Acartia was only absent in February when it was replaced by E. americana. At station D5, Acartia was dominant only in November. During June and July, T. longicornis, O. similis, and C. typicus dominated, while during February and March O. similis and P. minutus dominated copepod communities.

Table 6. Summary of experimental conditions at the start of feeding experiments.

	Date	Temp °C	Live-C[1] (mg/l)	Phytoplankton-C[2] (mg/l)	Detrital-C (mg/l)	Total-C (mg/l)	% Detritus
STATION A3							
	5/13	13.0	0.18	0.53	1.00	1.18	85
	6/8	19.2	0.37	0.62	0.49	0.86	57
	6/18	19.5	0.39	0.19	0.27	0.66	40
	6/24	19.8	0.55	0.19	0.26	0.83	32
	7/10	20.5	0.09	0.51	0.23	0.77	88
	11/22	14.1	0.05	0.06	0.63	0.73	93
	11/24	11.1	0.08	0.04	0.68	0.76	90
	2/21	3.6	0.57	0.47	1.29	1.25	70
	3/31	7.5	0.11	0.02	1.02	1.13	91
STATION D5							
	5/13	12.0	0.11	0.08	0.10	0.20	50
	6/8	19.0	0.13	0.08	0.30	0.43	70
	6/18	19.5	0.11	0.16	0.33	0.44	75
	6/24	21.0	0.28	0.06	0.24	0.52	46
	7/10						
	11/12	14.6	0.18	0.09	0.07	0.25	28
	11/24	12.2	0.06	0.15	0.28	0.34	82
	2/21	4.0	0.31	0.26	0.19	0.51	38
	3/31	7.3	0.09	0.10	0.08	0.84	90

1. Live-C calculated from the ratio of C:ATP of 250.

2. C: chlorophyll *a* ratio of 72 used from 5/13 - 11/24, 46 used from 2/21 - 3/31.

Rates of total carbon specific assimilation at station A3 ranged from 0.03 to 1.56 day^{-1}. Rates of assimilation increased from May to a maximum of 1.56 day^{-1} in late June. Rates were lower in November and decreased to a minimum in March. While temporal patterns at station D5 paralleled those at station A3, rates were less variable and ranged from 0.06 to 0.43 day^{-1} (Table 8).

Estimates of live and phytoplankton carbon assimilated calculated from ATP and chlorophyll a showed fairly good correspondence ($r = +0.78$). The regression of chlorophyll-C on ATP-C had an x-intercept not significantly different from zero and a slope not significantly different than 1 ($p < 0.01$), indicating that most of the living carbon assimilated was attributable to phytoplankton.

Greatest deviations between the two estimates of living matter were found during May and June at both stations. At these times, estimates of phytoplankton carbon obtained from the ratio of C:Chl a yielded values more than twice that of total live carbon obtained from the ratio of C:ATP. During May and June, estimates of assimilated phytoplankton-C accounted for more than the total loss of carbon during incubation. On these occasions estimates of phytoplankton-C did not overestimate total carbon present in incubation

Table 7. Dominant species of copepods at stations A3 and D5 from May 1975 to March 1976. Lists include the smallest number of species necessary to obtain a cummulative total of 75% of copepods. and include only dates on which feeding experiments were performed.

	STATION A3		STATION D5	
Date	Species	Cummulative %	Species	Cummulative %
5/13/75	Eurytemora americana	36.6	Pseudocalanus minutus	47.4
	Acartia clausi	68.9	Temora longicornis	92.3
	Harpacticold spp.	92.1		
6/6/75	Acartia tonsa	67.5	Oithona similis	63.0
	T. longicornis	76.6	Temora spp.	89.7
6/18/75	Acartia sp. A*	44.7	Centropages spp.	
	A. clausi	66.6	(hamatus & typicus)	37.5
	A. tonsa	86.7	O. similis	69.8
			T. longicornis	99.4
6/24/75	Acartia sp. A	83.9	T. longicornis	65.4
			C. typicus	79.7
7/11/75	Acartia sp. A	43.2	T. longicornis	48.3
	A. clausii	81.0	C. typicus	70.7
			O. similis	86.9
11/12/75	A. tonsa	94.6	A. clausi	53.4
			Acartia copepodites	83.0
11/24/75	A. clausi	49.4	A. clausi	40.6
	A. tonsa	80.7	C. typicus	56.5
			A. tonsa	72.1
			O. similis	86.2
2/21/76	E. americana	70.6	O. similis	71.6
	O. similis	90.6	P. minutus	92.5
3/31/76	A. tonsa	38.9	O. similis	44.7
	E. americana	60.3	Calanus sp.	65.8
	T. longicornis	77.0	Oithona sp.	78.9

* Unidentified species of Acartia.

bottles at the start of the experiment, but did at the conclusion. This might be due to a shift in the ratio of C:Chl a in experimental bottles which resulted from selective grazing or a change in the chemical composition of the algae population during the incubation. Since many species of algae synthesize chlorophyll a in the dark, it is possible that the C:Chl a ratio at the end of the incubation was lower than at the beginning. Similarly, shifts in the C:Chl a ratio would result if Chl a degradation was not proportional to phytoplankton carbon uptake.

Sporadically throughout the year ATP-C exceeded chlorophyll-C assimilated by 10% - 50%. This could be due to the differential rates of degradation of ATP and chlorophyll in the gut of the copepod, or the assimilation of live organisms other than phytoplankton, specifically bacteria adhering to detritus or microzooplankton.

Since detritus assimilation was estimated as the difference between total carbon assimilated and live carbon assimilated, and since the ratio of ATP was considered to be the most reliable estimator of total live biomass, the ratio of C:ATP was used throughout this section for all calculations of detrital assimilation.

Assimilation of live carbon at station A3 ranged from a low of 0.02 day^{-1} in March to a maximum of 1.24 day^{-1} in late June (Table 8). Most of the seasonal variability in assimilation of total carbon was due to the variability in assimilation of live carbon The proportion of total carbon assimilated that was live ranged from 44% - 74%.

Assimilation of live carbon at station D5 ranged from a minimum of 0.01 in March to a maximum of 0.20 day^{-1} in late June. During May and June, live carbon accounted for less than 24% of total carbon assimilated (17% - 22%), rising to greater than 45% (45% - 69%), in August through February.

During May through June the quantity of live carbon assimilation and its proportion of total assimilation were generally 2 to 5 times greater at station A3 than D5. In November and February, rates of assimilation of live carbon were comparable at the two stations.

Assimilation of detrital carbon at station A3 ranged from a maximum of 0.32 in late June to a minimum of 0.01 day^{-1} in February. Temporal variability, as indicated by the ratio of maximum/minimum observed rates, was 30, as opposed to 60 for live-carbon assimilated. Detritus accounted for 26% - 56% of total carbon assimilated.

Assimilation of detrital carbon at station D5 ranged from 0.35 in early June to 0.03 day^{-1} in February. The

Table 8. Summary of rates of assimilation, respiration and growth during all feeding experiments at stations A3 and D5. Each value represents mean of 3 replicates ± S.E.[1] expressed as µgC/µg Copepod-C/day. [2]

	ASSIMILATION					RESPIRATION	GROWTH
Date	Live-C	Phyto-C	Detrital-C	Total-C	% Detritus		
STATION A3							
5/13	0.06±0.01	0.35±0.02	0.04±0.02	0.11±0.04	40	0.05±0.005	0.06
6/8	0.21±0.04	0.14±0.03	0.04±0.03	0.24±0.03	42	0.11±0.003	0.13
6/18	0.34±0.02	0.59±0.03	0.18±0.01	0.52±0.005	46	0.26±0.002	0.27
6/24	1.24±0.02	1.15±0.02	0.32±0.01	1.56±0.20	26	0.56±0.003	1.00
7/10	0.25±0.03	0.20±0.01	0.14±0.006	0.39±0.03	34	0.19±0.004	0.20
11/12	0.07±0.008	0.05±0.02	0.05±0.01	0.13±0.02	39	0.03±0.001	0.09
11/24	0.16±0.02	0.01±0.007	0.13±0.02	0.29±0.03	44	0.09±0.004	0.19
2/21	0.02±0.005	0.02±0.008	0.01±0.004	0.03±0.006	30	0.01±0.003	0.17
3/31	0.03±0.004	0.03±0.004	0.05±0.01	0.08±0.02	56	0.05±0.002	0.03
STATION D5							
5/13	0.07±0.01	0.13±0.03	0.14±0.02	0.17±0.02	78	0.13±0.002	0.04
6/8	0.08±0.02	0.08±0.02	0.35±0.02	0.43±0.02	83	0.39±0.004	0.04
6/18	0.06±0.01	0.05±0.005	0.26±0.01	0.34±0.005	81	0.30±0.006	0.03
6/24	0.20±0.03	0.31±0.04	0.21±0.02	0.41±0.01	52	0.21±0.005	0.20
7/10							
11/12	0.12±0.04	0.13±0.02	0.06±0.03	0.18±0.008	31	0.09±0.006	0.09
11/24	0.17±0.04	0.16±0.04	0.13±0.03	0.30±0.007	42	0.11±0.004	0.19
2/21	0.03±0.01	0.19±0.02	0.03±0.01	0.06±0.01	52	0.03±0.008	0.02
3/31	0.01±0.009	0.01±0.005	0.06±0.02	0.07±0.02	80	0.03±0.006	0.02

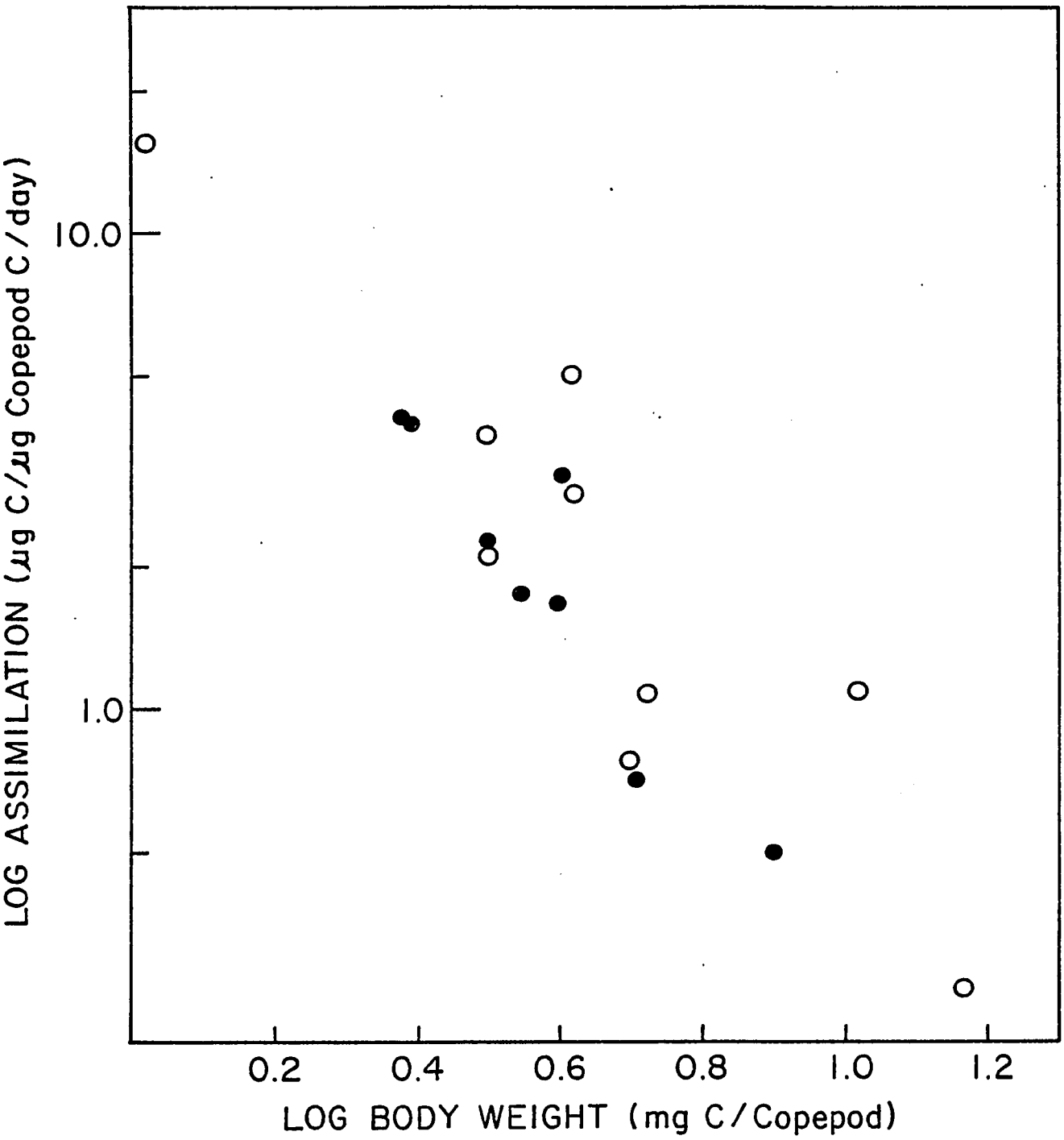
1. Standard error (S.E.)
2. Copepods carbon calculated as 40% of dry weight (Beers, 1966).

ratio between maximum and minimum rates in both cases was 12. Detritus accounted for greater than 50% (52% - 83%) of total carbon assimilated on all dates except in November when it accounted for only 31% - 42%.

Rates of utilization of detritus and its proportion of total dietary carbon during May through June, were generally higher at station D5, in spite of general lower concentrations of available detritus. Differences in utilization of detritus at the two stations were much less pronounced during November through March.

Rates of carbon specific assimilation of total carbon were found to be inversely related to body weight (Fig. 21). The correlation was not significantly different at the two stations, so all data were pooled to yield a combined correlation coefficient of -0.86 ($p < 0.01$). While larger organisms had higher total rates of assimilation per individual, smaller organisms had a higher rate of assimilation per unit body weight.

Figure 21. Correlation between log assimilation (µgC/µgCopepod-C/day) and log dry weight of copepods (mg). Data pooled for stations A3 (O) and D5 (●), ($r = -0.88$, $p < 0.01$).


LOG ASSIMILATION (µg C/µg Copepod C/day)
10.0
1.0
0.2
0.4
0.6
0.8
1.0
1.2
LOG BODY WEIGHT (mg C/Copepod)

Assimilation rates were positively related to temperature (Fig. 22). In the range of 5 - 23°C, assimilation rates at both stations increased exponentially with increasing temperatures. The relationship was not different at the two stations, and pooled data yielded a correlation coefficient of +0.86 ($p < 0.01$).

The correlations between assimilation and POC were different at the two stations (Fig. 23). At station D5, where concentrations of POC ranged between 0.2 to 0.8 mgC l^{-1}, there was a positive correlation ($r = +0.70$, $p < 0.05$). At station A3, where concentrations ranged between 0.7 - 1.28 mgC l^{-1}, there was a negative correlation ($r = -0.82$, $p < 0.01$). The intersection of lines fitted to the data by regression occurs at 0.63 mgC l^{-1}. Since ranges of POC at the two stations are essentially non-overlapping, it is unclear if there are functionally different types of responses at the two stations (as described by two line of opposite slopes), or if it is a response to increasing concentrations of POC that would occur at either station. That is, perhaps a better hypothetical curve would be one that increased linearly up to some threshold concentration between 0.4 and 0.6 mgC l^{-1}, remained constant over the range of 0.6 to 0.9 mgC l^{-1},

Figure 22. Correlation between log assimilation (µgC/µgCopepod-C/day) and temperature. Data pooled for stations A3 (O) and D5 (●). ($r = +0.86$, $p < 0.01$).

