AN ABSTRACT OF THE THESIS OF

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The structural capabilities and functional grazing responses of the developmental stages (CI to adult) of Pseudocalanus sp. and Acartia clausi were studied in the laboratory to determine the onset of adult feeding behavior in each species, and the probable mechanisms employed in feeding by the different developmental stages. Based on the distribution of intersetule spacings on the second maxilla, all developmental stages of Pseudocalanus could theoretically specialize on small cells (5 um) within a particle spectrum. In the laboratory, grazing experiments using two food particles (the diatom, Thalassiosira fluviatilis = T. weissflogii; and the flagellate, Isochrysis galbana), overall selection patterns on the 2-15 um cells were not considered significantly different from random feeding for Pseudocalanus copepodites, and for the younger stages of Acartia. The Acartia female was the only stage which selected particles not expected by the mechanistic model of feeding in copepods.

The grazing impact of natural populations of Pseudocalanus sp. and Acartia clausi were studied during the spring bloom period in a semi-enclosed embayment within Puget Sound, Washington. The combined copepodite population of Pseudocalanus (stages CI-CV) theoretically grazed 1.6 - 2.9 times more than the female population during low and high food levels, respectively. Acartia females theoretically removed 0.6 - 0.8 times the combined removal of cells by all its copepodite stages. The grazing removal by adult females was the highest stage-specific rate cal-

culated for both species. Pseudocalanus may maintain high population levels by specializing on abundant small cells. Acartia may maintain equivalent population levels in the field by actively assessing changes in the quality and/or quantity of cells within natural particle spectra, and by modifying their food ration to take advantage of particle peaks as they develop in time and space.

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult)

by

Barbara Lynne Dexter

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as the waves pull me down
and the frothy turbulence rises 'round me,
i lose sight of the world i have known
and begin a new journey:
for i have not passed this way before
and the unknown sends out it's chilling fingers
to numb my core and test my strength.

with my head subsurface now
i am falling fast, flowing free
yet bouyed up from below
by the incessant swash of wave upon wave,
knowing all too well
that this same life-giving force
will take me out to sea again:
for each day the current grows stronger,
the waves more eroding;
but here, too, lies my destiny.

my heels sink deep into the garnet sands of "B Street",
my ears roaring with the crash of each wave,
the lonely cries of seagulls fishing overhead
i stop to save a crab shell from its fate
on an incoming wave,
to remember one last time all that I've shared here,
and then to forget the tears of living
and go on.

my hair grows tangled and matted by the offshore breeze,
the sky softly clouded with a comforting bank of fog
lying just offshore,
just out of reach;
and my steps slowly turn
in their rightful direction
as i walk to my beginning
and toward my end.

bld
B Street Beach
Newport, Oregon

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CHAPTER 1

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult).

General Introduction

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult).

General Introduction

Statement of the Problem

A major focus of research by planktonologists over the past several years has been a study of the feeding responses of zooplankton under a variety of experimental and field conditions. From both an experimental and an ecological point of view, a central point of interest in these studies has been the feeding patterns and grazing capabilities of calanoid copepods. The apparent plasticity of their feeding responses under varying food situations, the mechanisms by which food capture occurs, and even such basic physical information as the hydrodynamic forces which act at the size and space scales on which feeding occurs for marine plankton, have all recently been investigated as theoretical considerations (Lam and Frost 1976, Lehman 1976, Donaghay 1980b, Poulet and Marsot 1980), in laboratory experiments (e.g., Richman *et al.* 1977, Donaghay and Small 1979, Landry 1981, Harris 1982), and through direct, behavioral observations (e.g., Alcaraz *et al.* 1980, Koehl and Strickler 1981, Strickler 1982).

Historically, feeding in copepods has been described as a filtering process in which swirls of water established by the synchronous beating of the feeding appendages move particles toward the mouthparts (Cannon 1928, Marshall and Orr 1956, Marshall 1973). Based on these early studies, particles were reportedly sieved from the water by impingement on the second maxillae, and transferred to the mouth by the first maxillae. The second maxillae and mandibles have thus been considered the appendages of primary importance in the feeding processes of herbivorous copepods, and several studies have indicated their

relationship to the size, type, and range of particles eaten by copepods (Anraku and Omori 1963, Frost 1972b, Marshall 1973, Schnack 1975, Boyd 1976, Nival and Nival 1976). However, microcinematographic observations of large calanoid copepods (e.g., Eucalanus pileatus) have indicated that copepods live and eat at scales in which viscous rather than inertial forces operate (Alcaraz et al. 1980, Zaret 1980, Koehl and Strickler 1981). Rather than working as sieves, recent studies have indicated that the second maxillae may be functionally smooth, and may act as paddles to preferentially position and redirect water parcels containing algae toward the body. The feeding appendages may also be used to reorient the body with respect to a parcel of water containing food particles. Once in the vicinity of the mouthparts, these direct observations indicated that only water containing particles was actually squeezed through the mesh of the second maxillae, and transferred to the mouth for ingestion.

The mechanisms of food capture in copepods may thus be quite different from the textbook descriptions of filtration, although ultimately, cells are removed from the water by the filtering apparatus, and some form of selection must occur when a particle is approached or encountered, and/or when a particle is transferred to the mouth orifice for ingestion. Although the microcinematographic technique is an important tool to use in understanding copepod feeding behavior, it must be extended to observations of small copepods as well before the above interpretation is accepted for copepods in general. These direct observations of feeding indicate a response appropriate for a large copepod with limited setular complexity. However, different capabilities may have evolved in smaller, coastal copepods which have complicated arrangements of setules on the filter, and live in a high-particle-abundance environment.

Another concept which has engendered a great deal of interest is whether copepods are able to actively assess

the quality or quantity of their food resource on other than a mechanistic, size-selective basis (Boyd 1976, Richman et al. 1977, Donaghay and Small 1979, Donaghay 1980a, Poulet and Marsot 1980). Selection of cells on the basis of particle size appears to be an important component in the feeding responses of large, oceanic copepods (Frost 1972a, Cowles 1979, Donaghay 1980b, Harris 1982). However, a number of studies with small, coastal copepods have indicated (1) the apparent active selection of particular cell types on other than a size-related basis (e.g., the preconditioning effects of Donaghay and Small 1979), (2) the ability to "track" the temporally changing shape of the food distribution, and to respond by sequentially ingesting cells from a variety of different abundance peaks (the "tracking behavior" of Richman et al. 1977), (3) the ability to switch between plant and animal prey as the relative concentrations varied (Landry 1981), and (4) the ability to select a higher quality item over a low quality food (Poulet and Marsot 1980, Huntley 1982), or to actively reject a non-food particle (Donaghay and Small 1979). These data have been used to hypothesize that at least some copepods have the ability to actively assess the quality of their food resource, perhaps by a chemosensory mechanism (Friedman and Strickler 1975, Poulet and Marsot 1980), or behavioral capability (Richman et al. 1977, Donaghay 1980b), or by a physiological acclimation response (Mayzaud and Conover 1976, Cox 1982). However, several studies have also indicated the importance of adequately testing the simplistic null hypothesis of mechanistic size selection (Frost 1972a, Boyd 1976), and of specifically ruling out the possibility of experimental artifacts or biases which may occur in a laboratory grazing experiment (e.g., particle production, Deason 1980; particle modification, Gifford et al. 1981; ammonia excretion or other containment effects, Roman and Rublee 1980; and errors introduced by the use of electronic particle counters, Harbison and McAllister 1980).

Although in a sense, all planktivores may be considered selective feeders, researchers remain divided as to whether true, behavioral selection of food types occurs in herbivorous copepods. However, the variety of mechanisms which have been proposed as feeding responses in copepods are not necessarily contradictory interpretations. Instead, the apparently different responses which have been described may be indicative of the range of capabilities typical for oceanic vs. coastal and estuarine planktonic grazers.

Ecologically, copepods are a dominant taxon in the zooplankton of temperate marine ecosystems (Steele 1974, Steele and Mullin 1977, Steele and Frost 1978, Landry 1981). They play a major role in the transfer of energy through marine food chains (Parsons and LeBrasseur 1970, Steele 1974, Steele and Mullin 1977, Koehl and Strickler 1981), and may have significant effects on phytoplankton growth, abundance, and species composition (Raymont 1980, Koehl and Strickler 1981, Landry 1981). Planktonic grazers may thus also affect the overall stability of aquatic systems (Steele 1974, 1976; Landry 1976, 1981). In this regard, herbivorous copepods have been included as an important loss term for the phytoplankton in marine ecosystem models (Steele 1974, Steele and Mullin 1977, Steele and Frost 1978), since they are the major trophic link through which all primary productivity must pass (Steele and Mullin 1977).