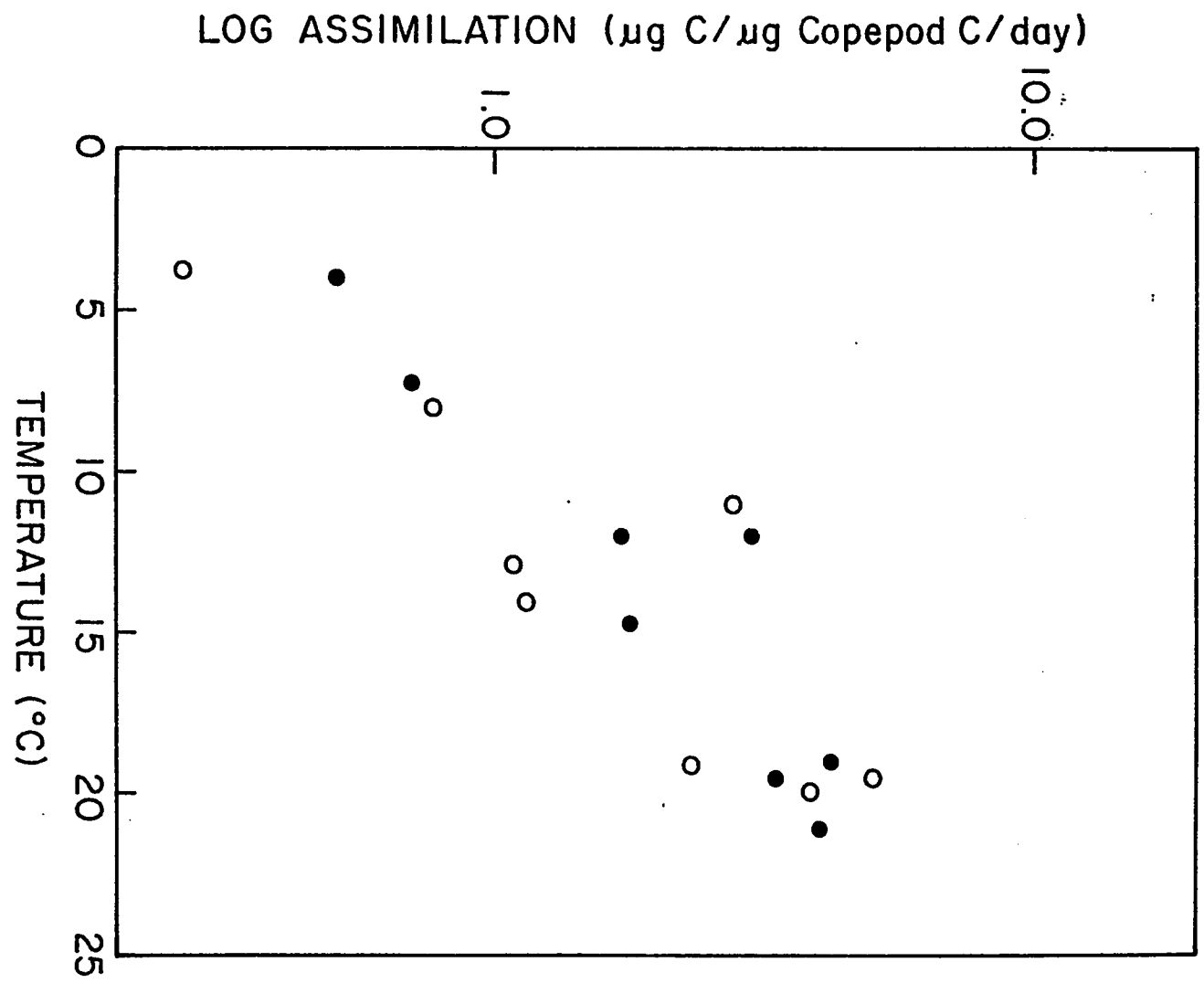
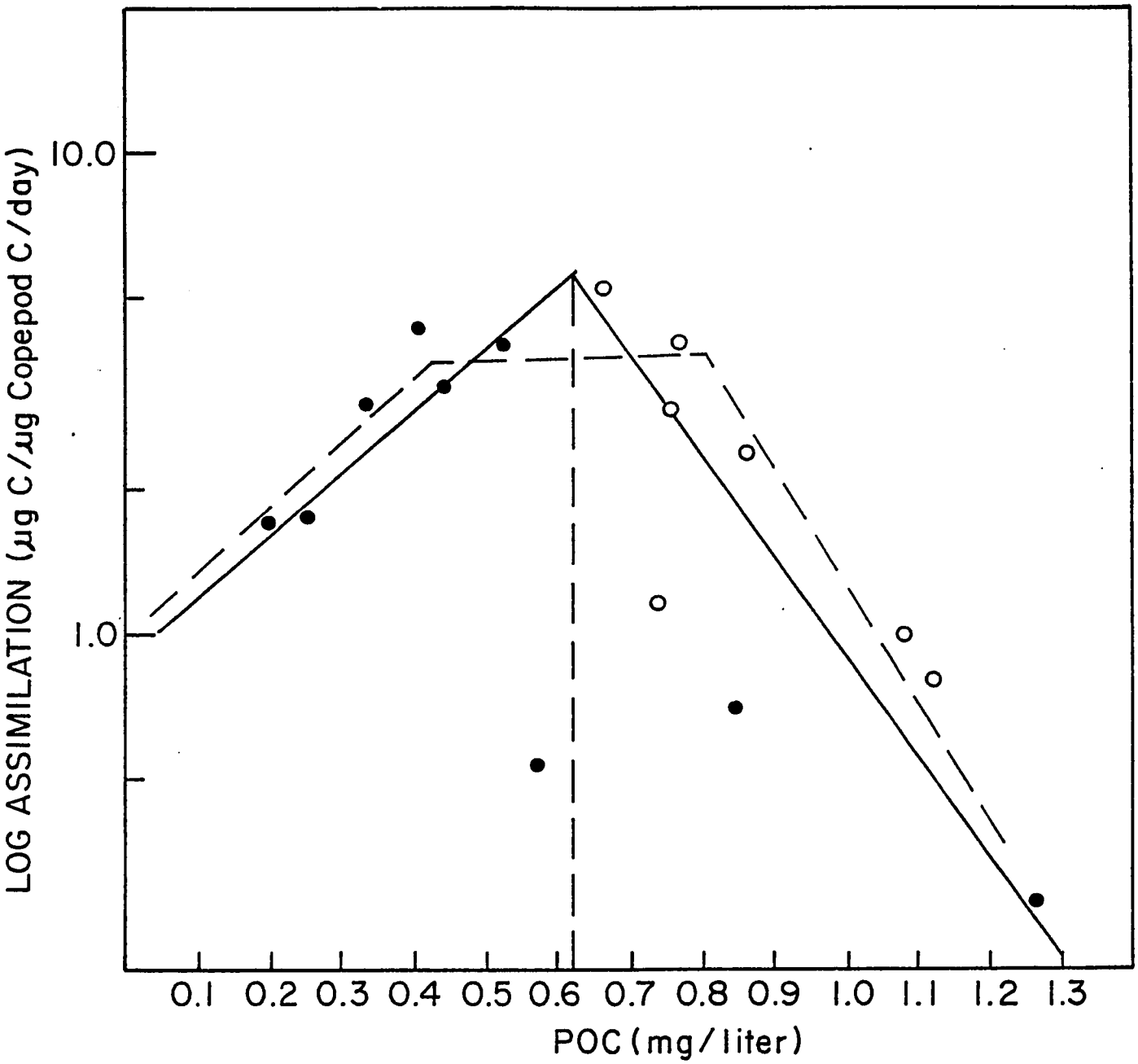

LOG ASSIMILATION (µg C/µg Copepod C/day)
1.0
10.0
0
5
10
15
20
25
TEMPERATURE (°C)

Figure 23. Correlation between assimilation (μgC/μgCopepod-C/day) and POC (mg l^{-1}) at station A3 (0) and D5 (●) Data pooled for concentrations less than 0.6 mgC l^{-1} ($r = +0.71$, $p < 0.05$); and for concentrations of greater than 0.6 mgC l^{-1} ($r = -0.82$, $p < 0.01$). Dashed line represents hypothetical saturation feeding curve, see text for explanation.

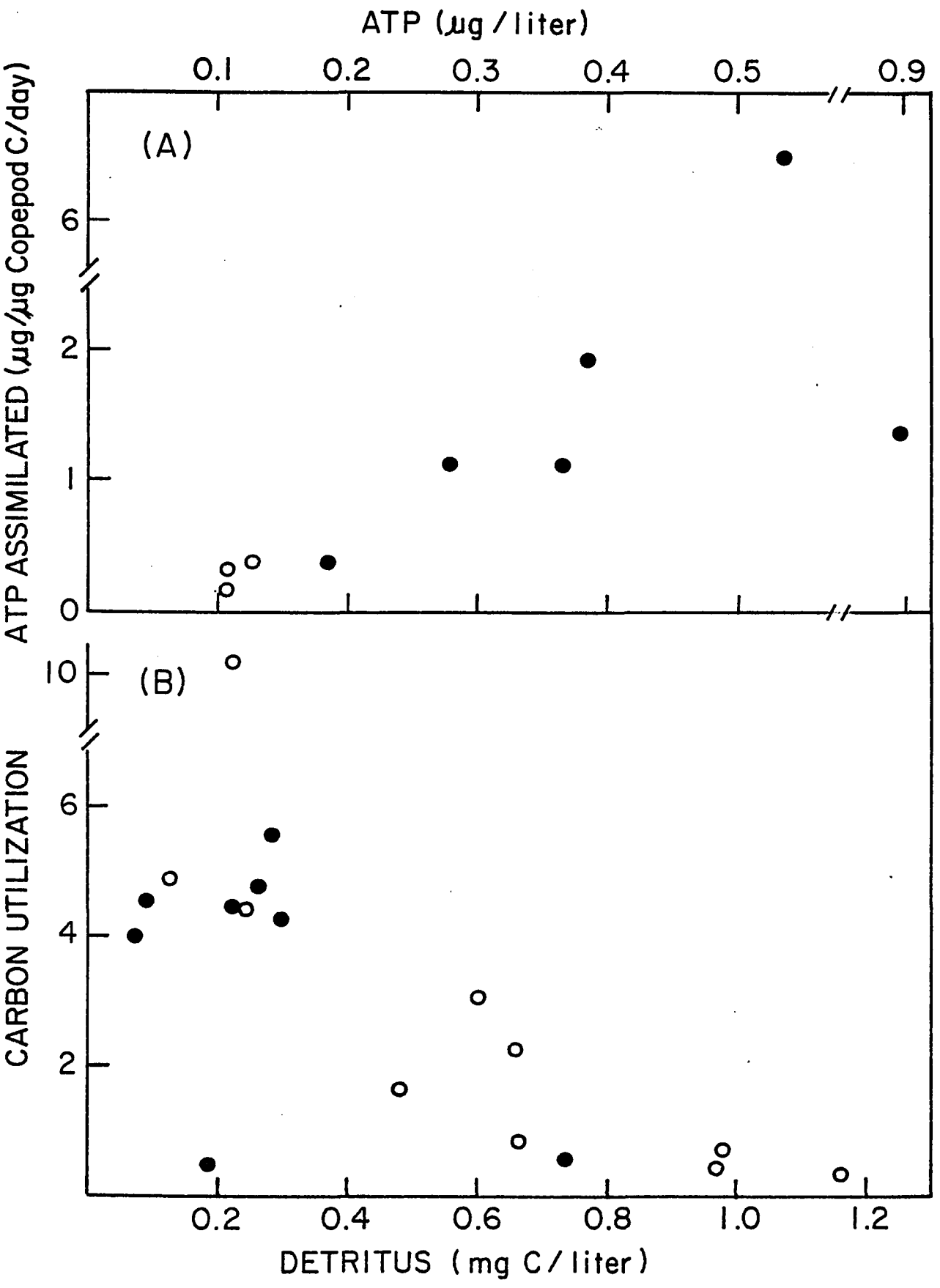

LOG ASSIMILATION (µg C/µg Copepod C/day)
10.0
1.0
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3
POC (mg/liter)

and then decreased rapidly at concentrations greater than 0.9 mgC l^{-1} (Fig. 23). It is of interest to note that on the dates that concentrations of POC at station D5 exceeded 0.63 mgC l^{-1}, assimilation rates were greatly reduced.

Relationships between rates of assimilation of live and detrital carbon and concentrations of these particulates were difficult to discern. During the spring, when phytoplankton blooms caused increases in concentrations of live carbon, rates of assimilation of live-carbon showed a corresponding increase (Fig. 24a). At concentrations of ATP between 0.1 and 0.4 μg l^{-1}, rates of ATP assimilation at both stations increased in a similar fashion.

There was no obvious relationship between concentrations of detritus and rates of detritus assimilation. However, there was a negative relationship between the presence of detritus and the ability of copepods to utilize POC (indicated by the ratio of POC assimilated/POC available) (Fig. 24b). At concentrations of detritus greater than 0.5 mgC l^{-1}, which includes only one point from station D5 and a number from A3, utilization rates were uniformly low (less than 4.0). At concentrations of less than 0.5 mgC l^{-1}, which includes points from both stations A3 and D5, carbon utilization increased to between 4 and 6, with values as high as 10.

Figure 24. Rates of assimilation and utilization of pools of carbon as a function of concentrations of detritus and ATP. (A) ATP assimilation (μg ATP/μg Cop-C/day) as a function of ATP ($\mu g\ l^{-1}$) concentrations at stations A3 (0) and D5 (●); (B) Carbon utilization (POC available/POC assimilated) as a function of detritus concentrations (mg l^{-1}) at stations A3 (0) and D5 (●).


ATP (µg / liter)
0.1
0.2
0.3
0.4
0.5
0.9
(A)
ATP ASSIMILATED (µg/µg Copepod C/day)
6
2
1
0
10
(B)
CARBON UTILIZATION
6
4
2
0.2
0.4
0.6
0.8
1.0
1.2
DETRITUS (mg C / liter)

Since some of the factors affecting rates of assimilation (temperature, body weight, and POC) were correlated in the field data, partial correlation coefficients were employed to sort out their independent affects on assimilation (Table 9). The correlation between concentrations of POC and assimilation was shown to be both positive and negative, so two separate analyses were run with data grouped on the basis of POC concentrations. The two groups were; 1) high levels of POC, where concentrations were greater than 0.6 mgC l^{-1} and 2) low levels of POC, where concentrations were less than 0.6 mgC l^{-1}.

At high levels of POC partial correlation coefficients for the independent variables, temperature, body weight, and POC concentration, were all significant and differed by less that 30% in their aboslute magnitude. In order of decreasing importance they were; temperature (+0.44), POC (-0.35) and body weight (-0.33). The combined correlation coefficient was 0.929, and explained 85% of the variability in assimilation.

Table 9. Partial correlation coefficients and multiple correlation coefficients of log assimilation (A') in µg c/µg copepod C/day and log respiration (R') in µg C/µg Copepod C/day versus; temperature T°C), log body weight (W) in mg dry wt copepod^{-1}, POC in mg C l^{-1} and total carbon assimilation. All partial correlation coefficients significantly larger than standard errors (S.E.) at $p < 0.01$.

Station	Dependent Variable	Independent Variable	β	r
A3 and D5 when POC > 0.6 mgl^{-1}	Assimilation	Temperature Body Weight (POC)	+0.44 -0.33 -0.35	0.929
A3 and D5 when POC < 0.6 mgl^{-1}	Assimilation	Temperature Body Weight (POC)	+0.44 -0.56 +0.10	0.940
A3 and D5 all points	Assimilation	Temperature Body Weight	+0.48 -0.54	0.930
A3 and D5 all points	Respiration	Temperature Body Weight	+0.40 -0.62	0.935
A3 and D5 all points	Respiration	Temperature Body Weight % Detritus assimilated	+0.41 -0.55 +0.20	0.957

At low levels of POC, the partial correlation coefficients of temperature and body weight were much larger than that for POC. Body weight had a higher coefficient (-0.56) than temperature (-0.44). The partial correlation coefficient of temperature was equal to that found in the analysis at high levels of POC, while the coefficient accounted for 88% of the observed variability in assimilation.

With the removal of the dependence of POC on temperature, the independent effect of POC on assimilation was seen to be less important than temperature and body weight. If POC is excluded from the analysis and all data are pooled, temperature and body weight account for 87% of observed variability.

5.2 Selectivity

The question of copepod feeding selectivity was analyzed with respect to: (1) the ability of copepods to discriminate between phytoplankton and detritus, and (2) within the phytoplankton, the ability of copepods to select one size class over another. The extent to which size affected assimilation of detritus could not be evaluated in this study.

Assimilation experiments showed that while the concentrations of detritus and its relative percentage in the water column were greater at station A3, its relative proportion as a dietary component was higher at station D5 (Fig. 25a). The relationship between the percentage of detritus available and that assimilated is different at the two stations (Fig. 25b). If no selectivity were exhibited we would expect to see a linear relationship between availability and assimilation. Percent assimilation at station D5 increases linearly to 50% availability and then is independent of further increases. Assimilation at station A3 appears to be independent of availability over the entire range of relative concentrations (30% - 90%).

The degree to which an animal preferentially selects a prey can be expressed as an Electivity Index (E), described by Ivlev (1961):

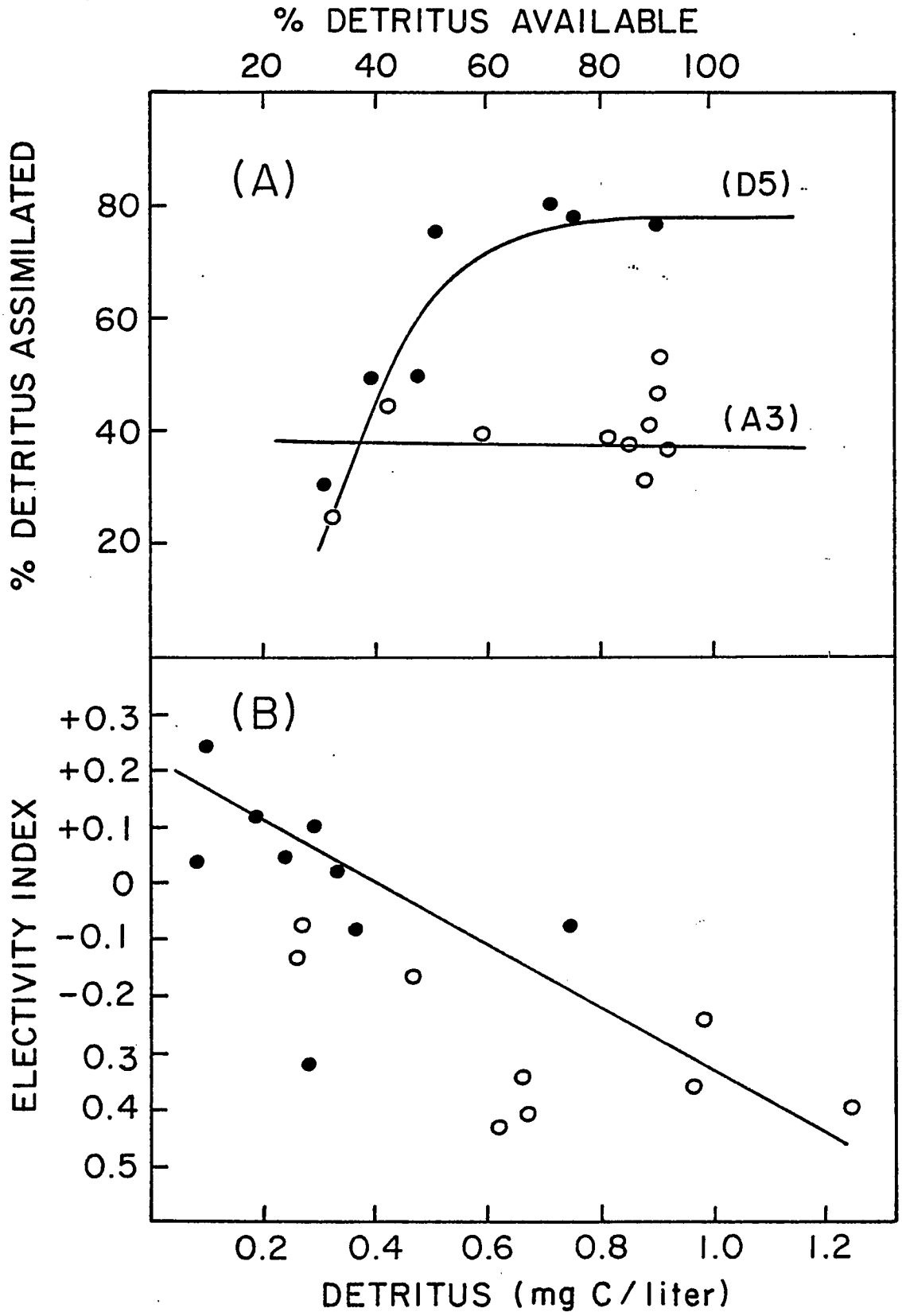
$$E = (r_i - p_i)/(r_i + p_i)$$

Where r_i is the percentage of the prey item in the diet

p_i is the percentage of the prey available

E ranges from +1 to -1

Figure 25. Copepod selectivity on the basis of live and detrital particles. (A) Proportion of diet composed of detritus (detritus assimilated/ total-C assimilated x 100) as a function of proportion of total POC available composed of detritus (detrital-C/total POC x 100) at stations A3 (0) and D5 (●); (B) Electivity Index for detritus (see text for explanation) as a function of detritus concentrations (mg l^{-1}) at stations A3 (0) and D5 (●).


% DETRITUS AVAILABLE
20
40
60
80
100
(A)
(D5)
(A3)
% DETRITUS ASSIMILATED
80
60
40
20
(B)
ELECTIVITY INDEX
+0.3
+0.2
+0.1
0
-0.1
-0.2
0.3
0.4
0.5
0.2
0.4
0.6
0.8
1.0
1.2
DETRITUS (mg C / liter)

All values of E are negative at station A3, indicating selection against detritus (or for live carbon), while most values at station D5 were positive, indicating selection for detritus (or against live carbon) (Fig. 23b). The value of E seems to be related to the concentration of detritus such that as concentrations of detritus increased, selection for detritus decreased. The inflection from positive to negative values of E occurred at a detritus concentration of about 0.4 mgC l^{-1}.

The proportion of net chlorophyll *a* available in incubation bottles at station A3 fluctuated widely from 11 - 74%, with proportions greater than 50% occurring only in February (74%) and March (58%). Netplankton composed from 35 - 68% of total chlorophyll *a* assimilated during May, June and July (Table 10). This decreased to 10% in November and less than 1% by March.

Netplankton available in incubation bottles at station D5 ranged from 32 - 87%. On all dates but June 6 and November 12, netplankton composed greater than 45% of total chlorophyll, and was highest during February and March. The proportion of netplankton available was generally higher here than at station A3. Netplankton comprised the greatest proportion of chlorophyll assimilated in May through June

Table 10. The proportion of netplankton assimilated relative to its availability in experimental bottles and corresponding Electivity Indexes. (% netplankton = net-chlorophyll a/ total chlorophyll a; E = r_i+p_i/r_i-p_i, see text for further explanation).

Date	% Netplankton Available		% Netplankton Assimilated		Electivity Index	
	A3	D5	A3	D5	A3	D5
5/13	35	48	66	54	+0.31	+0.06
6/6	12	25	68	52	+0.70	+0.39
6/18	28	45	37	50	+0.14	+0.16
6/24	45	49	35	29	-0.12	-0.61
7/10	11	-	64	-	+0.71	-
11/12	33	32	10	32	-0.53	0.00
11/24	20	57	10	25	-0.33	-0.39
2/21	74	82	8	10	-0.81	-0.78
3/31	58	87	0	0	-1.00	-1.00

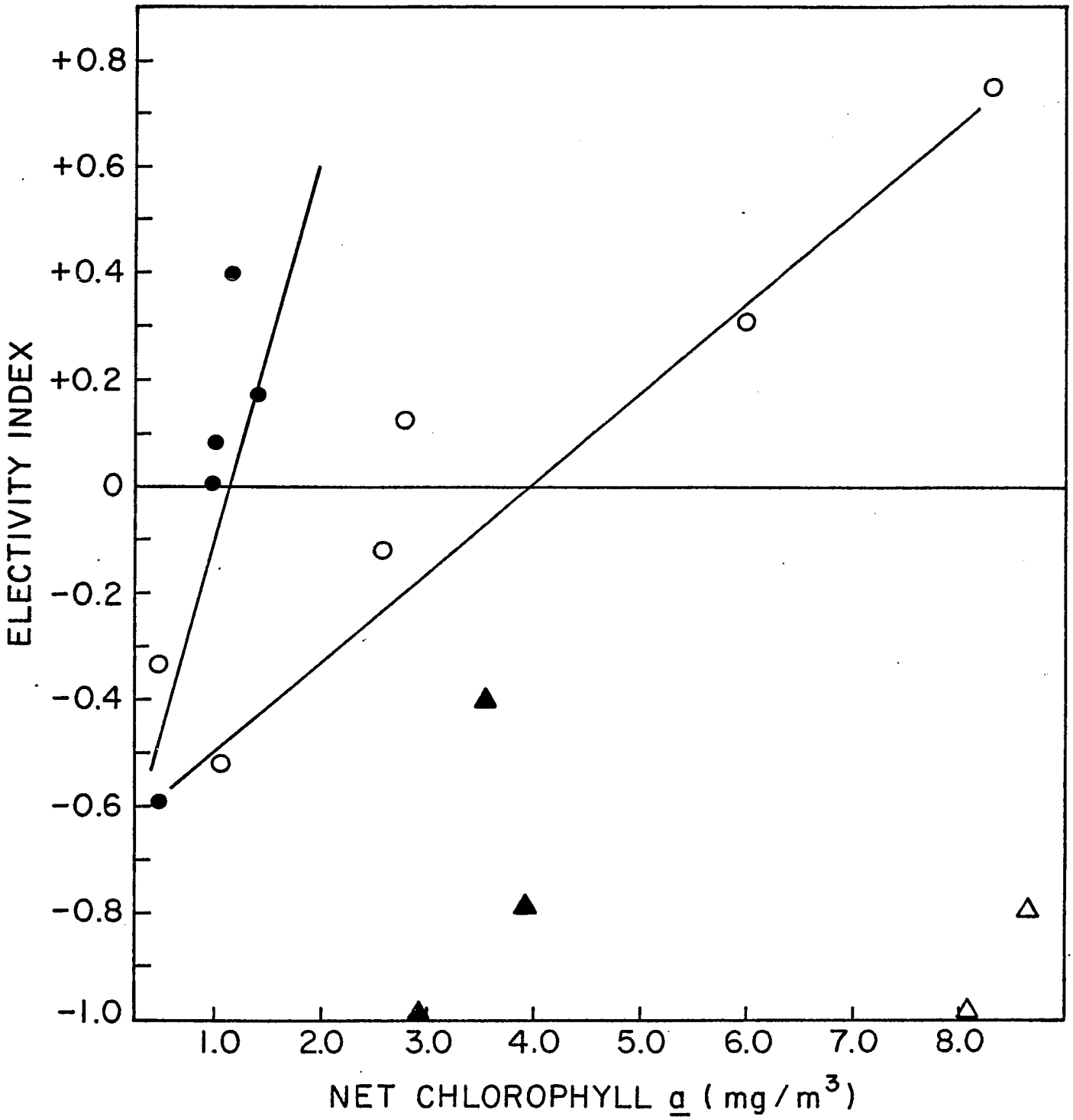
(29% - 54%), decreasing in November to 25% - 32% and less than 1% by March.

At both stations, while netplankton dominance was minimal during the spring and summer and maximal in the winter, the proportion of netplankton in the diet was maximal in the spring. This was most apparent in March, when the proportion of netplankton available was greater than 50% at both stations, but it comprised less than 1% of the diet.

During the spring, at both stations, E for netplankton was positive during the spring, with generally higher values occurring at station A3 (Table 10). E became negative at both stations in late June and decreased to -1.00 in late March.

Excluding February and March, when almost no netplankton was assimilated, there was a positive relationship between E and concentrations of netplankton chlorophyll *a*. The line describing this relationship had a much steeper slope at station D5 than A3 (Fig. 26), suggesting differences in either the species of phytoplankton or behavior of species of copepods indigenous to the two areas.

Figure 26. Relationship between electivity index for net-plankton and concentrations of net-chlorophyll a ($\mu g\ l^{-1}$) present during the spring and summer at stations A3 (0) and D5 (●); and during the winter at stations A3 (△) and D5 (▲).


+0.8
+0.6
+0.4
+0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
ELECTIVITY INDEX
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
NET CHLOROPHYLL a (mg / m3)

Carbon specific respiratory rates at station A3 ranged from 0.01 to 0.56 day^{-1}. Highest rates occurred in June and lowest in February. At station D5 rates ranged from 0.03 to 0.39 day^{-1}, with highest rates occurring in early June and lowest in February (Table 8).

Respiratory rates in almost all cases but late June and July were higher at station D5. This was especially pronounced during May and June when rates at station D5 were up to 3 times as great. Temporally, respiration varied by a factor of 50 at station A3 and 12 at station D5.

Rates of respiration were found to be inversely related to body weight (Fig. 27). The correlation was not significantly different at the two stations and had a combined correlation coefficient of -0.86 ($p < 0.01$) for pooled data. As was found for assimilation, the metabolic processes of smaller organisms was greater, per unit body weight, than for larger organisms.

Increases in respiration were correlated with rising temperatures. Correlations at the two stations were not significantly different and the combined correlation coefficient of pooled data was +0.85 ($p < 0.01$) (Fig. 28).

The interaction of temperature and weight and their combined affect on respiratory rates was examined by partial

Figure 27. Correlation between log respiration (µgC/µgCop-C/day) and log body weight of copepods (mg dry wt copepod^{-1}). Data pooled for stations A3 (0) and D5 (●); ($r = -0.86$, $p < 0.01$).