Although typically younger life cycle stages vastly outnumber adult stages in copepod populations, most feeding studies have centered on the basic responses of adults, and primarily on adult females (with exceptions being the classic studies by Marshall and Orr 1956, and by Fernández 1979 for Calanus; Allan et al. 1977 for Acartia species; and the studies on Pseudoclanus reviewed by Corkett and McLaren 1978). The direct comparison of the feeding behaviors of different species under similar experimental or

field conditions has also been minimal (Harris 1982, but see Richman et al. 1977, Gamble 1978, Poulet 1978, Cowles 1979). Yet we are accruing a variety of data which indicate that at least some copepod feeding responses may be species-specific, and that it may be overly simplistic to model the grazing removal of a copepod species based solely on feeding responses of the adult, or on a weight basis for species comparisons.

Purpose of the Study

The objective of the present study was to directly compare the feeding capabilities and grazing responses of the developmental stages (CI to adult) of Pseudocalanus sp. and Acartia clausi. Three aspects of the ontogeny of feeding responses in these copepods were investigated:

(1) the structural limitations and capabilities imposed upon the different developmental stages of each species by the morphology of their feeding apparatus,

(2) the effects of phytoplankton size and concentration on the functional response of each copepodite stage under exactly the same experimental conditions, and

(3) preliminary behavioral observations and interpretation of the experimental grazing results to determine the onset of adult feeding responses, and the probable mechanisms employed in feeding by the different stages and species.

Measurements of the mandible and second maxilla were taken for specimens of each copepodite stage (CI to adult). These data were used to determine the theoretical structural capabilities which existed in each copepodite stage for the selection of particles, assuming a mechanistic, passive filtration model of copepod feeding. That is, the comparative morphology study (Chapter 2) used the working hypothesis that setal and setular dimensions of the filter, and mandibular dimensions of the jaws, were the primary morph-

ological characteristics of the mouthparts by which the range of particles eaten by a particular size of copepod was determined. Laboratory grazing experiments were then conducted using two species of cultured phytoplankton cells offerred as food items at four concentration levels (Chapter 3). The null hypothesis used for these experiments was that no differences in cell selection should occur due to (1) cell size or type, or (2) copepod size or developmental stage. It was assumed that the generally observed functional response of increasing ingestion rate with increasing cell concentration would be observed over the range of particle concentrations used (Frost 1972b). The grazing data were analysed on an individual (per animal) and a weight-specific basis for each developmental stage. The patterns of particle selection were determined using a variety of statistical techniques.

The species chosen to study were Pseudocalanus sp. and Acartia clausi. These copepods typically co-occur in temperate to boreal, nearshore to estuarine environments (Brodski 1964), and become dominant members of the zooplankton community in the coastal northeastern Pacific off Oregon (Peterson and Miller 1979) and Washington (Koeller et al. 1979). Based on studied of adult female feeding patterns, these species represent the probable range of feeding capabilities of small, herbivorous copepods. In the literature, Pseudocalanus has been primarily considered an herbivorous, passive filterer and a non-selective, "opportunistic" feeder (Poulet 1974) similar to Calanus species (Frost 1972b). Although Acartia species may feed omnivorously at times (Conover 1956, Marshall 1973, Lonsdale et al. 1978), A. clausi appears to have a wide range of feeding capabilities which allow it to actively select phytoplankton particles not expected by a mechanistic theory of passive filtration, and to reject non-food particles (Donaghay and Small 1979, Donaghay 1980a). Both species have been classified as "small" copepods in

the literature (e.g., Parsons et al. 1969, Koeller et al. 1979, Harris 1982). Yet they are sufficiently different in size and body weight to hypothesize differences in their developmental feeding capabilities, and thus in their subsequent grazing impact on a phytoplankton community (Frost 1972b). Considering the extensive overlap in the distributions of these two species, the high abundances typically reached during spring and summer in the coastal northeastern Pacific, and the fact that the total range of particles eaten by marine copepods is considered to be quite narrow (Raymont 1980, Harris 1982), one may hypothesize the existence of strong biotic interactions, and the potential for intense intraspecific and interspecific competition for food.

In order to study the grazing impact of natural populations of copepods, the laboratory grazing results were applied to a field situation in which populations of Pseudocalanus and Acartia developed together and became the dominant grazers in a semi-enclosed embayment within Puget Sound, Washington (East Sound, Orcas Island, the San Juan Island Archipelago, Washington, U.S.A.). Maximum and minimum estimates of the stage- and weight-specific grazing removal of each species were calculated in order to assess the impact of each population on the phytoplankton community in East Sound. Phytoplankton concentrations and zooplankton abundances from several dates representative of the biological and physical conditions present in the bay during winter, spring, and summer were used. The grazing impact of each species was calculated for each day, and for the mean conditions observed during periods of high phytoplankton abundance (bloom conditions), low phytoplankton abundance (background conditions), and for the seasonal mean conditions.

CHAPTER 2

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult)

I. Effects of Ontogenetic and Seasonal Body Size Variations on the Feeding Appendage Morphology of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult)

Developmental Grazing Capabilities of Pseudocalanus sp. and Acartia clausi (CI to Adult). I. Effects of Ontogenetic and Seasonal Body Size Variations on the Feeding Appendage Morphology of Pseudocalanus sp. and Acartia clausi (CI to Adult).

Introduction

The role of active versus passive selection for suspended food particles by herbivorous copepods remains a controversy for planktonologists (Rubenstein and Koehl 1977, Donaghay 1980a, Koehl and Strickler 1981). Recent studies have investigated whether the feeding process is primarily by chemosensory or tactile sensation (Friedman and Strickler 1975; Poulet and Marsot 1978, 1980), by some type of passive mechanistic filtration (Frost 1972a, Boyd 1976, Frost 1977), or by the active, behavioral selection of particular cells (Wilson 1973, Richman et al. 1977, Donaghay and Small 1979). Morphological measurements of copepod feeding appendages have been used to study the probable mechanisms involved in feeding, to estimate clearance rates or capture efficiencies for a spectrum of cell sizes, and to predict the type and size of particles eaten by presumably herbivorous, "filter-feeding" copepods (Anraku and Omori 1963, Marshall 1973, Schnack 1975, Nival and Nival 1976, Boyd 1976, Lam and Frost 1976, Lehman 1976, Rubenstein and Koehl 1977, Bartram 1981).

The present study reports morphological measurements of the major feeding appendages, the mandible and second maxilla, for the copepodite stages (CI to adult) of Pseudocalanus sp. and Acartia clausi. The working hypothesis for this comparative morphology study was that there was a direct and functional relationship between the pattern of setule spacings on the second maxilla and the dimensions of the mandible, and the spectrum of algal particles available to these copepods. Within this theoretical framework, the data were used to estimate the filtration or capture

efficiency for different-sized phytoplankton particles by each developmental stage. The maxillary setular patterns of these copepods are species-specific and quite complicated, composed of several different types of setae with a variety of setular patterns across the filter. A comparison of the setular patterns on the filter, and the intra- and interspecific morphometric and allometric relationships are presented for the developmental stages of both species. These characteristics are discussed in light of recent evidence that mechanisms other than the classical filtration of particles may occur on the scale at which copepods feed (Alcaraz et al. 1980, Zaret 1980, Koehl and Strickler 1981, Strickler 1982).

In addition to ontogenetic variations in feeding capabilities, seasonal variations in body size may affect the size of feeding structures, and thus contribute to differences in feeding capabilities. Obvious seasonal variations in body size were noticed in animals of both species collected from Puget Sound, Washington, U.S.A. The cephalothorax length of individuals collected from March through July, 1980, was measured in order to document the seasonal variations in body size in adult females of Pseudocalanus and Acartia clausi collected from East Sound, a semi-enclosed embayment within Puget Sound. The results were compared with other morphology studies from the literature to determine the potential effects that both ontogenetic and seasonal variations in body size could have on feeding appendage morphology, and consequently on the feeding capabilities of the copepodite stages of Pseudocalanus and Acartia.

Materials and Methods

Six to ten individuals of each copepodite stage of Pseudocalanus sp. and Acartia clausi were sorted from preserved zooplankton samples collected from a mid-bay station within East Sound. The copepods were sorted by species and stage from samples taken in June 1979 (for Pseudocalanus) and July 1980 (for Acartia). After measuring the cephalothorax length of a specimen, the feeding appendages were dissected off, mounted in and stained with a drop of polyvinyl-lactophenol (Schnack 1975, and personal communication) which had been dyed with lignin pink (Schnack 1982). The appendages were positioned by gently moving the cover slip on the slide as the media solidified over a three to six day period. A pressure-sensitive, electric ocular measuring device mounted on a Wild M-40 inverted microscope provided a dimensional accuracy of 0.1-0.5 µm (depending on the level of magnification at each of three magnifications. Measurements taken at 300X and 900X were recorded vocally on tape and transcribed later onto data sheets.