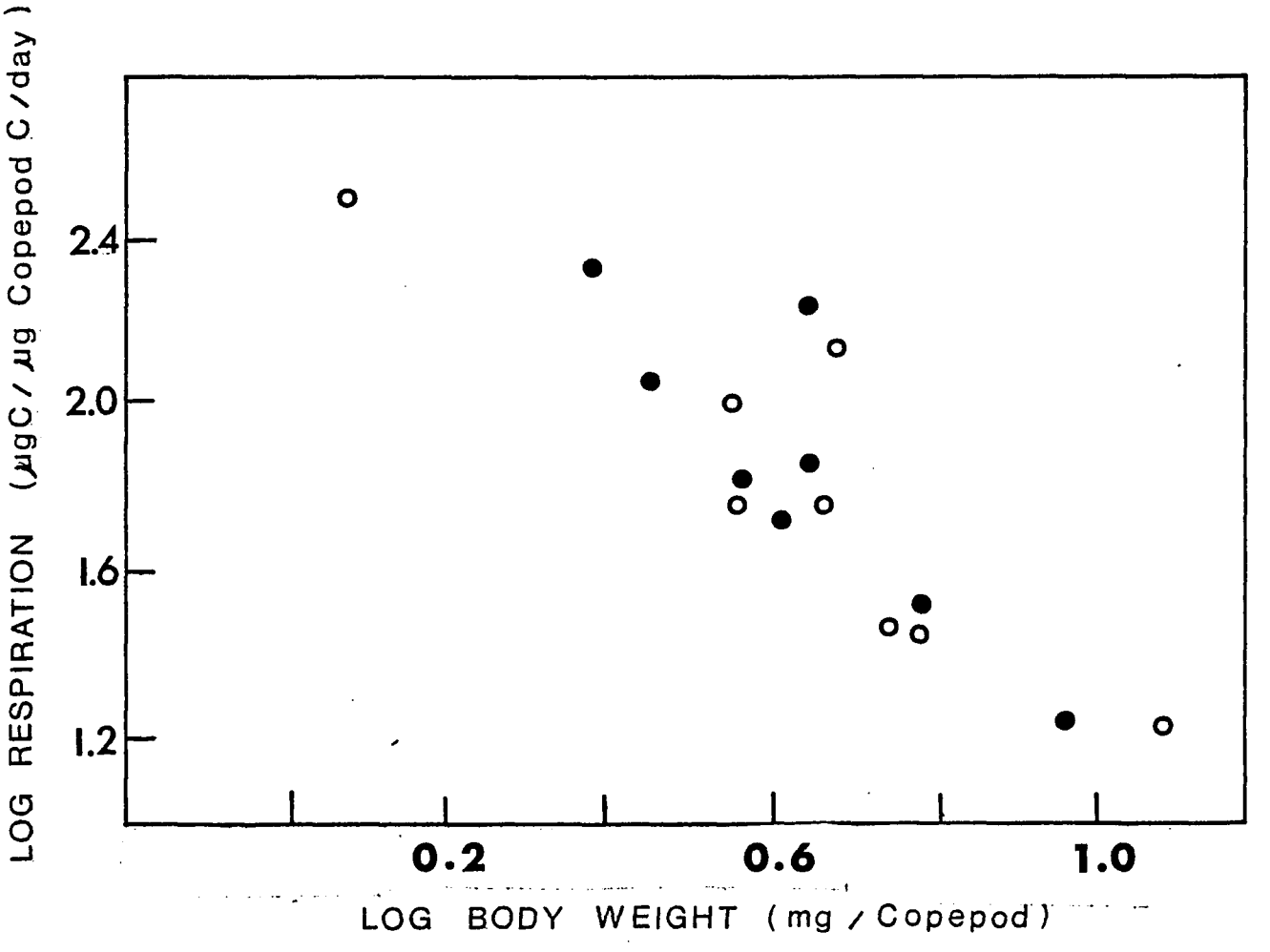
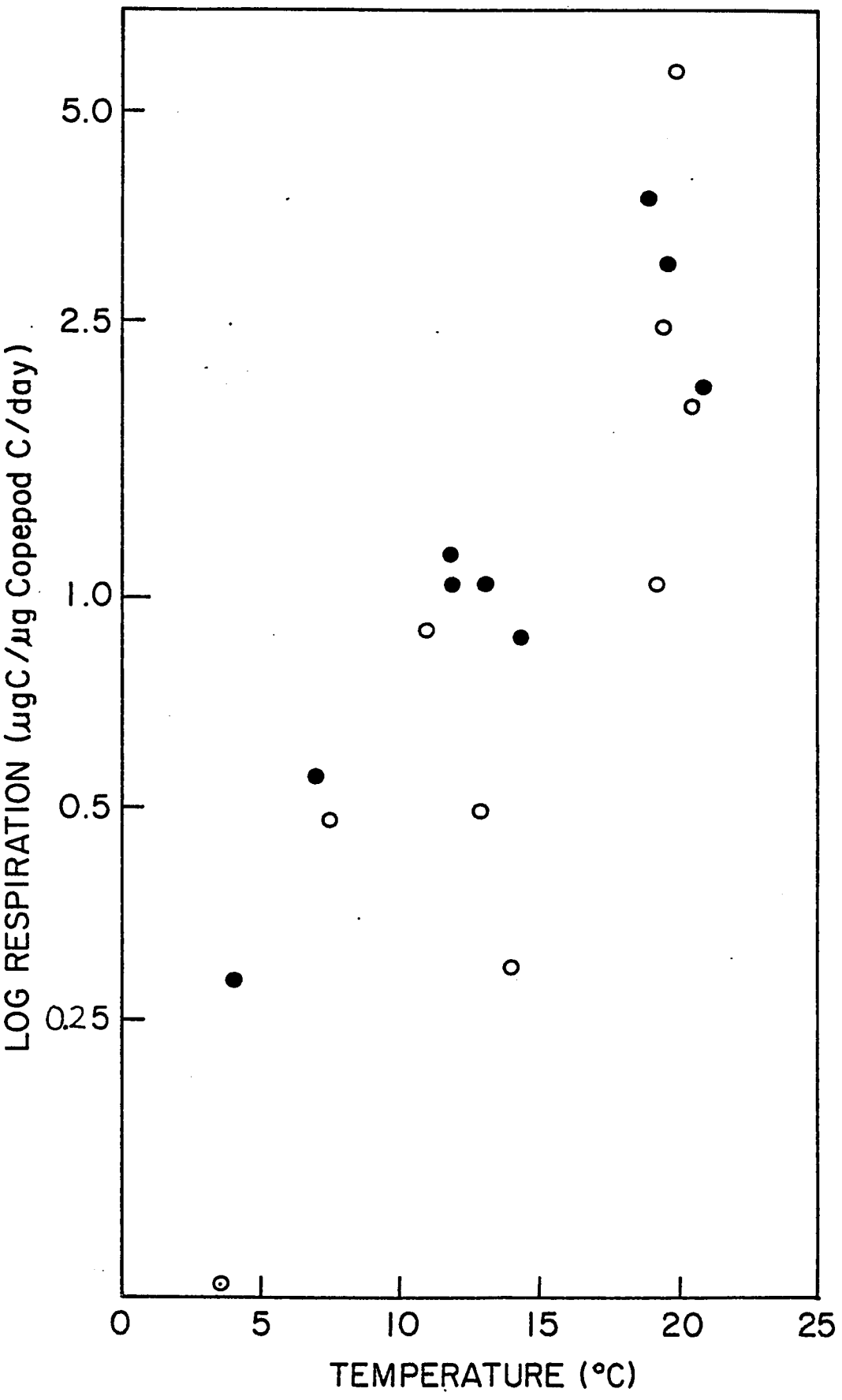

LOG RESPIRATION (μgC / μg Copepod C / day)
2.4
2.0
1.6
1.2
0.2
0.6
1.0
LOG BODY WEIGHT (mg / Copepod)

Figure 28. Correlation between log respiration (µgC/Cop-C/day) and temperature (°C). Data pooled for stations A3 (0) and D5 (●); ($r = +0.85$, $p < 0.01$).


5.0
2.5
1.0
0.5
0.25
LOG RESPIRATION (µgC/µg Copepod C/day)
0
5
10
15
20
25
TEMPERATURE (°C)

correlation coefficients (Table 9). The partial correlation coefficient of body weight (-0.61) was greater than that for temperature (+0.40) and together they accounted for 87% of the observed variability or respiration.

Rates of respiration were also correlated with quantity and quality of food assimilated. There was a positive relationship between levels of assimilation and respiration (Table 8) with some indication that the response might be different at the two stations. Respiration at any rate of assimilation was generally higher at station D5.

Respiration was also found to be positively related to the percent of detritus in the diet. When the percentage of dietary detritus is included in the partial correlation analysis, it has a correlation of +0.20, and increases the combined correlation slightly (Table 9).

5.4 Growth and net growth efficiencies.

The excess of assimilation over respiration was considered to be that quantity of carbon converted to animal tissue. Rates of growth at station A3 increased from less than 0.1 day^{-1} in May to a maximum of 1.0 day^{-1} in June.

Rates decreased through November and February to a minimum of 0.03 day^{-1} in March. Growth rates at station D5 similarly increased from less than 0.1 in May to a maximum of 0.20 day^{-1} in June. Values decreased to a minimum of 0.16 day^{-1} in March (Table 8).

Rates of growth at station A3 were usually greater than those at station D5. This difference was due to higher respiratory rates at station D5, rather than higher assimilation rates at station A3.

Net efficiencies of growth (K_2) at station A3 fluctuated between 38% - 76%, with highest values occurring in November and lowest in June (Table 11). At all times, but especially during June, K_2 was higher at station A3 than D5. There was a negative relationship between K_2 and the percent detritus in the diet (Fig. 29). Correlation coefficients at the two stations were not different, and there was a combined correlation coefficient of -0.88 ($p < 0.01$).

6.0 DISCUSSIONS AND CONCLUSIONS

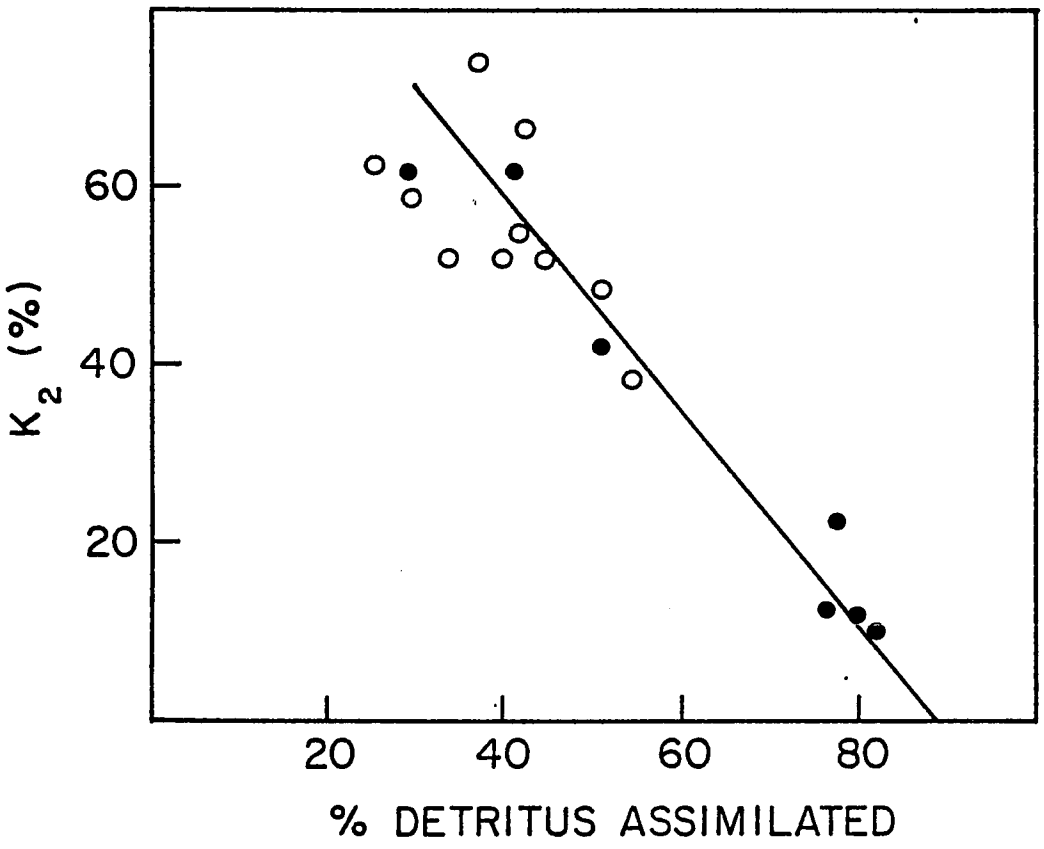
6.1 Assimilation rates

It is difficult to compare rates of assimilation obtained in this study to various feeding parameters reported

Table 11. Seasonal variations in Net Growth Efficiencies (K_2) at stations A3 and D5

Date	Station A3 %	Station D5 %
5/13/75	52	25
6/8/75	56	9
6/18/75	51	9
6/24/75	64	48
7/10/75	52	-
11/12/75	76	63
11/24/75	68	63
2/21/76	59	43
3/31/76	38	23

Figure 29. Correlation between Net Growth Efficiency (K_2) and the proportion of the diet composed of detritus (detrital-C assimilated/total-C assimilated x 100). Data pooled for stations A3 (0) and D5 (●);($r = -0.88$, $p < 0.01$).


60
40
20
K_2 (%)
20
40
60
80
% DETRITUS ASSIMILATED

in previous studies. Commonly, estimates have been made of rates of ingestion or filtration and reported as daily rations (carbon ingested per unit body carbon per unit time x 100). Such values are somewhat comparable to my reported estimate of carbon assimilated per unit body carbon per day x 100). Since rates of assimilation must be equal to or less than rates of ingestion, my estimates of "rations" will be lower,in proportion to the assimilation efficiency of copepods, than previous studies.

"Rations" in my study ranged between 2.7 and 156% of body weight daily, with most values between 10 and 50%. These are within the range of values reported in the literature. Gaudy (1974) found that at moderately low food concentrations, Calanus heloglandicus ingested roughly 50% of its body weight daily. Similarly, rations for Centropages typicus were 50 - 75% and those for Acartia clausi were 33 - 45%. Under optimal conditions, he found rations of 250 - 400%. Petipa et al., (1968) studying epipelagic herbiverous

zooplankton in the Black Sea, calculated values of between 45 and 140% of body weight. Corner (1961) used natural suspensions of particulates and found rations of 25 - 63% for C. helgolandicus. Under conditions of phytoplankton blooms, Cushing and Vucetic (1963) calculated rations of up to 399%. Much lower values of 0.8 - 45% were calculated by Gaudy (1974) using the data of Richman (1958) for a mixture of Pseudocalanus minutus and Oithoma similis. Poulet (1973) calculated rations of P. minutus when fed natural suspensions of particulates of only 5.5 to 11%.

The extreme variability of rations is in part due to the effects of differences in temperature (Anraku, 1964), body weight (Mullin and Brooks, 1970), quantity of food (Reeve, 1963; Mullin, 1963; Parsons et al., 1967; Suschenya, 1970) and quality of food (Conover, 1966c; Richman and Rogers, 1964; Gaudy, 1974) on rates of ingestions and assimilation.

The inverse relationship found between body weight and weight specific assimilation in the present study supports the generalization that smaller animals metabolize faster per unit body weight than larger animals under similar conditions. Mullin and Brooks (1970) found that rations obtained

by copepods decreased with increasing age and size of copepods.

The positive relationship between temperature and assimilation found in this study is well documented for other copepods. At temperatures below 5°C, species of coastal temperate copepods had been found to feed at extremely slow rates, if at all (Anraku, 1964; Martin, 1968).

Concentrations of POC were found to be less important in accounting for variability of assimilation rates than either body weight or temperature. In the apex, where concentrations during feeding experiments were between 0.2 and 0.7 mgC l^{-1}, there was only a slight positive correlation between rates of assimilation and increases in POC. Similarly it was found that in field observations correlations between POC and copepod abundance only occurred during April to May and July, when water column concentrations of POC fell significantly below 0.6 mgC l^{-1}. This suggests that food was generally not limiting to copepods in the apex, except perhaps intermittantly during the spring and summer.

In the estuary, where concentrations during feeding experiments were always in excess of 0.8 mgC l^{-1}. there was a negative relationship between POC and assimilation rates.

In the water column, concentrations of POC never dropped below 0.4 mgC l^{-1} and only fell between 0.4 and 0.6 mgC l^{-1} during early June and early July. The lack of field correlations on standing crops of POC and abundance, coupled with the negative assimilation response, suggests that food rarely became limiting to copepods in the estuary. If such limitation did occur, it was likely to do so during the spring and summer. Extremely high concentrations of POC seemed to actually cause a decrease in assimilation rates.