Five measurements on the mandible and 13 measurements or calculations from the second maxilla were routinely made along with cephalothorax length (Table 1). Mandible cutting area was calculated as the product of the measured width and height of the mandible (Amand = W*H, Table 2). An estimate of minimum filter area, A min, was calculated by representing the filter (second maxilla) as a rectangular area equal to the width of the filter at the base of the setae multiplied by the mean length of the long filter setae (A min = Wb*Ll, Table 2). The estimated number of setules on the second maxilla (Se, Table 1) was calculated as twice the number of setules actually counted (Sc), since measurements were taken for setules from only one side of each setal shaft, whereas setules regularly protruded from both sides of each shaft on the long, filter setae.

Table 2-1 Morphological measurements taken for the developmental stages of *Pseudocalanus* sp. and *Acartia clausi*. The morphometric calculations and allometric relationships derived from these measurements are listed in Table 2.

MEASUREMENT	SYMBOL NOTATION
Cephalothorax Length	Lc
Mandible:	
1. Mandible width	W
2. Mandible height	H
3. Diastema width	Wd
4. Diastema height	Hd
5. Number of teeth	T
Second Maxilla:	
1. Filter width at base of setae	Wb
2. Total number of setae	Nt=Nl+Ns
a. number of long, filter setae	Nl
b. number of short, non-filter setae	Ns
3. Total length of each seta	
a. measured directly for short setae	Ls
b. calculated from ISS measurements for long setae	$Ll = \sum ISS+t+b$
4. Measurements for long filter setae:	
a. successive intersetule spacings from base to tip of seta	ISS
b. distance from last setule to tip	t
c. distance from base of seta to first setule	b
d. number of setules counted	s
e. number of ISS (= pores) counted	p
f. total number of ISS counted on a filter	$P = \sum p$
g. total number of setules counted on a filter	$Sc = \sum s$
h. estimated number of setules on a filter	Se = 2(Sc)

Table 2-2 Morphometric calculations and allometric relationships for the developmental stages of *Pseudocalanus* sp. and *Acartia clausi* derived from the measurements listed in Table 1. Allometric relationships were graphed by stage (means) or against cephalothorax length. *i* = setal number; *j* = size class category.

A. MORPHOMETRIC CALCULATION	SYMBOL NOTATION
Mandible:	
1. Mandible cutting area	A mand=W H
Maxilla:	
1. Filter area	
a. minimum filter area calculated as the filter width at base of filter times mean length of filter setae	A min = Wb Ll
2. Estimated number of setules on the filter	Se = 2(Sc)
3. Maximum, minimum, and modal pore sizes	p max p min p mode
4. Relative % frequency of ISS size categories	p_{ij}/P
5. Cumulative % frequency of ISS size categories	p_{ij}/P
6. Mean pore size across filter along different axes of variance:	
a. pore size at 1/4 maximum setal length	p-1/4
b. pore size at 1/2 maximum setal length	p-1/2
c. pore size at 3/4 maximum setal length	p-3/4
d. pore size along diagonal across filter from proximal base to tip of distal seta	p-diag

B. ALLOMETRIC RELATIONSHIPS	
1. Mandible width	W
2. Mandible area	A mand
3. Maxilla width	Wb
4. Mean setal length	Ll
5. Estimated number of setules per seta	s_i
6. Minimum filter area	A min
7. Relative % frequency distribution of setules	
8. Cumulative % frequency distribution of setules	

Intersetule distances on the second maxilla were measured at 0.5 µm intervals and subsequently grouped into 1 um size categories. A pore size was defined as the intersetule spacing (ISS) directly measured on the filter. An effective pore size was defined as an intersetule spacing that would theoretically capture and retain a cell of a given equivalent spherical diameter (ESD), assuming that some overlap between the measured ISS andthe ESD of the cell was required to effectively retain the cell on the filter. For example, a pore size category of 5 µm contained intersetule spaces actually measured to be 4.5 and 5 µm. It was then assumed that a pore of this size would not retain a cell of 5 µm ESD, but could effectively retain a cell of 6 µm. Therefore, a measured pore size of 5 µm was classified as an effective pore size of 6 µm, and so on. The maximum, minimum, and modal size categories measured on the filter were also calculated for each developmental stage (Table 2). The relative percent frequency of each measured pore size category was calculated as a percentage of the total number of pores counted on the filter, and the frequencies sequentially summed to represent the cumulative percent frequency of pores $\leq$ each size category. The mean pore size measured at distances of 1/4, 1/2, 3/4, the mean setal length, and diagonally across the filter, were also measured for several adult females for each species. The morphological measurements (Table 1 and 2) were plotted against developmental stage (means) and against cephalothorax length (for each specimen), and the data were fit to the appropriate linear or curvilinear allometric expression.

In order to study the seasonal variation in body size for adult Pseudocalanus and Acartia from East Sound, individuals were sorted from representative plankton samples collected over the survey period (March through July, 1980) at the same station and depth. The selected sampling station was in a mid-bay location, where large

zooplankton and phytoplankton biomass and abundance peaks developed at 5 meters during the spring-summer period (see Chapter 4). Samples from this station were considered representative of the general zooplankton populations within the bay. Cephalothorax length was measured for 50 adults of each species sorted from each sample. The mean cephalothorax length was calculated for each group.

Results

Pseudocalanus sp.

Eight primary silicious teeth were present on the mandibles of Pseudocalanus, plus one or two smaller, non-silicious spines on the posterior edge of each mandible (Table 3). Some specimens of stage CI indicated one less tooth on the mandibles for this stage, but often the worn condition of the teeth precluded an accurate count, especially just prior to molting (C.B. Miller, personal communication; personal observation). The maxillary setal number was constant at 16 long setae (> 100 µm in length), and 8 shorter setae (Nt = 24 setae, Table 3). Long setae (> 100 µm long) had a row of setules extending from either side of the setal shaft and were considered to be those setae actively used in the filtering process. These setae were thus designated "filter" setae. Shorter setae, which often projected out at an angle to the plane formed by the filter setae, were designated "non-filter" setae. (These terms are used for convenience throughout the rest of this paper).

The areal distribution of intersetule spacings on the maxillary filter of an adult female Pseudocalanus is shown in Fig. 1. Mean pore size increased distally across the filter and along a setal shaft. The smallest intersetule spaces were located as a fringe at the bases of setae and on the two proximal setae. The largest pores were located approximately midway along the distal setae (seta #18-24, Fig. 1). This pattern was observed in all stages of Pseudocalanus. The setules composing the main filter of the second maxilla projected out at an angle from, but lay within the plane formed by the long setal shafts. Many of these setae also had short spines or spikes protruding from the shaft at a 90 degree angle to the filter plane. The shorter, presumably "non-filter" setae were setulate only

Table 2-3 Stage-specific morphometrics for Pseudocalanus sp. developmental stages. Data are means from 4-6 specimen for each stage. Symbol notations are as listed in Table 1 and 2. Dimensions for each measurement are listed in parentheses.

MEASUREMENT/CALCULATION	SYMBOL	CI	CII	CIII	CIV	CV	ADULT
Cephalothorax length (µm)	Lc	431	531	593	739	893	967
Mandible width (µm)	W	28	35	36	45	53	64
Mandible height (µm)	H	5	7	8	10	10	29
Diastema width (µm)	Wd	6	8	10	12	14	16
Diastema height (µm)	Hd	3	4	4	7	9	11
# Teeth (+ spines)	T	7+1	8+1	8+1	8+1	8+1	8+1
Mandible cutting area (μm^2)	A mand	152	272	285	460	667	1866
Filter width at base (µm)	Wb	57	61	71	63	72	89
Number of short setae	Ns	8	8	8	8	8	8
Number of long setae	Nl	16	16	16	16	16	16
Total number of setae	Nt	24	24	24	24	24	24
Length of short setae (µm)	Ls	38	48	51	49	74	77
Length of long setae (µm)	Ll	75	88	98	98	125	151
Length, base to first s (µm)	b	3	3	3	3	3	3
Length, last s to tip (µm)	t	11	5	6	7	8	12
# setules/seta counted	Sc	16	25	29	29	34	40
Total # ISS/Nl counted	ISS	219	303	549	423	448	551
	Nl_c	10	13	12	15	14	14
Estimated # of setules	Se^c	>598	>606	>722	>876	>923	>1001
Maximum pore size (µm)	p max	10	11.5	15	9.5	12.5	16.5
Minimum pore size (µm)	p min	1	1	1.5	1	1.5	1
Modal pore size (µm)	p mode	2	2	2	2	2.5	2
Pores 5 um or smaller (%)		91	90	92	92	99	98
Pores 10 um or smaller (%)		100	100	100	100	99	98
Pores larger than 10 μm_2(%)		0	0	0	0	1	2
Minimum filter area (μm^2)	A min	4424	5290	6987	6373	9005	12,930