Studies by Ivlev (1945) on the feeding behavior of fish, showed that the quantity of food ingested was a function of food density, up to some maximum rate of ingestion. The concentration at which rates of ingestion are maximal is termed the maximum or upper threshold. Further increases in concentrations of food above this threshold would not yield increases in ingestion rates. The work of Reeve (1963), Frost (1962), Mullin (1963), Suschchenya (1970) and others, have shown that copepods respond in a similar fashion. It has been further shown that there is evidence of a lower threshold, below which feeding did not occur (Adams and Steele, 1966; Parsons et al., 1967; Nassogne, 1970). This lower threshold has been found to be dependent on the species of both grazer and food item, and ranged between 0.04 and 0.13 mgC l^{-1}.

(Parsons and LeBrasseur, 1970). Since concentrations in both the estuary and the apex were between 0.2 and 2.0 mgC l^{-1}, it is unlikely that feeding patterns were much affected by lower threshold phenomenon.

The range over which increasing food concentrations yield increases in ingestion rates has been found to be affected by the nature of the grazer, and the quality and size of food particles (Conover, 1966; Paffenhopper, 1970; Frost, 1972). The upper threshold has been found to vary between 0.2 and 1.0 mgC l^{-1}. Adams and Steele (1966), using natural suspensions of particulates as a food source, found that the maximum threshold was 0.4 mgC l^{-1}. The upper threshold concentrations seem to be set by the ability of copepods to filter and digest food particles.

Mullin (1963) found that the rate of ingestion of C. hyperboreus increased over the range of 200 - 4000 cells ml^{-1}, but then decreased to 25% of maximum over the range of 4000 - 8000 cells ml^{-1}. Inhibition of ingestion at extremely high concentrations has been observed by Marshall and Orr (1955a) for Calanus, and Conover (1956) for Acartia. The mechanism causing this decrease is unclear, but may be related to the decrease in filtering efficiency caused by clogging of filtering surfaces. It has also been suggested that it is a response to

toxins excreted at high concentrations of phytoplankton.

In order for there to be a direct correlation between my estimates of assimilation rates and estimates of ingestion, a relatively constant proportion of carbon ingested must be assimilated (the ratio of assimilation to ingestion x 100 is termed assimilation efficiency). Conover (1966) concluded that assimilation efficiencies were in the range of 70 - 80% and were unaffected by food concentration. Gaudy (1974) found some evidence that a decrease in assimilation efficiency occurred at low food concentrations, but at moderate to high levels of food, it remained constant. Feeding patterns as indicated by rates of assimilation in this study and rates of ingestion in other studies appear to follow similar trends including maximum threshold concentrations of 0.4 to 0.6 mgC l^{-1}, and the existence of inhibition at very high food levels.

If the decrease in assimilation rates at high concentrations of POC is purely a function of absolute increases in densities of particles, the same type of response would be expected to occur in the apex if concentrations of particulates exceeded approximately 0.8 mgC l^{-1}. Since concentrations of POC never reached these levels during feeding experiments, it is not possible to determine if the response would have been the same. It is possible that inhibition in the estuary might

not only have been a response to the greater quantity of particulates, but a qualitative difference between particles in the estuary and apex.

The extremely high concentrations of POC in the estuary have been seen to be largely due to detritus. If such particles were less suitable for feeding than either phytoplankton cells or detritus found in the apex, increases in their concentration would result in observed increases in POC but would not yield proportional increases in food availability. The result would be a negative relationship between increasing POC and assimilation rates. The effect of unsuitable particles could be manifested by a rejection of such particles during filtering or a decrease in assimilation efficiency. Conover (1966c) observed that raptorial feeding copepods could reject food particles even after they had been seized. Such rejection might occur on the basis of size, shape or chemical composition.

Conover (1956c) found that assimilation efficiencies of copepods decreased as a function of percent ash weight of particles. The reasons for this were unclear, but might have been related to varying enzyme efficiencies. Detritus particles might be expected to have variable percent ash compositions (dependent on their origin) which are generally greater per-

centages than contained in live cells. If the concentrations of these unsuitable particles increased, while ingestion rates might not be affected, rates of assimilation efficiency would be decreased. The lowered efficiencies would then be reflected in the observed decreases in total carbon assimilation. Thus it appears that sewage derived detritus is not a good food source for copepods.

A number of observations made in both feeding experiments and in the field support the hypothesis that the nature of detritus and the response of copepods to detritus are different in the estuary and the apex. Since the origin of most detritus in the estuary is probably sewage, while that in the apex was more related to phytoplankton production, it is likely that the chemical composition and suitability of detritus is different in the two areas. Patterns of assimilation at station A3 were different from those at station D5. The percentage of detritus in the diet was uniformly higher at station D5, while the percentage of detritus available was generally higher at station A3. Electivity indexes for detritus were always negative at station A3 and either slightly negative or slightly positive at station D5. This suggests that copepods could discern differences in live and dead particles and select against dead particles in the estuary on the basis of unsuitability.

The inverse relationship between growth efficiencies (K_2) and the proportion of detritus in the diet might be caused by a relatively lower assimilation efficiency of copepods feeding on detritus as opposed to phytoplankton. Saunders (1969) found that the assimilation efficiency of Daphnia fed artifically produced detritus (3.9 - 13.9%) was considerably lower than when fed algae (47 - 88%). He concluded that detritus was refractory to digestion.

6.2 Seasonal variability in phytoplankton-zooplankton interactions

Copepod size selectivity varied seasonally, with netplankton being selected against during the winter, and for during the spring and summer. Positive selection on the basis of larger size cells has been found to occur by many authors (Mullin, 1963; Frost, 1972; Gaudy, 1974). Poulet (1974) found that selectivity of copepods varied seasonally in relation to the abundance of particles. This was not seen to occur in this study since the most abundant group during the winter, netplankton, was selected against.

The occurrence of selection against netplankton during the winter was probably due to the presence of high concentrations of Ceratium tripos, which bloomed during February and March. C. tripos is a large, spined dinoflagellate species

that appears not to be assimilated by copepods. Conover (1976) observed that neretic copepods from Bedford Basin rarely ate any Ceratium and indeed showed negative selection for all species of this genera. When concentrations of Ceratium were artificially increased to high levels there was a complete cessation of feeding in their size range even though this was the preferred size range at ambient concentrations. Similarly in this study, if the contribution of C. tripos is subtracted from the total standing crop of netplankton, electivity indices calculated on the basis of the remaining netplankton are still negative. This observation supports Conover's conclusion that selection against a particular kind of particle can be so strong as to offer a refuge for particles of the same size.

During the spring-summer periods netplankton were selected for in both the estuary and the apex. At this time E was generally higher in the estuary. This might have been due to difference in the species composition of netplankton in the two areas. It could also have been due to the fact that detritus and nanoplankton are in the same size class (Odum, 1972) and that active avoidance of high detritus concentrations in the estuary would be most easily accomplished by selectivity for larger particles.

6.3 Respiration and growth efficiency

Rates of respiration observed in this study ranged between 1 and 58% of body weight daily, and were generally higher in the apex than the estuary. They were somewhat higher than most values reported in the literature. Menzel and Rhyther (1971) calculated that 12% of body weight was respired daily. Ivlev (1955) found that depending on temperature, respiration accounted for between 0.6 and 8.4% of body weight. Respiration is also commonly expressed as a proportion of carbon assimilated, and termed metabolic expenditure (T). This is the inverse of values reported here as K_2, net growth efficiency. T ranged from 36% in the estuary to 81% in the apex. Suschenya (1962), studying Artemia salina, found that T was 72 - 76%; Richman (1958) found values of 42 - 45% for Dapnia pulex; Corner (1961) studying Calanus heloglandicus, estimated values of 48 - 57%.

The rate of oxygen consumption is a good index of metabolic expenditure and is sensitive to stress. As such, respiratory rates can be used to indicate the suitability of various food particles with respect to the metabolic cost of processing. The great variability associated with described respiratory rates has been found to be related to

the effects of body size, temperature, feeding activity and quantity and quality of food assimilated.

In general, it is found that for both interspecific and intraspecific comparisons, there is an inverse relationship between weight specific respiration (R') and the log of body weight (Raymount and Gauld, 1951; Vernberg, 1962). Equations describing this relationship are usually expressed in the exponential form of:

$$R' = aw^{b}$$

Where R' is the weight specific consumption of oxygen;

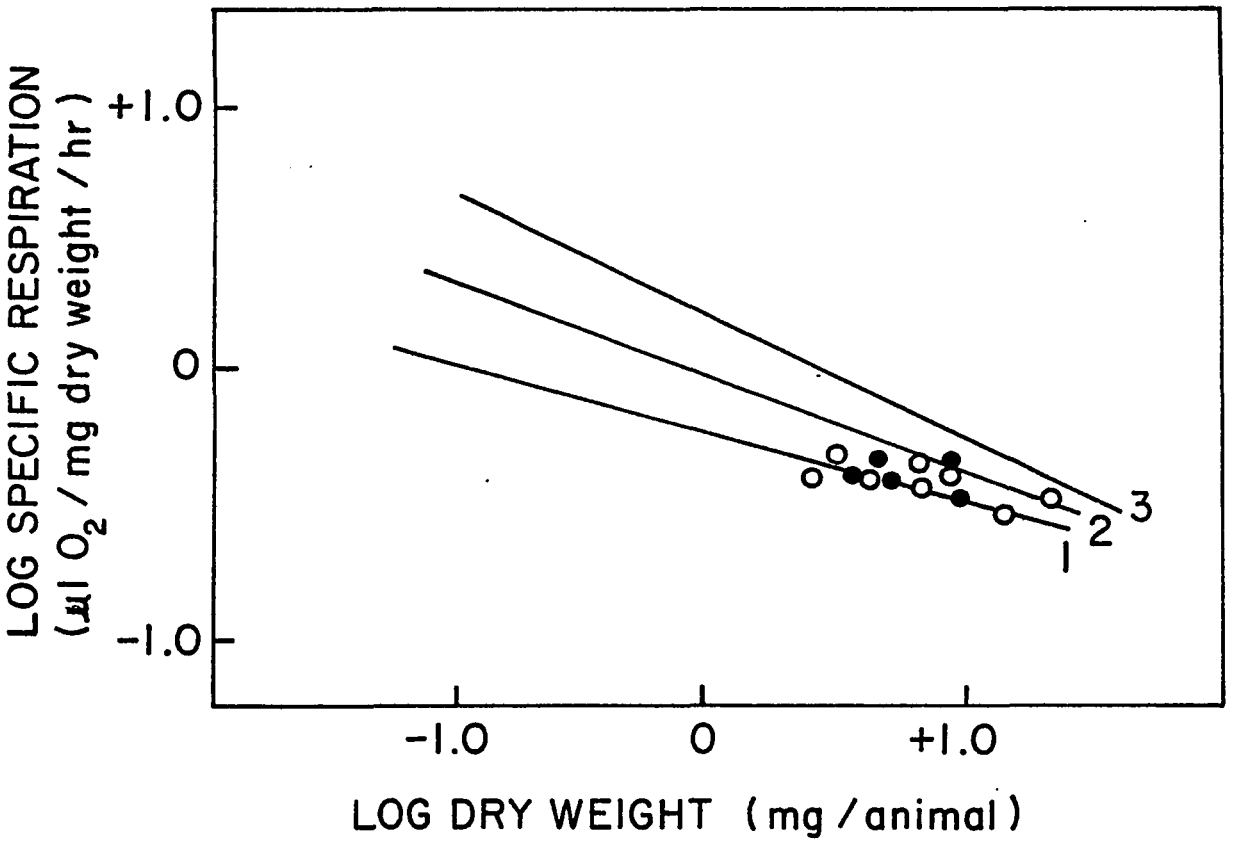
a is the intercept of the regression line on the y axis; and

b is the slope of the regression line

Ikeda (1970) described this relationship for copepods taken from tropical, temperate and boreal areas. My results (Fig. 30) correspond to those predicted by his equations for boreal and temperate areas.

The proportionality constant "a" defines the level of metabolism of the organism and is affected by temperature and food quality. The exponent "b", which defines the effect of weight on respiration, is generally found to be unaffected by these factors (Small, 1966; Paranjape, 1967; Comita, 1968) and is used to compare rates observed in this and other studies. The equation generated from all data from stations A3 and D5 was:

Figure 30. Log specific respiration rates (µl O_2/mg dw/hr) versus log dry weight (mg) in boreal (1), temperate (2) and tropical (3) areas. Redrawn from Ikeda (1970). Data from this study indicated by (O) for station A3 and (●) for station D5.


LOG SPECIFIC RESPIRATION
(μl O2 / mg dry weight / hr)
+1.0
0
-1.0
-1.0
0
+1.0
LOG DRY WEIGHT (mg / animal)
1
2
3

$$R = 0.30W^{0.72}$$

The value of 0.72 is similar to those found for copepods by other authors (Table 12) which are in the range of 0.60 - 0.86.

Respiration in poikilotherms is known to be greatly influenced by temperature. This relationship is usually described by a temperature coefficient, the most common of which is Q_{10}:

$$Q_{10} = 10(\log k_1 - \log k_2)/t_1 - t_2$$

Where k_1 is the rate at temperature 1

k_2 is the rate at temperature 2

Q_{10} for all pooled data was 1.7. This is slightly lower than values reported in the literature of between 2 and 3.

Analyses in this study indicated that the independent effects of body weight and temperature accounted for most of the observed variability in respiration. Comita (1968) generated a multiple linear regression equation to predict respiration on the basis of temperature and body weight for the copepod Diaptomus:

$$\text{Log}_{10}R' = 0.036T - 0.34W + 0.618$$

Where R' is the oxygen uptake expressed as µl O_2/mg dry weight copepod/hour

Table 12. Comparison of values of respiratory coefficients (b)*

Organism	T°C Range	Weight Range (mg dry weight)	b	Author
Crustacea	10-25	0.01-10,000	0.826-0.810	Weymouth (1944)
Neretic Copepods	20	0.002-0.015	0.86	Conover (1956)
Multi-species copepods	20		0.75	Winberg (1950)
Herbiverous plankton	4-18.5	0.004-3.681	0.652	Conover (1960)
Carniverous plankton	4-18.5	0.820-27.300	0.649	Conover (1960)
Artemia salina	5	0.090-0.590	0.860	Conover (1960)
	13	0.110-0.610	0.730	Conover (1960)
Multi-species copepods	17	based on length	0.730	Raymont and Gauld (1951)
Herbiverous plankton	3-5	0.219-4.516	0.76	Conover and Corner (1968)
Carniverous plankton	3-5	0.021-97.403	0.78	Conover and Corner (1968)
Artemia salina	25	0.040-0.400	0.633	Gilchrist (1950)
Diaptomus spp.	5	0.003-0.300	0.669	Comita (1968)
	10		0.721	
	20		0.626	
	25		0.622	
Acartia clausi	24-26	0.0006-0.006	0.811	Petipa (1966b)
Daphnia pulex	20	0.003-0.046	0.881	Richman (1958)
Euphausia	5	0.020-14.000	0.962	Small et al (1962)
	10		0.935	
	15		1.141	
E. pacifica	5	0.976-8.018	0.985	Paranjape (1967)
	10	0.868-6.146	1.008	
	15	0.946-15.064	0.992	
	20	2.070-7.056	1.052	
Multi-species copepods	3-23	0.003-0.042	0.720	present work

* $Q = aW^b$, where Q is oxygen consumed/unit time; W is the weight of organism (mg); a is the constant defining level of metabolism expenditure per unit time; b is the range of change of metabolism with body weight.

W is the dry weight of copepods expressed as mg/copepod

T is the temperature (°C)

Similarly a multiple regression equation based on my data was; $Log_{10}R' = 0.031T - 1.07W + 1.23$. While the coefficient of temperature was almost identical to that obtained by Comita, the coefficient of weight and the y-intercept were approximately double in my study. Part of the discrepancy may be due to differences in the quality of food assimilated, acclimation to different food concentrations or geographic differences in copepods (Ikeda, 1970).