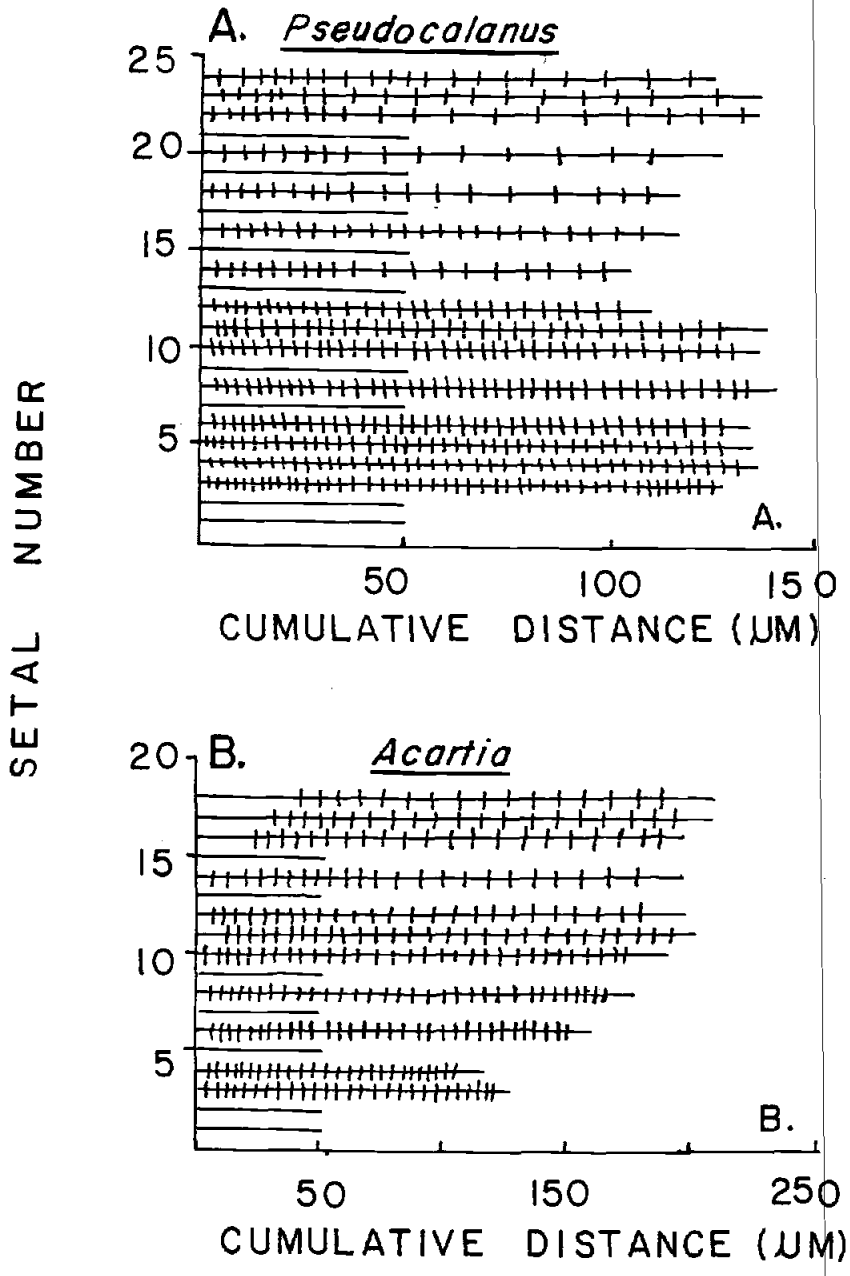

Figure 2-1 Areal distribution of intersetule spacings on the second maxilla of (A.) Pseudocalanus sp. adult female and (B.) Acartia clausi adult female. Non-filter setae are schematically shown without setules. Basal setules of setae 16-18 on A. clausi females were not regularly visible

on the proximal two-thirds of the shaft, forming a three-dimensional spiralling pattern of irregular intersetule spacings around the setal shaft. These spacings varied from less than one micron to about three microns. The setules on the distal portion of each non-filter seta appeared to be naked. These spacings were not consistently visible, and could not be measured accurately since the setae often did not lie in the plane of the filter. The non-filter setae were therefore not included in the setular calculations, and only total length was measured for these setae (Ls, Table 2).

Stage-specific morphogenesis resulted from the allometric growth of all the features measured (Table 3 and 5, Fig. 2 and 3). Mean mandible width increased with developmental stage (Fig. 2), with a growth stanza (Miller et al. 1978) between stages CII and CIII which was not apparent in the regression against cephalothorax length (Fig. 3). The relationships between mandible width vs. developmental stage or cephalothorax length were best described by a linear regression model (Table 5). Mandible cutting area (Fig. 2) increased only slightly from stage CI to CV, again showing a growth stanza between stages CII and CIII. However, there was a four-fold increase in mandible cutting area between stage CV and the adult female. A similar increase was noted in the relationship between cutting area and cephalothorax length (Fig. 3). Both sets of data were better described by an exponential rather than a linear regression model (Table 5), although two intersecting straight lines may be the more appropriate fit to the data (Fig. 3). The mean maxilla width increased from CI to CIII, and from CIV to the adult stage (Fig. 2). An apparent decrease in mean filter width occurred between stage CIII and CIV, a trend also present in the plots of mean setal length vs. developmental stage for both filter and non-filter setae (Fig. 2), and for the estimated number of setules per seta. Except for this break between stage CIII

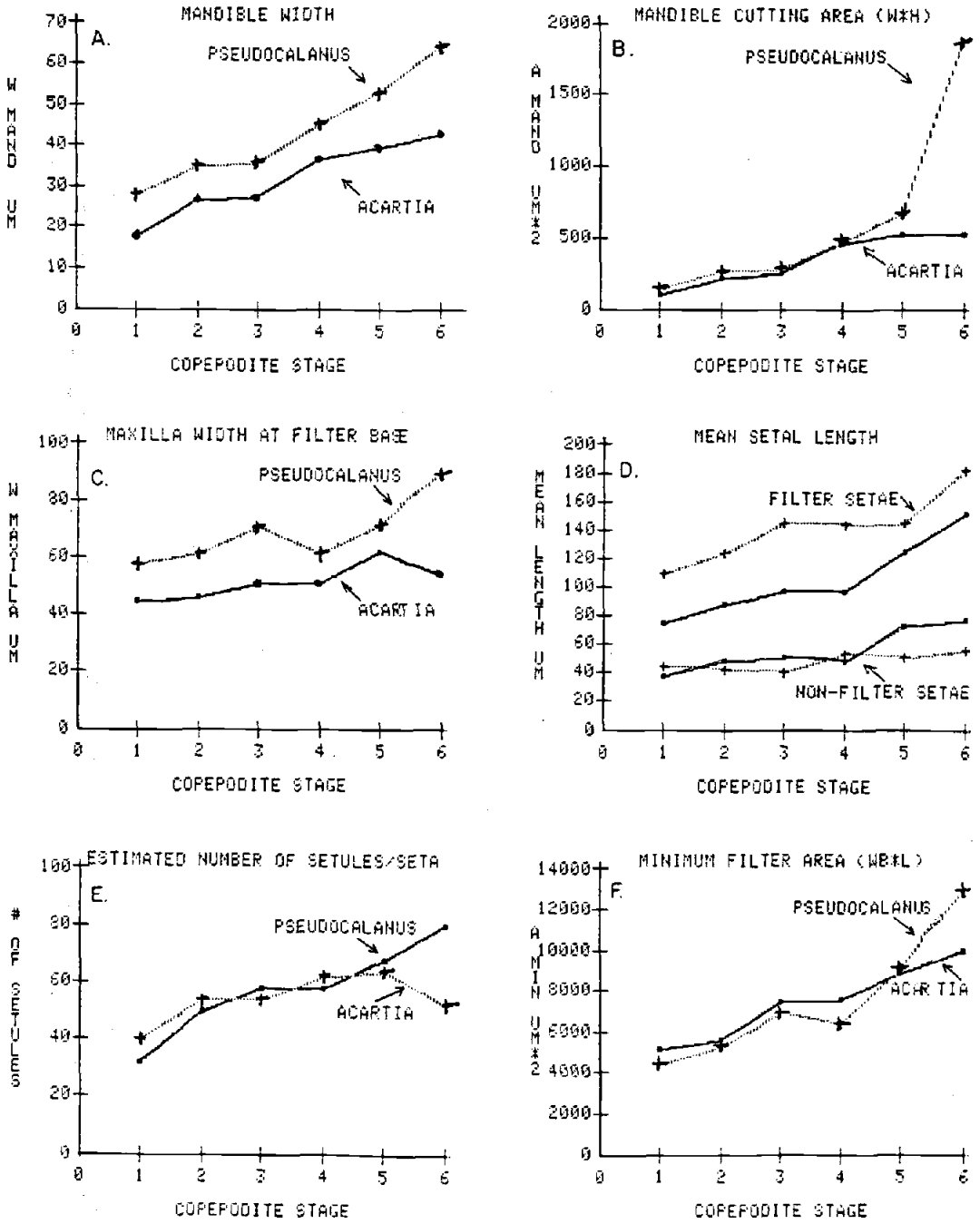

Figure 2-2 Mandibular and maxillary measurements for Pseudocalanus sp. and Acartia clausi developmental stages. Each data point represents the mean from 4-6 specimens for each stage as listed in Table 3 and 4.

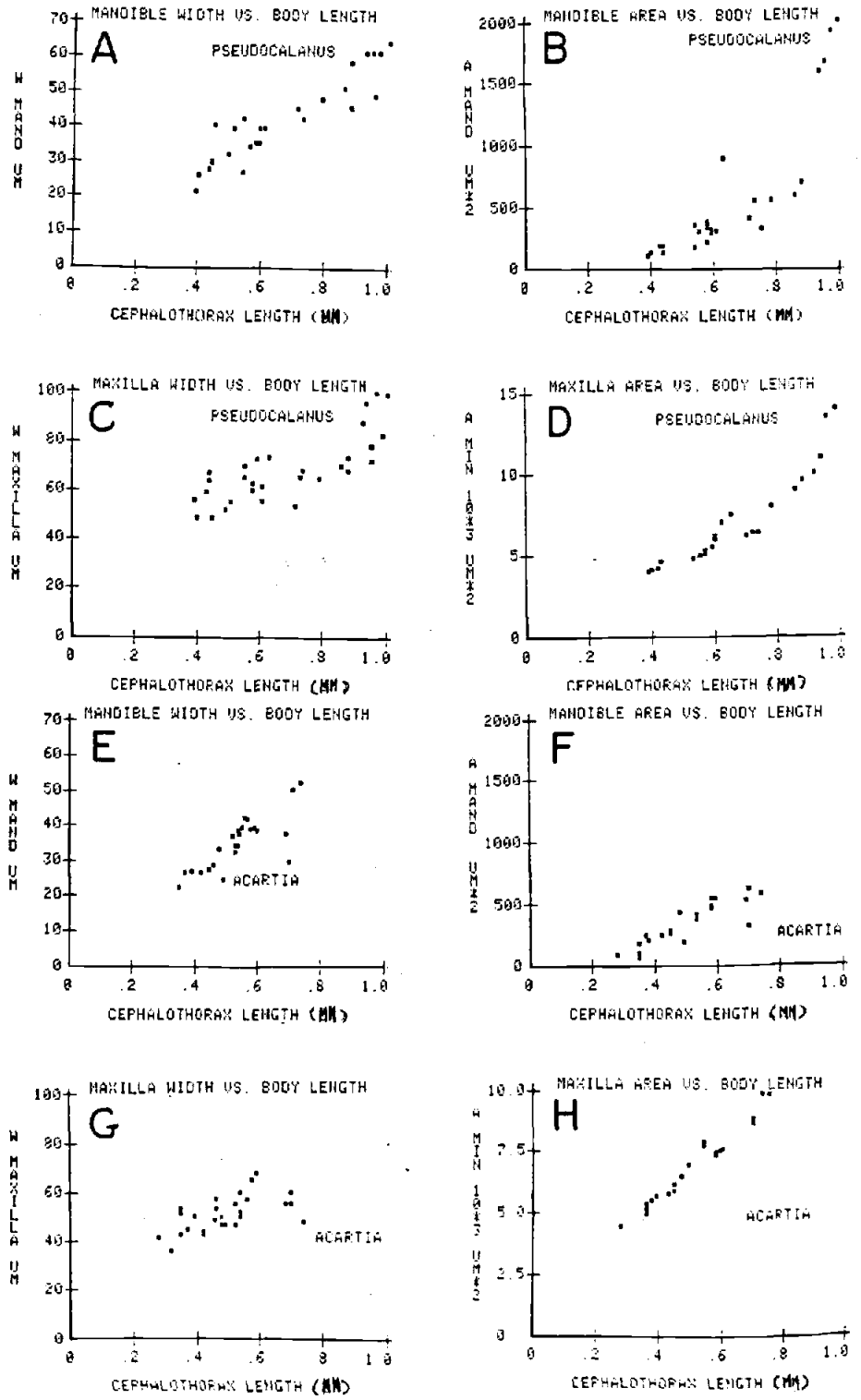

Figure 2-3 Mandibular and maxillary measurements for each specimen of Pseudocalanus sp.(A-D) and Acartia clausi (E-H). The allometric equations calculated for each species from these data are listed in Table 5.

and CIV, maxilla width, mean setal length, and the number of setules per seta increased linearly with developmental stage (Table 3 and 5). An exponential model fit the data for maxilla width vs. developmental stage, and mean setal length vs. developmental stage as well as a linear model (Table 5).

The mean estimate for minimum filter area (A MIN, Table 2) plotted against developmental stage (Fig. 2) and cephalothorax length (Fig. 3) indicated an interrupted allometric increase between stage CIII and CIV, resulting from both the decrease in maxillae width and in mean setal length in these two stages. The data were best fit by an exponential relationship between minimum filter area and cephalothorax length (Table 5). The minimum filter area of the adult female (A MIN = 13,000 μm^2) was almost three times that for stage CI (A MIN = 5000 μm^2), and increased rapidly from stage CIV to adult (Fig. 2). The estimated number of setules on the filter increased with copepod stage and size, from about 500 setules in stage CI to over 1000 setules on the filter of the adult female (Table 3). This increase was due to the allometric increase in setal length and a subsequent increase in the number of setules per seta.

The relative frequency distribution of measured intersetule spacings on the second maxilla (Fig. 4) indicated a strong modal size class at 2.5 - 3.0 µm for all developmental stages of Pseudocalanus. The variance around this mode increased with stage as the number of setules on the filter and the maximum pore size increased. The cumulative frequency curve of effective intersetule spacings grouped into one micron intervals (Fig. 5) was curvilinear for all developmental stages of Pseudocalanus, indicating a distribution which is skewed to the right (Sokal and Rohlf 1969), as indicated in the relative frequency distribution; this analysis therefore suggested that pore sizes on the filter of Pseudocalanus were not normally distributed (Sokal and