The quantity of food assimilated has been seen in both this and other studies to be correlated with rates of respiration. Conover (1956) found the vigorously feeding animals had higher rates of respiration than nonfeeding ones. Gaudy (1974) found that respiration increased with increasing food supply. This has been called the "specific-dynamic affect", or the energy needed to metabolize food (Conover, 1968).

The higher respiration rates observed in this study may be related to the fact that copepods were not starved prior to

the experiment, or to differences in the nature of food particles assimilated. The cost of respiring food items has been found to be related to the chemical composition of the food particle. For example, it is known that more oxygen is required to metabolize fat than carbohydrate (Conover, 1960). The higher rates of respiration observed in the apex may thus be related to the increased specific dynamic cost of processing detritus.

Growth efficiencies in this study ranged between 38% and 76% in the estuary, and 9% - 63% in the apex. Values reported by other authors ranged between 3% - 90% (Table 13). While the methodology employed to determine K_2 varied greatly, previous studies showed that K_2 was unaffected by temperature, and decreased with increasing age of the organism.

Seasonal variations in K_2 may be good indicators of the metabolic cost of food processing. Data presented here indicated that assimilation of detritus depressed K_2. Heinle (1974) also found that while detritus was assimilated, growth efficiencies and egg production were significantly lower than when copepods were fed phytoplankton. Field data presented here cannot take into account the concommitant effects of seasonal variations in sex or reproductive stage on K_2.

Table 13. Literature values of Net Growth Efficiencies (K_2)

Species	Stage	Basis of Calculation	K_2	Author
Daphnia pulex	5 days 15 days	Calories	42.3 30.3	Ivlev (1938)
Penilia avirostris	Juvenile Adult	Calories	53.4 21.2	Pavlova (1964)
D. pulex	Pre-adult Adult 40 days	Calories	55.4-58.6 3.0-4.0 56-73	Richman (1968)
Calanus hyperboresus	Stage IV-V Stage IV-V	Calories Dry weight	34-90 25-63	Conover (1964)
Diaptomus sp.	Egg prod-uction	Calories	4.2-19.8	Comita (1964)
Euphausia pacifica	Adult Field pop.	C^{14}	17.1 33.6	Lasker (1966)
Acartia clausi	Nauplli C. I-IV C. V	Calories	17 21-29 14	Petipa (1967)
Calanus helgolandicus	Nauplii C. I-IV C. V	Calories	37 22-55 6	Petipa (1967)
Calanus finmarchicus	Growth + egg. prod.	Nitrogen	38.6	Corner et al., (1967)
Mixed copepods	Estuarine Coastal	Carbon	38-76 9-63	present work

III. SECONDARY PRODUCTIVITY, GRAZING PRESSURE AND TRANSFER EFFICIENCIES

7.0 RESULTS

7.1 Secondary productivity and water column respiration

Rates of gross productivity (GP) at station A3 ranged from less than 0.1 to 18.3 mgC m^{-3} day^{-1} (Table 14). During May, June and August, GP always exceeded 3.5 mgC m^{-3} day^{-1} and reached highest values in mid-June and August. Rates in November, February and March never exceeded 2.0 and were usually less than 1 mgC m^{-3} day^{-1}.

GP at station D5 ranged from 0.6 to 41.3 mgC m^{-3} day^{-1}. Temporal variability paralleled that at station A3, with maximum values in mid-June and lowest values during November, February and March.

During May and June, in spite of higher rates of assimilation per organisms at station A3, the greater density of organisms at station D5 resulted in generally higher values of GP at D5. Peaks in GP at station A3 were due to increased assimilation of both detritus and live carbon, while at station D5 they were due to proportionally greater increases in detrital assimilation.

Water column respiration (mgC m^{-3} day^{-1}), and the proportion of NP that was lost to respiration at station A3 were

Table 14. Comparison of Gross Secondary Productivity (GP) expressed as mgC m^{-3} day^{-1}; Net Secondary Productivity (NP) expressed as mgC m^{-3} day^{-1}; Water Column Respiration (R) expressed as mgC m^{-3} day^{-1}; Primary Productivity (PP) expressed as mgC m^{-3} day^{-1} and Transfer Efficiency (E) at stations A3 and D5.

Date	Temp.	Copepod Abundance (No./m^3)		GP		R		NP		PP		TE	
		A3	D5	A3	D5	A3	D5	A3	D5	A3	D5	A3	D5
5/13	11	1978	1305	3.5	2.8	1.6	2.1	1.9	0.7	79	72	2	0.1
6/6	17	3566	6036	8.6	17.4	3.8	15.7	4.8	1.6	231	40	2	4.0
6/18	19	2608	10,003	18.3	41.3	8.9	37.8	9.4	3.5	57	82	16	4.0
6/24	20	1805	12,575	9.5	40.2	3.4	20.2	6.1	20.2	63	30	10	66.0
7/11	22	3984	-	15.5	-	5.2	-	8.1	-	62	-	13	-
11/12	15	138	527	0.6	1.1	0.2	0.5	0.4	0.5	2	7	20	7.0
11/24	12	118	571	0.5	1.7	0.2	0.6	0.3	1.1	1	24	33	4.0
2/21	4	44	18	0.1	0.1	0.1	0.1	0.1	0.1	27	41	1	0.1
3/31	7	1756	2122	2.1	2.6	1.3	2.0	0.8	0.6	21	49	4	1.0

highest in June. During this time respiration rates were 8.9 mgC m^{-3} day^{-1}, and accounted for 49% of the total GP. Lowest rates occurred in November and February when less than 1 mgC m^{-3} day^{-1} or 24% of GP was respired.

At station D5, a maximum of 37.8 mgC m^{-3} day^{-1} or 91% of GP was respired during June and a minimum of less than 1 mgC m^{-3} day^{-1} or 37% of GP was respired in November and February. Both rates of respiration and the proportion of GP lost to respiration were always greater at station D5. The higher rates were due to both higher rates per organism and higher densities or organisms in the water column.

Net productivity (NP) at station A3 ranged from less than 1 to 9.4 mgC m^{-3} day^{-1}, with maximal rates in May through August. NP at station D5 ranged from less than 1 to 3.5 mgC m^{-3} day^{-1}, with the exception of one anomalously high value of 20.2 mgC m^{-3} day^{-1} on June 24.

In spite of higher rates of GP at station D5, increased respiratory costs (45 - 91% at D5 as opposed to 41 - 49% at A3) resulted in lower rates of NP at station D5 during May and early June. During the fall and winter months, NP at both stations was uniformly low.

7.2 Water column grazing pressure

The impact of copepod grazing on phytoplankton can be estimated as the product of daily ingestion rates per copepod and total abundance of copepods. Estimates of the removal of phytoplankton from the water column from my data will be underestimates since rates of assimilation are used instead of ingestion. Grazing pressure was calculated as phytoplankton-carbon assimilated [mgC copepod^{-1} day^{-1} x copepod abundance (number of organisms m^{-3})] (Table 15).

Grazing pressure at both stations was highest during May, June and August. During this period, grazing pressure at station A3 ranged from 3.1 to 10.1 mgC m^{-3} day^{-1}. This amounted to the assimilation of 1 - 13.8% of the standing crop of netplankton daily during May and June and 32.4% in August. Less than 4% of the standing crop of nanoplankton was assimilated daily at this time.

At station D5 grazing pressure increased from 0.7 in May to 18.9 mgC m^{-3} day^{-1} in June. This accounted for the assimilation of 0.5 to 17.2% of the standing crop of phytoplankton daily. The percentage of netplankton standing crop removed daily increased from 0.3% in May to 10% in late June. Daily assimilation of nanoplankton accounted for less than 6% during May and early June, and increased to 24.3% of the standing crop in late June.

Table 15. Comparison of water column grazing pressure (calculated as rates of assimilation per copepod x copepod density) expressed as mgC m^{-3} day^{-1} on netphytoplankton-c, nanophytoplankton-c and total phytoplankton-c; percent of standing crop of net-phytoplankton, nanophytoplankton and total phytoplankton assimilated daily.

Date	Water Column Grazing Pressure						Percentage of standing crop assimilated daily					
	Net-C		Nano-C		Total-C		Net-C		Nano-C		Total-C	
	A3	D5	A3	D5	A3	D5	A3	D5	A3	D5	A3	D5
5/13	2.31	0.37	1.20	0.31	3.5	0.68	0.9	0.7	0.3	0.3	0.5	0.5
6/6	3.4	1.54	1.60	1.42	5.0	2.96	7.8	3.5	0.2	2.5	0.7	3.0
6/18	3.67	3.93	6.20	3.91	9.9	7.84	13.8	5.8	3.4	5.8	4.7	6.1
6/24	2.42	5.48	4.70	13.40	7.2	18.92	7.5	10.0	3.0	24.3	3.8	17.2
7/11	6.46	-	3.64	-	10.1	-	32.4	-	2.4	-	5.9	-
11/12	0.03	0.23	0.27	0.49	0.30	0.72	0.14	1.2	0.5	1.0	0.4	1.0
11/24	0.03	0.24	0.27	0.72	0.03	0.96	0.40	0.2	0.8	0.8	0.8	0.4
2/21	0.003	0.001	0.04	0.01	0.04	0.008	0.00	0.00	0.0	0.02	0.01	0.003
3/31	0.00	0.00	0.90	0.52	0.90	0.52	0.00	0.01	0.01	0.90	0.24	0.16

At both stations, grazing pressure on phytoplankton was reduced to 0.001 - 0.96 mgC m^{-3} day^{-1} in November, February and March. During this time less than 1% of the standing crop of phytoplankton were assimilated daily, and assimilation of netplankton was negligible. Thus, at both stations, the highest grazing pressure in terms of percent removal corresponded to periods of highest phytoplankton growth rates.

7.3 Transfer efficiencies

The apparent efficiency of energy transfer (E') can be calculated as the ratio of net secondary productivity to net primary productivity. It is termed apparent because the common usage of this term deals only with cases where all food available to herbivores is produced by phytoplankton and utilized as either live cells or phyto-detritus. In this study, especially at station A3, there is an additional source of carbon in the form of terrigenous and sewage derived detritus.

There is a good deal of confusion in the terminology of efficiencies in the literature. Transfer efficiency as described here, has been considered analogous to Slobodkins (1962) ecological efficiency, which is defined as the ratio of yield from trophic level "n" to the yield from trophic level "n-1". Since transfer efficiencies deal with total

net production at n, values must be less than or equal to those of ecological efficiencies. The term transfer efficiency has also been considered synonomous with food chain efficiency. This is only true when populations are in steady state, so that the population of herbivores consumes all the net production of food. This is rarely the case in temperate areas, although it may be approximated in the tropics.

Primary productivity on a per volume basis was approximately equal at both stations during May and November, but was higher at station A3 during June, and lower during February and March. Maximum rates at both stations occurred in June with values of 231 at station A3 and 83 mgC m^{-3} day^{-1} at D5. Minimum values at both stations occurred during November, and were less than 10 mgC m^{-3} day^{-1}.

Except for one anomalously high value at station D5, all values of E' were between 0 and 33%. Higher efficiencies occurred during the summer and fall at both stations with a maximum of 66% in June at station D5 and 33% in November at A3. Values decreased to 0 - 4% at both stations during February and March.

The extremely low efficiencies found during the winter were related to the differential response of copepods and phytoplankton to low temperatures. During February and March,

while rates of primary productivity and biomass of phytoplankton were high, copepod assimilation and NP were at a yearly low, thus resulting in low trophic efficiencies.

The ratio of GP due to phytoplankton primary productivity was less than 0.1 when temperatures were below 8°C, but increased rapidly with rising temperatures (Fig. 31). This was due to both the direct effects of temperatures and the blooms of C. tripos. Transfer efficiency was inversely related to primary productivity when temperatures were greater than 8°C (Fig. 32) and reflected increasing feeding activity and growth of copepods.

8.0 DISCUSSION AND CONCLUSIONS

8.1 Net secondary productivity

The estimates of NP are compared to those found by other authors for mixed zooplankton and copepod populations in Table 16. In similar shallow coastal areas, such as Long Island Sound and Georges Bank, annual rates of NP ranged between 166 and 200 mgC m^{-2} day^{-1}. Weighted yearly averages of NP were 33 and 145 mgC m^{-2} day^{-1} in the estuary and apex, respectively. Heinle's (1966) estimate of 77 mgC m^{-2} day^{-1} for the dominant copepod, Acartia tonsa, during the summer in Chesapeake Bay, is very similar to an estimated 67 mgC m^{-2} day^{-1} found in the estuary in June of this study.

Figure 31. Ratio of gross secondary productivity derived from phytoplankton assimilation to primary productivity, as a function of temperature at stations A3 (0) and D5 (●).

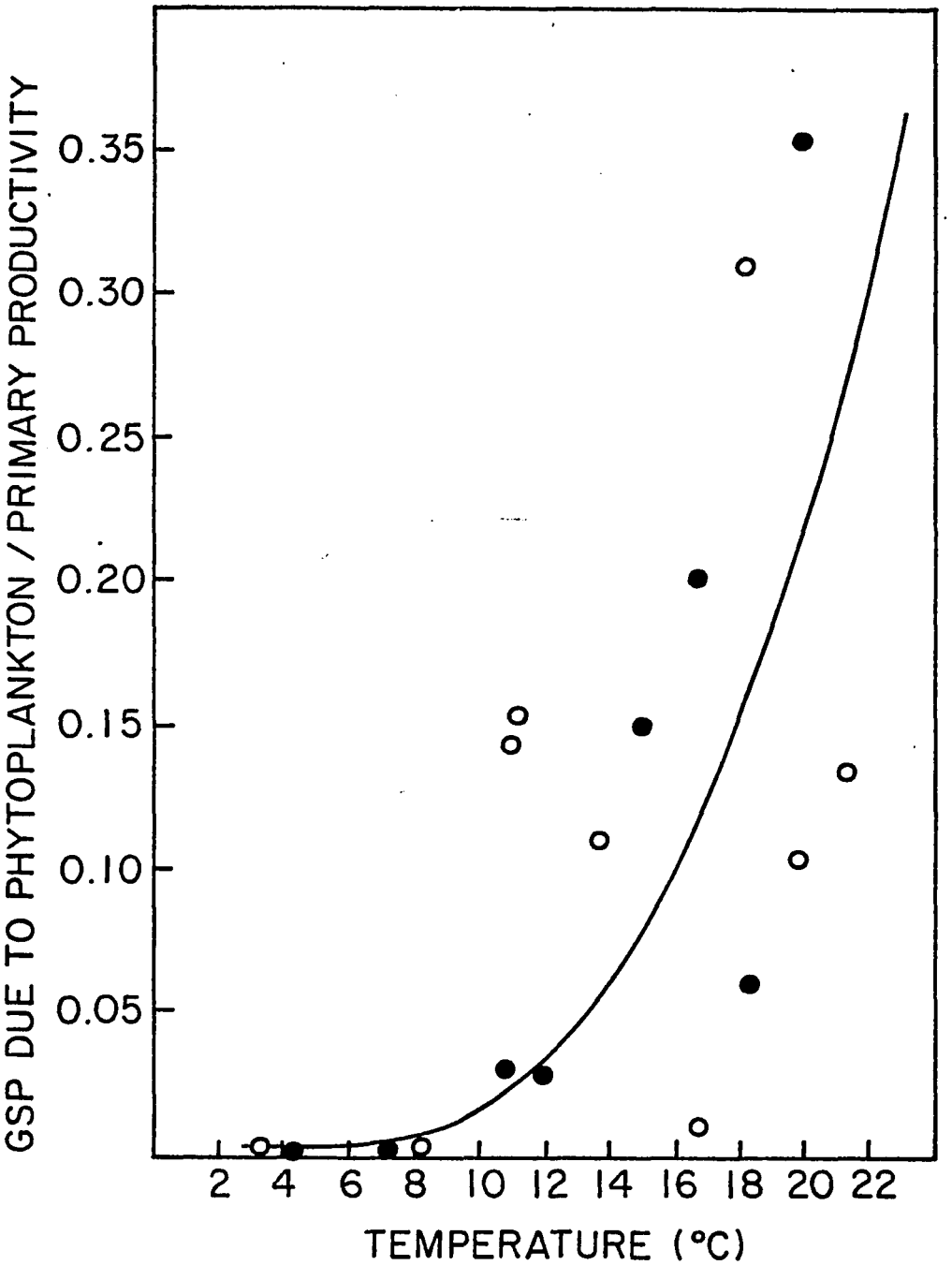

GSP DUE TO PHYTOPLANKTON / PRIMARY PRODUCTIVITY
0.35
0.30
0.25
0.20
0.15
0.10
0.05
2 4 6 8 10 12 14 16 18 20 22
TEMPERATURE (°C)

Figure 32. Transfer Efficiency (E') as a function of primary productivity (mgC m^{-2} day^{-1}) at stations A3 (0) and D5 (●). Dashed regression line redrawn from Cushing (1961).