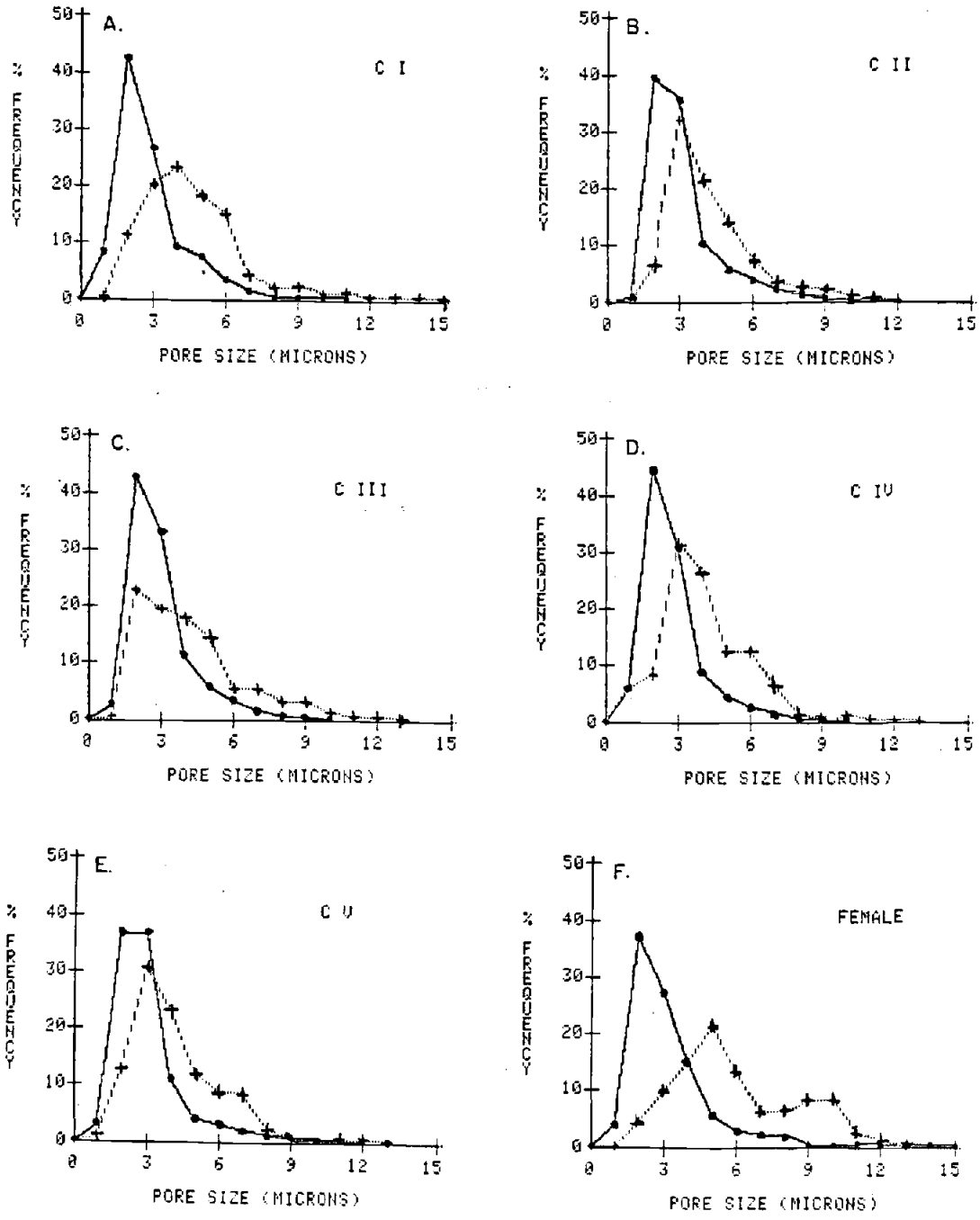

Figure 2-4 Relative percent frequency distributions of intersetule spacings (= pore sizes) measured on the second maxillae of the developmental stages of Pseudocalanus sp. (●) and Acartia clausi (+).

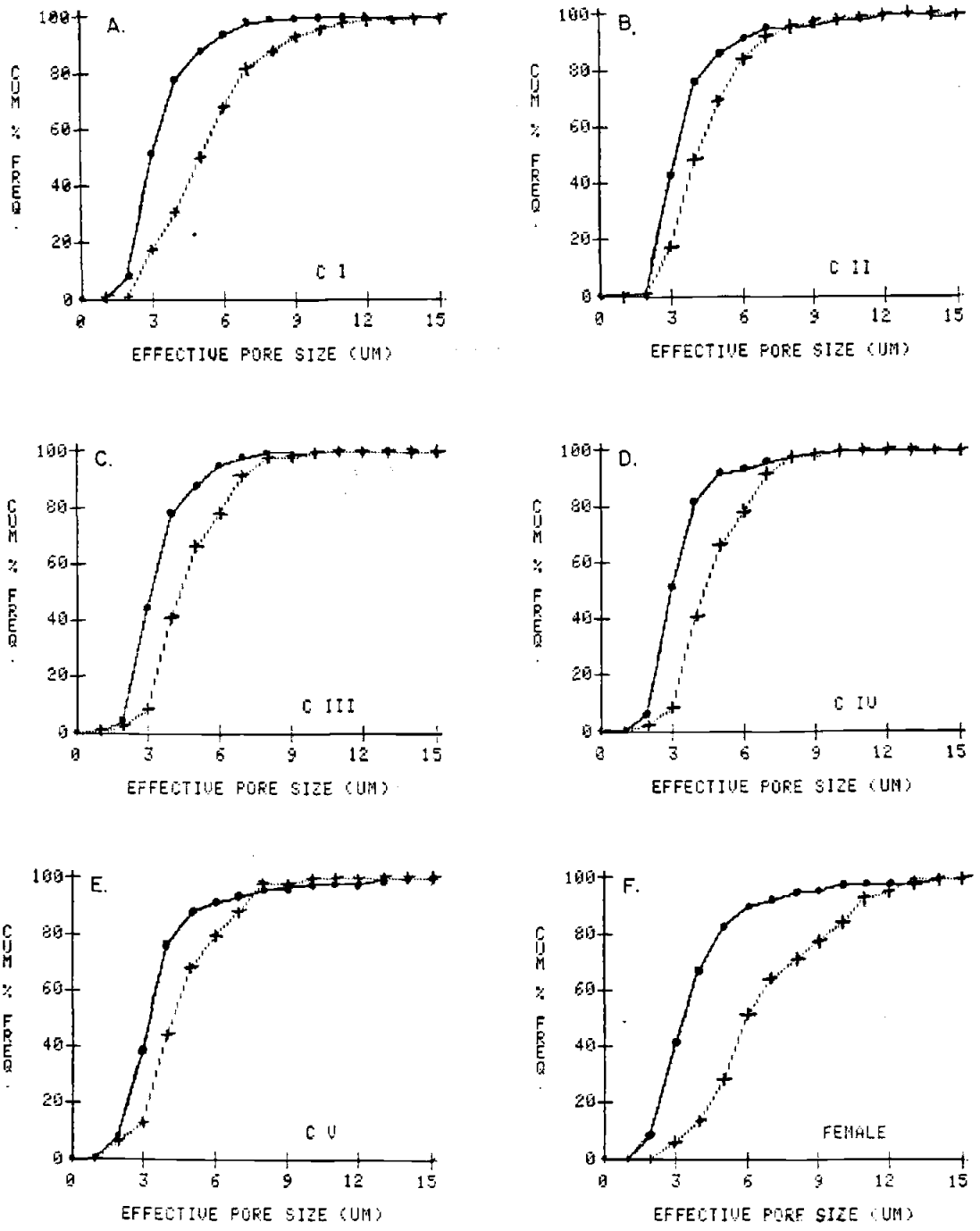

Figure 2-5 Cumulative percent frequency distributions of intersetule spacings (= effective pore size) on the second maxillae of the developmental stages of Pseudocalanus sp. (●) and Acartia clausi (+). Effective pore size refers to an intersetule spacing that would theoretically retain a cell of the given equivalent spherical diameter. See text for details.

Rohlf 1969). Although the maximum intersetule spacing varied slightly between stages, the smallest intersetule spacing (i.e., the lower pore size threshold, Frost 1972a), remained constant at 1.0 - 1.5 µm (Table 3, Fig. 4). Close to 90% of the measured spacings on the filter of all stages of Pseudocalanus were 5 µm or less (Table 3, Fig. 5), ranging from a mean of 91.3 (+/- 2.6) % in stage CI to 87.7 (+/- 3.5) % in the adult female. Only 1-2% of the spacings were greater than 10 µm (Table 3), and these larger spacings were only present on individuals of stage CV and adult females. A maximum pore size of 16.5 µm was measured on one adult female. The mean pore size measured at successive distances from the base of the filter of adult females increased gradually from 4.2 (+/- 1.8) µm at 1/4 the mean setal length, to 6.0 (+/- 2.6) µm at 3/4 mean setal length. An average pore size of 5.4 (+/- 3.2) µm was measured diagonally across the filter.

Acartia clausi

All stages of Acartia clausi had seven siliceous mandibular teeth, with one or two non-siliceous spines at the posterior edge of each mandible (Table 4). The adult compliment of maxillary setae (Nt = 18, Table 4) was not present on specimens of stage CI due to the apparent absence of one of the basipods on which three long, filter setae and one short, non-filter seta were present in the older developmental stages. All 18 maxillary setae were present by stage CII, including seven non-filter setae which lay at an angle to the filter plane, and 11 filter setae which formed the plane of the filter (Fig. 1). The non-filter setae appeared to be without setules in younger copepodites. In the older stages (CIV to adult), some of the non-filter setae were setulate, with setules arranged in a three dimensional pattern around the shaft similar to that observed in Pseudocalanus. As with the Pseudocalanus

Table 2-4 Stage-specific morphometrics for *Acartia clausi* developmental stages. Data are means from 4-6 specimen for each stage. Symbol notations are as listed in Table 1 and 2. Dimensions for each measurement are listed in parentheses.

MEASUREMENT/CALCULATION	SYMBOL	CI	CII	CIII	CIV	CV	ADULT
Cephalothorax length (um)	Lc	329	398	467	538	570	705
Mandible width (μm)	W	18	27	28	37	40	43
Mandible height (μm)	H	6	9	9	13	13	12
Diastema width (μm)	Wd	6	9	9	12	13	16
Diastema height (μm)	Hd	5	6	7	8	7	7
# Teeth (+ spines)	T	7+1	7+1	7+1	7+1	7+1	7+1
Mandible cutting area (μm^2)	A mand	109	227	262	470	515	523
Filter width at base (μm)	Wb	45	46	51	52	62	54
Number of short setae	Ns	6	7	7	7	7	7
Number of long setae	Nl	8	11	11	11	11	11
Total number of setae	Nt	14	18	18	18	18	18
Length of short setae (μm)	Ls	45	42	41	53	52	56
Length of long setae (μm)	Ll	109	124	145	144	145	182
Length, base to first s (μm)	b	6	4	4	4	5	5
Length, last s to tip (μm)	t	10	10	12	10	11	13
# setules/seta counted	Sc	20	27	27	31	32	26
Total # ISS/Nl counted	ISS	133	243	262	249	294	223
	Nl	7	9	10	8	10	9
Estimated # of setules	Se	>266	>486	>524	>550	>590	>600
Maximum pore size (μm)	p max	13	11	14	9	9	12.5
Minimum pore size (μm)	p min	1.5	1.5	1.5	1.5	1.5	2
Modal pore size (μm)	p mode	4	3	2	3	3	5
Pores 5 um or smaller (%)		59	78	62	76	76	45
Pores 10 um or smaller (%)		98	99	98	100	100	95
Pores larger than 10 μm (%)		2	1	2	0	0	5
Minimum filter area (μm^2)	A min	5128	5648	7678	7553	8837	9901

specimens, intersetule spacings were not routinely measured for these setae, since the non-filter setae generally lay outside of the filter plane, and were not consistently visible. Only total length was measured for non-filter setae (Table 4).

The first two proximal setae (seta #1 and 2, Fig. 1) appeared to have setules spiralling around the shaft, arranged three-dimensionally at very small intervals of 1-3 µm. Although in some specimens these setae lay within the plane of the filter, like the non-filter setae they were difficult to measure and were not included in the pore size calculations. The long setae (> 100 µm) composing the maxillary filter of Acartia were setulate along the full length of the shaft. Setules near the tips of seta #3 and 4 (Fig. 1) were quite long (10-15 µm) and gave a bushy appearance to these setae. Seta #15 on the distalmost basipod was noticeably shorter than the surrounding filter setae and often lay outside the filter plane. Small spines protruded from the shafts of several of the filter setae at a 90 degree angle to the setular plane. As in Pseudocalanus, the areal distribution of intersetule spacings on the filter of the adult female revealed a gradual gradation from small to larger pore sizes across the filter and from base to tip along a setal shaft. A fringe of smaller spacings near the tips of all the filter setae and on the setae around the exterior of the filter was also present. The largest measured intersetule spacings for Acartia (10-15 µm) were located on the distal setae (seta #16-18, Fig. 1).

Mandible width, mandible height, diastema width, diastema height, mandible cutting area, mean setal length, and the number of setules per seta all generally increased with stage and cephalothorax length in Acartia (Table 4 and 5). Mean height of the mandible and diastema (Table 4) decreased in the adult female, due primarily to the worn condition of the teeth in several individuals. The decrease

Table 2-5 Allometric equations for the comparative morphology data shown in Fig. 3, for *Pseudocalanus* sp. and *Acartia clausi* developmental stages. Measurement data were regressed against cephalothorax length using the linear model: $Y = aX+b$ or the exponential model: $Y = aX^b$.

Measurement	Model	a	b	r
Pseudocalanus sp.				
Mandible width (µm)	Linear	0.56	0.06	0.96
Mandible area (µm^2)	Exponential	61.78	0.01	0.89
Maxilla width (µm)	Linear	37.52	0.05	0.69
Maxilla area (µm^2)	Linear	2195.4	1516.03	0.84
	Exponential	3541.0	0.20	0.91
Acartia clausi				
Mandible width (µm)	Linear	-1.81	0.07	0.92
Mandible area (µm^2)	Linear	-257.80	1.21	0.86
Maxilla width (µm)	Linear	35.04	0.03	0.52
Maxilla area (µm^2)	Linear	838.18	13.21	0.93
	Exponential	2919.17	0.20	0.91

in mandible height also affected the calculation of mandible cutting area in the older copepodite stages (Fig. 2, Table 4), resulting in a linear relationship between mandible cutting area and cephalothorax length (Fig. 3, Table 5). Maxilla width also apparently decreased in the adult female, while mean length of the filter setae increased (Fig. 3 and 4). The estimate for minimum filter area (A MIN. Table 2, Fig. 2) increased linearly for stages CI to CIII and from CIV to the adult female, from ca. 5000 μm^2 in the youngest stages (CI and CII) to almost 10,000 μm^2 in the adult female (Fig. 2). The filter setae were quite long for all stages of Acartia, extending to over 200 µm in some adult specimens. As setal length increased, the estimated number of setules per seta (Fig. 2) and the total number of setules counted on the filter (Table 4) increased for stages CI to CV. In the adult female, however, the number of setules per seta and the total number of setules counted on the filter both decreased, due to the relative increase in the number of large intersetule spacings as mean setal length and body length increased (Table 4). The estimated number of setules on the female maxilla was approxmately the same as in the stage CV.

The relative percent frequency distribution of intersetule spacings on the maxillary filter of Acartia indicated the development of a strong mode at 3 - 4 µm in copepodite stages CI-CV (Fig. 4). The modal pore size increased with developmental stage from 3 - 4 µm in the youngest copepodites to ca. 5.5 µm in the adult female (Table 4). The development of a secondary peak was evident in the later stages of Acartia at 9 - 10 µm. The cumulative frequency curves of intersetule spacings on the maxillary filter of Acartia were curvilinear and only slightly sigmoidal, indicating a platykurtic or slightly bimodal distribution of pore sizes (Sokal and Rohlf 1969). At all stages, Acartia copepodites had a higher percentage of larger pore sizes on the filter compared to Pseudocalanus. The minimum pore

size was constant at 1.5 - 2.0 µm, whereas the maximum measured intersetule spacing varied between stages. The modal pore size was largest in the youngest and oldest stages, due to the lower number of setules per seta on the filter in these stages (Table 4). From 45 to 78% of the pores were 5 µm or smaller. Greater than 95% of the pores were $\leq$ 10 µm, with only a few percent (0 - 5%) larger than 10 µm (Table 4). Mean pore size increased along the shaft of the filter setae, from 6.1 (+/-0.9) µm measured at 1/4 the mean setal length to 7.3 (+/- 2.1) µm measured at 1/2 mean setal length, and 7.6 (+/- 2.8) µm measured at 3/4 the mean setal length in adult females. A mean pore size of 6.7 (+/- 2.1) µm was measured along the diagonal of the filter setae.

Seasonal Body Size Variations

Mean cephalothorax length of adult females of both species decreased from March to June in East Sound, Washington (Fig. 6). Pseudocalanus females were over 1 mm long (maximum size = 1.04 mm) throughout the winter period, and decreased in size to 0.88 mm by July. This represented a 15.4% decrease in cephalothorax length between winter and summer for Pseudocalanus females. Acartia females were largest in spring, ranging from 0.82 mm in April and May to 0.68 mm in July, a decrease of 17.1% in cephalothorax length over the same period.

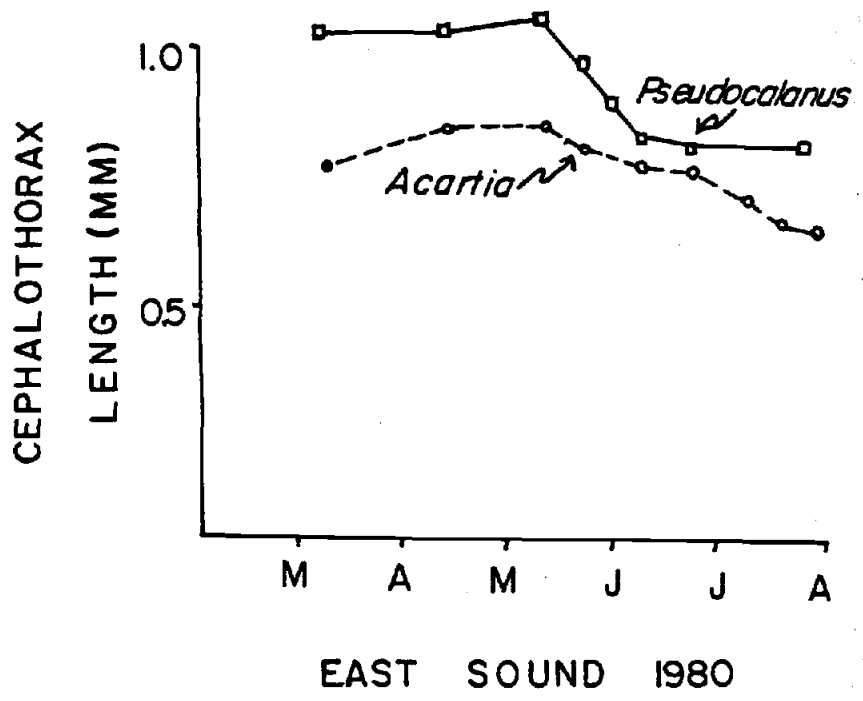

Figure 2-6 Seasonal changes in cephalothorax length of Pseudocalanus (□) and Acartia clausi (○) adult females sampled from East Sound, Wash. Data were calculated as the mean body length for 50 females from each date.