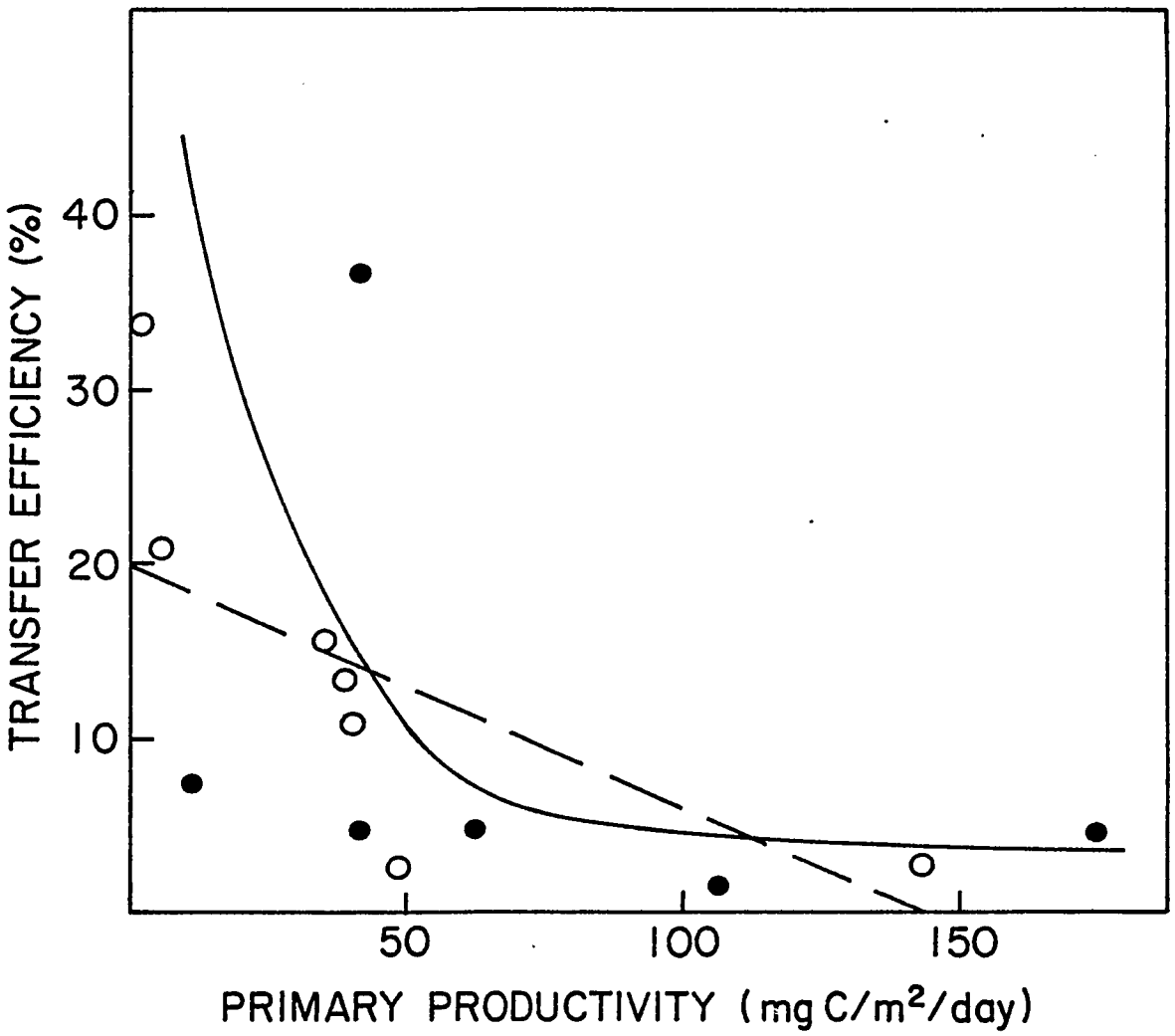

TRANSFER EFFICIENCY (%)
40
30
20
10
50
100
150
PRIMARY PRODUCTIVITY (mg C/m²/day)

Table 16. Literature values for secondary productivity (net) and efficiency of energy transfer (after Mullin, 1966).

Group	Area and Period	Net Prod. MgC/m^2day^{-1}	Daily Prod./ Standing Crop	Net Second. Prod./ Net Primary Prod.	Ref.
Zooplankton	Georges Bank; year	200	0.03	25.0	1
Zooplankton	English Channel; year	75	0.10	30.0	2
Zooplankton	Long Island Sound; year	166	0.17	30.0	3
Zooplankton	North Sea; April - Sept.	180	0.06	57.0	4
Herbiverous Copepods	North Sea; January-June	5	0.08	14.0	5
Mixed Copepods (mainly *Calanus*)	North Sea; March-June	46	0.10	20.0	6
Acartia tonsa	Chesapeake Bay Estuary; Summer	7-	0.50	5.0	7
Mixed Copepods	Hudson River Estuary				
	May	19.4	0.16	2.0	present work
	June	67.0	0.54	8.0	
	November	3.5	0.36	26.0	
	February - March	4.2	0.07	2.0	
	Average	33.2	0.34	12.0	
	New York Bight				
	May	18.5	0.01	0.1	
	June	211.0	0.35	24.0	
	November	20.0	0.36	6.0	
	February - March	7.5	0.04	0.5	
	Average	145.2	0.28	8.0	

References:
(1) Riley (1947)
(2) Harvey (1950)
(3) Conover (1956)
(4) Steele (1958)
(5) Cushing (1959)
(6) Cushing and Vucetic (1963)
(7) Heinle (1966)

Comparisons of this sort are of limited value due to the variety of means employed in obtaining the estimates of production but they at least indicate the correct order of magnitude of NP. It is not possible, however, to determine if the differences seen in Table 15 are real or a function of diverse methodology.

Rates of NP are affected by two classes of factors; 1) those that influence growth rates, such as temperature, body weight, quantity and quality of food, etc., and 2) those that affect the standing crops of organisms, such as growth, entrainment or wash out of organisms due to water circulation, and predation by carnivores.

The latter category has been seen to include mixing, advection, wash out of estuarine organisms during spring runoff, and influxes of swarms of carniverous ctenophores during the late summer.

While factors such as temperature and body weight affected NP uniformly at both stations, the concentrations of food and the proportion of the diet composed of detritus were quite different. The greater utilization of detritus at station D5, and its higher metabolic cost, resulted in decreased growth efficiencies and NP at station D5.

It is possible that the influence of temperature on NP was moderated by diurnal vertical migrations of copepods (McAllister, 1968). Such migrations are probably of little importance in the shallow, estuarine area of A3, but may have been important in the deeper, more thermally stratified apex region. Under conditions of thermal stratification, vertically migrating copepods would feed at the surface at a relatively warm temperature and return to the deeper, cooler layer during the night. The effect of such migrations would be a reduction of metabolic rates during the time spent at cooler temperatures, and higher growth rates than those predicted by incubation copepods for 24 hours at the warmer surface temperatures. Consequently, estimates of net growth efficiency may have been too low if such a phenomenon were of importance. The total gain of energy from such migrations would be offset somewhat by loss of energy expended in migrations.

At both stations, the combined effects of low biomass, low temperature and the abundance of C. tripos, probably resulted in low NP during the winter.

8.2 Grazing pressure of copepods on phytoplankton

In both the estuary and the apex, peaks in copepod assimilation rates, abundance and resultant grazing pressure closely followed spring and summer nanoplankton blooms.

During this time, up to 17% of the standing crop of phytoplankton was assimilated daily. Feeding experiments indicated that copepods showed size selectivity during the spring-summer period and were preferentially removing netplankton cells. Copepods removed up to 32% of the standing crop of netplankton daily.

The winter months were characterized by depressed assimilation rates, copepod abundance and resultant grazing pressure, and periods of netplankton blooms. At this time less than 0.01% of the standing crop of phytoplankton was assimilated daily, and there was a strong selection against netplankton cells.

The seasonal changes in selectivity for netplankton coupled with the inverse relationship between netplankton biomass and copepod grazing pressure, suggests that copepods were important in regulating netplankton populations. The observation by Malone (1976a) that winter increases in netplankton blooms were not associated with increased growth rates, is consistent with the conclusion that release from grazing pressure was important in triggering the netplankton blooms.

Riley et al. (1949) and Margalef (1958) point out that even a slight preference for certain phytoplankton species, exerted over just a few weeks, could have a profound effect

on the species composition of phytoplankton communities. Mullin (1963) concluded that copepod feeding would result in the removal of a greater biomass of large or chain form phytoplankton species than small unicellular forms due to size selectivity.

8.3 Transfer efficiencies (E')

Transfer efficiencies found in this study were in the range of reported values (Table 16). Values averaged for the entire year or selected seasons for total zooplankton were reported by authors as between 25% and 57%, with values of 5% - 20% for mixed herbivore or copepod populations. Calculations of E, in my study, are not comparable since they are estimated only over a daily period and do not take into account the animals life cycle, reproductive patterns and egg production. The daily efficiencies ranged from 0 - 66%, and if averaged over the year, were 12% and 8% at A3 and D5 respectively. These low efficiencies were due, in part, to the large quantities of detritus assimilated.

Slobodkin (1962) suggested that ecological efficiencies of 20% - 25% might be found in areas where herbivores were increasing under conditions of plentiful food (as occurred at station A3 in June). He also stated that anomalously high rates of greater than 25% were possible since 1) zooplankton and copepods represented more than one trophic level and so would yield apparently high efficiencies, 2) cannabilism or

predation by one group of animals on another of the same trophic level would also give rise to high apparent efficiencies, and 3) communities, such as temperate area, which are not in steady state would give rise to violent and rapid fluctuations such that efficiencies could temporarily appear to be quite high.

Cushing (1961) suggested that the inverse relationship between productivity and efficiencies was due to superfluous feeding as described by Beklemishev (1964). However, as shown by Conover (1966c) and Mullin (1963), assimilation efficiencies do not decrease with increasing food concentrations. The constancy of assimilation efficiency with respect to food concentrations makes Cushing's hypothesis doubtful. The explanation may lie in the type of food chain interactions that occur in areas characterized by high productivity.

Parsons and Takahasi (1975) pointed out that estimates of ecological efficiency may be misleading since they do not take into account either recycling of materials not respired or inputs other than phytoplankton derived material. Both of these factors are very important in the energetics of the estuarine-apex region.

If phytoplankton were limiting, the incorporation of detritus would allow communities of copepods to sustain themselves until more favorable conditions occurred. It is probable that while detritus may be used for maintenance, it is a poor substrate for active growth or reproduction. Dagg (1977) concluded that estuarine copepods are not able to

survive even short periods of starvation. The ability to assimilate detritus would thus be very important in their survival. The respiratory rates at station D5 and the direct relationship between respiration and detritus assimilation of detritus would thus increase secondary productivity (if detritus were of phytoplankton origin), act as a buffer between phytoplankton and zooplankton, and increase the efficiency of transfer from phytoplankton to herbivores.

In cases where both detritus and phytoplankton concentrations are high, detritus may act to decrease phytoplankton assimilation. This may be due to clogging of filtering processes or by decreasing the probability that any grazer will encounter a given phytoplankton cell. Further, since detritus is metabolized less efficiently than phytoplankton, its incorporation in the place of high quality phytoplankton would act to decrease net secondary productivity and apparent ecological efficiencies.

9.0 Summary

Changes in standing crops of copepods are related to rates of growth, reproduction, advection or predation. While at any one point in time they act concurrently, their relative importance was seen to vary seasonally. Data presented here suggest that (1) The increase in food available in the

form of phytoplankton during the spring was correlated with increases in copepod biomass. During this period a large proportion of nanoplankton (up to 24.3%) and netplankton (up to 32.4%) standing crop enters copepod food chains daily. Intense grazing pressure may thus be a primary limiting factor for spring phytoplankton blooms. (2) Phytoplankton production occurring during winter netplankton blooms was largely ungrazed by copepods, less than 0.1% of the phytoplankton standing crop being assimilated daily. The lack of response of copepods was due to the limiting effects of low temperatures. (3) The positive correlation between assimilation and temperature and the lack of any indication of temperature inhibition or food limitation, resulted in near optimal growth conditions for copepods during the summer. The observed decreases in copepod density coupled with increases in ctenophore populations suggest predation was an important limiting factor at this time. (4) Increases in copepod abundance during the late fall of 1973 were due to both advection of offshore immigrants and release from summer grazing pressure. (5) Copepod feeding preferences with respect to phytoplankton size classes varied seasonally. Preferential selection of netplankton during the spring and summer was responsible, at least in part, for the decline of netplankton biomass which occurred at this time in spite of increasing netplankton growth rates.

During the winter, netplankton were selected against. This was probably due to the avoidance of Ceratium tripos which dominated the netplankton. The negative selection against netplankton coupled with the sharp decrease in total grazing pressure removed copepods as a selective cropping factor and facilitated the onset of the winter netplankton blooms. (6) During most of the year concentrations of POC were so high as to not be limiting to copepod growth. Removal of POC by copepod grazing was not sufficient to obviously affect levels of POC. (7) Concentrations of approximately 0.6 mgC l^{-1} represent upper feeding thresholds. (8) Rates of assimilation and respiration were a function of seasonal changes in temperature and body weight of copepods. (9) Detritus is utilized as a food source by copepods in both the estuary and the apex. (10) Detritus is metabolized less efficiently than phytoplankton, and results in decreased growth efficiencies. (11) The incorporation of detritus in place of available phytoplankton results in decreased net secondary productivity and transfer efficiencies.

Appendix I. Taxonomic composition of zooplankton

Date	Copepoda	CLADOCERA Evadne	Penila	Others	MYSIDACEA	CHAETOGNATH	TUNICATA Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate	Mysis	Fish
9/28/73	6239	14	0	0	0	0	0	0	0	7	0	0	0	10
10/28/73	9125	266	2	0	0	0	0	0	0	0	12	0	0	0
11/17/73	43	1	0	0	0	0	0	0	0	0	0	1	0	0
12/15/73	38	0	0	0	+	0	0	0	0	0	0	+	0	0
1/26/74	54	0	0	0	0	+	0	0	0	0	0	0	0	0
2/16/74	275	0	0	0	+	+	0	0	0	0	0	0	0	+
4/10/74	194	2	0	0	0	0	0	0	0	0	1	0	0	0
4/27/74	958	1	1	0	0	0	0	0	0	0	2	0	0	0
5/25/74	146	45	0	0	+	0	0	0	6	0	+	0	0	0
6/ /74	6722	95	0	0	0	0	0	0	0	0	0	5	0	2
7/ /74	1571	680	0	0	0	0	0	0	0	0	0	0	0	0
8/1 /74	21404	0	0	0	0	0	0	0	0	0	0	0	0	0
4/21/75	1524	0	0	0	2	5	0	0	2	0	0	11	0	3
5/4/75	1213	0	0	0	6	+	0	0	1	0	0	108	6	0
5/13/75	1975	0	0	0	3	0	0	0	0	0	0	31	5	0
5/20/75	1268	146	0	20	0	0	0	0	0	0	0	102	3	1
5/27/75	1179	4	0	7	0	0	0	0	2	0	0	62	3	0
6/6/75	3566	24	0	47	0	3	0	0	0	7	0	104	2	5
6/10/75	1763	1	0	16	1	0	0	0	2	4	0	22	5	10
6/18/75	2608	0	0	60	0	0	0	0	0	0	0	47	5	0

(1) During 1973 counted as total Cladocera, and tun
(+) Less than $1/m^3$
(#) Present but could not be quantified

...ic composition of zooplankton at station A3

TUNICATA Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate	Mysis	Fish	Zoae	*Balanus* spp. nauplii	*Balanus* spp. cyprid	Lamellibranch	Others	CTENOPHORA	TOTAL
0	0	0	7	0	0	0	10	0	0	0	0	10	0	6290
0	0	0	0	12	0	0	0	0	0	0	17	0	0	9512
0	0	0	0	0	1	0	0	0	0	0	0	0	0	45
0	0	0	0	0	+	0	0	0	0	0	+	0	0	36
0	0	0	0	0	0	0	0	0	+	0	0	0	0	56
0	0	0	0	0	0	0	+	0	0	0	+	26	0	307
0	0	0	0	1	0	0	0	0	0	0	0	+	0	206
0	0	0	0	2	0	0	0	0	6	0	0	0	0	977
0	0	6	0	+	0	0	0	2	221	81	0	0	0	493
0	0	0	0	0	5	0	2	0	0	0	0	0	0	6972
0	0	0	0	0	0	0	0	8	0	0	0	0	#	2301
0	0	0	0	0	0	0	0	0	0	0	0	0	#	21410
0	0	2	0	0	11	0	3	0	0	1	0	0	0	1553
0	0	1	0	0	108	6	0	2	40	0	0	0	0	1368
0	0	0	0	0	31	5	0	0	777	0	0	0	0	2694
0	0	0	0	0	102	3	1	0	8182	40	0	0	0	9738
0	0	2	0	0	62	3	0	2	2552	54	0	0	0	3981
0	0	0	7	0	104	2	5	0	1993	161	0	0	0	5914
0	0	2	4	0	22	5	10	0	2591	170	0	0	0	4562
0	0	0	0	0	47	5	0	1	362	25	0	0	0	3109

...ed as total Cladocera, and tunicates.

... not be quantified

Appendix I. Taxonomic composition of zoop

TAXON / Date	Copepoda	CLADOCERA	Evadne	Penila	Others	MYSIDACEA	CHAETOGNATH	TUNICATA	Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE	Polycheate	Mysis	
6/24/75	1805	0		0	87	0	0	0		0	0	0	0		17	9	
7/10/75	3664	0		0	5	0	0	0		0	0	8	12		21	66	
7/16/75	5439	0		0	0	0	0	0		0	0	0	0		#	0	
7/25/75	1094	0		0	0	0	0	0		0	0	0	0		21	7	7
8/8/75	141	0		0	0	0	0	0		0	0	0	+		+	0	
10/29/75	104	0		0	0	1	0	0		0	0	0	0		0	0	
11/12/75	138	0		0	0	0	0	0		0	0	0	0		0	0	
11/24/75	118	0		+	0	+	+	0		0	0	0	0		+	0	
2/7/76	38	0		0	0	0	+	0		0	+	0	0		+	0	
2/21/76	44	0		0	0	2	0	0		0	0	0	0		0	0	
3/1/76	26	0		0	0	+	0	0		0	0	0	+		0	0	
3/6/76	59	0		0	0	0	+	0		0	0	+	0		0	0	
3/14/76	23	0		0	0	0	0	0		0	0	0	0		0	0	
3/20/76	736	0		0	0	0	4	0		0	0	0	0		0	0	
3/31/76	1756	0		0	0	4	7	0		0	5	22	0		15	0	

(1) During 1973 counted as total Cladocera and tunicates.
(+) Less than 1/m^3
(#) Present but could not be quantified

Taxonomic composition of zooplankton at station A3 (continued)

TUNICATA		MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE									
Doliolum	Okipleura				Polycheate	Mysis	Fish	Zoae	Balanus spp. nauplii	Balanus spp. cyprid	Lamellibranch	Others	CTENOPHORA	TOTAL
0	0	0	0	0	17	9	1	0	55	52	0	0	0	2060
0	0	0	8	12	21	66	0	0	154	20	0	0	#	3984
0	0	0	0	0	#	0	0	#	#	#	0	0	#	5450
0	0	0	0	0	21	7	77	2	10	2	0	0	#	1114
0	0	0	0	+	+	0	0	+	+	2	0	0	#	144
0	0	0	0	0	0	0	0	0	0	+	0	0	0	106
0	0	0	0	0	0	0	0	0	5	5	0	0	0	153
0	0	0	0	0	+	0	0	0	0	0	0	0	0	119
0	0	+	0	0	+	0	0	+	+	0	0	0	0	39
0	0	0	0	0	0	0	0	0	0	0	+	0	0	45
0	0	0	0	+	0	0	0	0	0	0	11	0	0	27
0	0	0	+	0	0	0	0	+	+	0	0	0	0	61
0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
0	0	0	0	0	0	0	0	0	0	0	0	0	0	744
0	0	5	22	0	15	0	2	0	21	0	0	0	0	1832

otal Cladocera and tunicates.

quantified

Appendix II. Taxonomic composition of zoopla

Date	Copepoda	CLADOCERA	Evadne	Penila	Others	MYSIDACEA	CHAETOGNATH	TUNICATA	Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate
9/28/73	2696	3116	0	0	3	3	85	0		0	0	18	3	
10/28/73	7993	6848	0	0	0	0	0	0		0	0	0	0	
11/17/73	7385	38	0	0	0	0	0	0		0	0	38	26	
12/15/73	267	0	0	0	+	4	0	0		0	0	+	0	
1/26/74	2309	0	0	0	6	0	0	0		0	0	0	0	
2/16/74	532	0	0	0	0	11	0	0		0	0	0	0	
4/10/74	168	2	0	0	0	2	+	0		0	0	1	5	
4/27/74	708	5	0	0	0	9	19	0		0	0	+	0	
5/25/74	5531	0	0	0	0	95	5	0		10	0	0	0	
6/ /74	3543	0	0	0	0	3	0	0		0	0	0	0	
7/ /74	1305	0	0	0	0	0	1576	0		0	0	0	0	
8/1/74	21404	191	0	0	0	0	542	0		0	0	0	0	
4/21/75	763	1	0	0	1	27	0	7		7	270	0	0	
5/4/75	681	107	16	1	0	51	0	10		3	242	0	9	
5/13/75	1305	399	0	+	0	23	0	0		+	259	0	11	
5/20/75	824	4458	159	0	0	64	0	0		0	73	0	31	
5/27/75	4861	4284	579	0	0	151	0	0		38	30	0	0	
6/6/75	6036	0	0	3	0	244	0	0		0	0	0	0	
6/10/75	2149	0	0	0	4	14	0	0		2	0	0	0	
6/18/75	10003	0	0	0	0	0	0	0		2	0	0	0	
6/24/75	12575	10	0	0	0	0	0	0		0	108	12	0	

(#) Present but could not be quantified.
(1) During 1973 counted as total Cladocera, and tunicate
(+) Less than 1/m^3

c composition of zooplankton at station D5.

Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate	Mysis	Fish	Zoae	Balanus spp. nauplii	Balanus spp. cyprid	Lamellibranch	Others	CTENOPHORA	TOTAL
85	0	0	0	18	3	0	0	0	0	0	54	69	0	6325
0	0	0	0	0	0	0	0	10	0	0	2318	0	0	17170
0	0	0	0	38	26	0	0	0	0	0	350	42	0	7930
0	0	0	0	+	0	0	0	0	0	0	14	6	0	286
0	0	0	0	0	0	0	0	0	0	0	98	12	0	2434
0	0	0	0	0	0	0	0	0	+	0	2	4	0	523
+	0	0	0	1	5	0	0	0	3	0	7	11	0	213
19	0	0	0	+	0	0	0	7	0	0	14	7	0	1185
5	0	10	0	0	0	0	5	+	0	0	0	124	0	5775
0	0	0	0	0	0	0	0	0	3	0	188	0	0	3741
76	0	0	0	0	0	0	12	3	0	0	0	0	#	2913
42	0	0	0	0	0	0	4	0	0	10	0	0	#	1186
0	7	7	270	0	0	0	2	2	+	0	0	0	0	1061
0	10	3	242	0	9	2	64	35	8	2	0	0	0	1267
0	0	+	259	0	11	7	3	3	2	0	0	0	0	2012
0	0	0	73	0	31	0	3	3	3	0	0	0	0	5620
0	0	38	30	0	0	22		130	268	109	0	0	0	10520
0	0	0	0	0	0	0	31	26	0	6	0	0	0	6356
0	0	2	0	0	0	0	0	0	0	14	0	0	0	2185
0	0	2	0	0	0	0	29	9	0	0	0	0	0	10229
0	0	0	108	12	0	0	13	0	0	10	0	0	#	13146

ntified.
Cladocera, and tunicates.

Appendix II. Taxonomic composition of zooplank

Date	Copepoda	CLADOCERA Evadne	Penila	Others	MYSIDACEA	CHAETOGNATH	TUNICA Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate	Mysis
7/10/75	16859	0	0	0	0	0	0	0	0	0	0	0	0
7/16/75	13658	0	0	0	0	26	0	67	0	0	0	20	20
7/25/75	-	0	0	0	0	0	0	0	0	0	0	0	0
8/8/75	249	0	297	5	0	0	551	11	5	0	0	0	0
10/29/75	73	0	3	0	0	0	0	+	0	0	0	1	0
11/12/75	527	0	30	0	0	0	0	+	1	0	0	0	0
11/24/75	571	0	27	0	0	2	+	0	2	0	0	0	0
2/7/75	237	0	0	0	0	7	0	0	+	4	0	+	0
2/21/75	18	0	0	+	+	+	0	+	0	+	0	1	0
3/1/75	54	0	0	0	0	0	0	0	0	0	0	0	0
3/6/75	250	0	0	0	0	0	4	0	4	0	0	0	2
3/14/75	47	0	0	0	0	0	0	0	13	0	2	0	0
3/20/75	1072	0	0	0	0	22	0	848	0	72	0	65	0
3/31/75	2122	0	0	0	0	61	0	410	8	0	0	0	0

(1) During 1973 counted as total Cladocera, and tunicate
(+) Less than $1/m^3$
(#) Present but could not be quantified.

xonomic composition of zooplankton at station D5 (continued)

CHAETOGNATH	TUNICA Doliolum	Okipleura	MEDUSAE	GASTROPODA	AMPHIPODA	LARVAE Polycheate	Mysis	Fish	Zoae	Balanus spp. nauplii	Balanus spp. cyprid	Lamellibranch	Others	CTENOPHORA	TOTAL
0	0	0	0	0	0	0	0	74	0	0	15	0	0	#	16934
26	0	67	0	0	0	20	20	0	0	0	0	0	0	#	13771
0	0	0	0	0	0	0	0	0	0	0	0	0	0	#	-
0	551	11	5	0	0	0	0	0	0	0	0	0	0	#	1122
0	0	+	0	0	0	1	0	+	0	0	0	0	+	0	79
0	0	+	1	0	0	0	0	0	0	0	0	0	5	0	603
2	+	0	2	0	0	0	0	0	0	0	0	0	+	0	603
7	0	0	+	4	0	+	0	0	+	0	0	0	2	0	250
+	0	+	0	+	0	1	0	0	0	1	0	1	0	0	22
0	0	0	0	0	0	0	0	0	0	1	0	11	0	0	66
0	4	0	4	0	0	0	2	0	0	2	12	42	14	0	301
0	0	0	13	0	2	0	0	0	0	0	0	4	3	0	68
22	0	848	0	72	0	65	0	0	0	65	0	158	16	0	2416
51	0	410	8	0	0	0	0	1	0	2	0	0	0	0	2604

as total Cladocera, and tunicates.

t be quantified.

Appendix III. Taxonomic composition o
on dates when feeding e

	COPEPOD SPECIE									
DATE	Acartia tonsa	A. clausi	A. species A	Eurytemora americana	Temora longicornis	Oithona similis	O. brevicornis	Pseudocalanus minutus	Centropages typicus	C. hamatus
5/13/75		638		723	67		20	34		
6/6/75	2407		221	189	325	189		100	103	
6/18/75	524	571	1166		130	120	5	31		4
6/24/75		107	1514		43	22			117	
7/10/75		1385	1583			88			44	
11/12/75	131								4	
11/24/75	37	58	9			2			9	
2/21/76				62		13				
3/31/76	683			376	293	14		14		

. Taxonomic composition of copepods at station A3 on dates when feeding experiments were run.

	COPEPOD SPECIES												
	Temora longicornis	Oithona similis	O. brevicornis	Pseudocalanus minutus	Centropages typicus	C. hamatus	Paracalanus parvus	Tortanus discaudatus	Calanus finmarchicus	Metridia sp.	Harpacticoid spp.	Eucalanus sp.	Immature (copepodites and nauplii)	TOTAL COPEPODS
3	67		20	34			8				460			1975
9	325	189		100	103					14				3566
	130	120	5	31		47		5						2608
	43	22			117									1805
		88			44								564	3664
					4								4	138
		2			9	2	3							118
2		13									5			44
6	293	14		14							106		269	1756

Appendix IV. Taxonomic composition on dates when feeding

	COPEPOD SPECIES									
DATE	Acartia tonsa	A. clausi	A. species A	Eurytemora americana	Temora longicornis	Oithona similis	O. brevicornis	Pseudocalanus minutus	Centropages typicus	
5/13/75					586	172	5	619	27	
6/6/75		79			1612	3802		127	320	
6/18/75					2961	3231	40		3751*	
6/24/75					8224	880		1622	1798	
7/10/75		169	253		8143	2731		1602	3776	
11/12/75	7	437				21			53	
11/24/75	89	232	4			81		23	91	
2/21/76				#		13	#	1	#	
3/31/76					113	949	278		113	

* Includes both C. typicus and C. hamatus

\# Present in concentrations of less than 1 org

x IV. Taxonomic composition of copepods at station D5 on dates when feeding experiments were run.

	COPEPOD SPECIES											
	Oithona similis	O. brevicornis	Pseudocalanus minutus	Centropages typicus	C. hamatus	Paracalanus parvus	Tortanus discaudatus	Calanus finmarchicus	Metridia sp.	Harpacticoid spp.	Eucalanus sp.	Immature (copepodites and nauplii)	TOTAL COPEPODS
36	172	5	619	27						5			1305
.2	3802		127	320								97	6036
51	3231	40		3751*		10							10003
24	880		1622	1798				25			38		12575
13	2731		1602	3776		169							16859
	21			53		7							527
	81		23	91		50		2					571
	13	#	1	#		#						2	18
.3	949	278		113				448				223	2122

typicus and C. hamatus

itrations of less than 1 organism m^3

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