Discussion

A number of studies have described the morphological characteristics of the developmental stages of copepods. However, these descriptions have been primarily for taxonomic (Oberg 1906, Lebour 1916, Corkett 1966, Lawson and Grice 1970, Grice 1971, Gibson and Grice 1977) or field identification purposes (Bjornberg 1961, Faber 1966), or were a part of a larger work on the general biology of the animal (Marshall and Orr 1956, Conover 1956, Mullin and Brooks 1967, Paffenhofer and Harris 1976, Corkett and McLaren 1978). Usually the adult stages of several different species have been treated in a comparative manner (Marshall 1977, Nival and Nival 1976, Schnack 1980). Few studies have recorded the development and allometric growth of feeding structures with respect to changes in the feeding capabilities of a particular species.

The allometric growth of the feeding appendages of Pseudocalanus and Acartia copepodites in the present study indicated a linear or curvilinear relationship to body size. Similar increases in the dimensions of the mouthparts between developmental stages up to stage CV were noted for both species. Mandible cutting area, maxilla width, minimum filter area and the estimated number of setules per seta increased considerably for Pseudocalanus females (Table 3), but decreased for Acartia females (Table 4). Although growth stanzas (Miller et al. 1978) were not readily apparent in the regression data (Fig. 3), the stage-specific means (Fig. 2) suggested that mandible growth between stage CIII-CIV may be arrested. Measurements of the maxilla indicated a cessation of growth between stages CIII and CIV for both species. The mandibular measurements in Acartia were affected by an apparent wearing of the teeth, a condition that was not as readily visible in Pseudocalanus females. This may indicate "old age"in females (P.L. Donaghay, C.B. Miller, pers. commun-

ication; personal observation). Although the width of the filter decreased for Acartia females, mean setal length increased, resulting in a larger value for the estimate of minimum filter area in the adult stage.

The fact that the pattern of allometric increase in the mandibular and maxillary measurements was similar for the copepodite stages of both species (CI to CV) may indicate from a morphological standpoint that the feeding capabilities of these developmental stages can, in fact, be appropriately modelled on a size or weight basis. The ontogeny of the feeding appendages was thus primarily achieved by the allometric growth of the structures prior to the molt to the adult stage, rather than by a change in shape or form. (The only exception to this pattern was the apparent addition of one basipod and three setae between stages CI and CII for Acartia clausi). However, the size and shape of the feeding apparatus changed considerably for the adult females of both copepod species, possibly reflecting a morphological component in the development of additional feeding capabilities.

A variety of different kinds of setae were present on the second maxillae of both species. The long setae, presumably composing the "filter" of both species, had setules extending at regular intervals from both sides of the setal shaft, and often had small spines or spikes protruding at a 90 degree to the plane of the filter formed by the setules. Although the function of these structures remains unknown, they have been observed on the maxillae of several copepod species (C.B. Miller, Personal communication, W.T. Peterson, personal communication). Theoretically, they could function to increase the area of the filter or to change the form of the boundary layer or flow of water around a seta (Koehl and Strickler 1981). The short, presumably non-filtering setae had setules placed three-dimensionally around the shaft and generally lay at an angle to the filter. These setae could have functioned in

the capture of algal chains, as a pre-filter to prevent large particles from reaching the filter (Marshall 1973), or have been used to position cells for raptorial capture (Conover 1966, Jorgensen 1966). Both copepod species also had one noticeably stiff seta on the distal-most basipod, which could be used for piercing larger cells (Corkett and McLaren 1978).

The cumulative frequency distributions for Pseudocalanus sp. and Acartia clausi developmental stages indicated a species-specific distribution of setules on the filter (Fig. 4 and 5). Although the minimum and maximum pore izes measured on the filter were quite similar for the two species, Pseudocalanus theoretically should have been more efficient than Acartia in capturing small cells (5 µm) due to the distribution and relatively greater abundance of small pore sizes on the Pseudocalanus filter. This result has been reported in a variety of field grazing experiments (Poulet 1974, Koeller et al. 1979, Harris 1982), indicating that the role of Pseudocalanus as a small cell specialist might allow it to feed, grow, and reproduce well during periods when the overall food concentration was low, and whenever small cells composed a large fraction of the particle spectrum. Pseudocalanus may thus be able to maintain a population during conditions when larger copepods (e.g., Calanus species) or copepods with larger setule spacings (e.g., Acartia) cannot (Koeller et al. 1979, Harris 1982). Acartia, on the other hand, seems to capture large particles quite effectively (Conover 1966), but not small cells, although in the present study the data indicated that the total size range of particles theoretically available to all the developmental stages of Pseudocalanus and Acartia clausi overlapped considerably.

A morphological study similar to the present report by Nival and Nival (1976) compared measurements of the second maxilla for all the copepodite stages of Acartia

clausi from the Bay of Villefranche, France. Their cumulative percent frequency distributions of intersetule spacings were strongly sigmoidal for all stages of Acartia. However, it was assumed in this study that there were only two mesh regions on the second maxillae of A. clausi: a "large mesh" and a "small mesh" region. Subsequently, only a few setae from each of these regions was measured. Although the relative percent frequency distributions of pore sizes on the filter of Acartia developmental stages in the present study revealed the development of a secondary peak at 9-10 μm in the older copepodite stages, when measurements from all the setae across the filter were taken, the data indicated a gradation from small intersetule spacings at the bases of all setae and on the proximal setae, to gradually larger spacings near the tips and on the distal setae of the filter. The data did not indicate two distinct mesh regions. A comparison of the pore sizes measured at successive distances from the base of the filter and diagonally across the filter also confirmed this pattern of a gradual increase in pore size along a setal shaft and distally across the filter, a pattern which has been observed for a number of copepod species (Marshall 1973). Although the data in the present study were generated in the same manner as those by Nival and Nival (1976), it would appear that the strong sigmoidal curves generated by Nival and Nival were an artifact of the small number of measurements taken in the intermediate size classes.

Seasonal changes in copepod body size have been reported for a variety of nearshore to estuarine species, and may affect the feeding capabilities of copepods by changing the size or shape of feeding structures. Schnack (1975) reported a transition to smaller morphs from winter to summer in populations of Pseudocalanus elongatus and Acartia longiremis from Kiel Bay, W. Germany (1970-1971). Evans (1981) reported successively smaller animals from spring to summer

for Pseudocalanus sp., Oithona similis, Acartia clausi, and A. longiremis sampled from the North Sea. Schnack (1982) reported that winter animals of P. elongatus (females) in Kiel Bay showed 20 - 30% larger mean setule spacings compared to females sampled in the summer, whereas Acartia species (A. longiremis, A. tonsa) had 15 - 30% larger mean setule spacings during the summer. Conover (1956) reported a 50% decrease in mean setule spacing for A. clausi from Long Island Sound in summer as compared to winter. However, Nival and Nival (1976) reported a larger mean mesh size and larger filter area for A. clausi collected from the Bay of Villefranche in August compared to animals collected in October.

These data indicate that seasonal changes in body size regularly occur in coastal and estuarine copepods, but body size changes may have a variable effect on the allometry of the feeding apparatus. Traditionally, studies have shown that planktonic copepods are smaller in the summer and autumn when the sea is warm, compared to winter or spring when it is colder, and that the size changes observed in copepods were a seasonal response to both water temperature and food supply (Deevey 1960, Evans 1981). For Pseudocalanus species, Corkett and McLaren (1978) concluded that final adult body size was determined solely by water temperature, and that a shortage of food during winter months only prolonged the developmental period, but did not change the final adult size. In East Sound, adult females of both species decreased 15 - 17% in body length from winter to summer. These size changes in the copepods from East Sound may have reflected both the increase in temperature of surface waters and the increase in particle concentration which occurred during the spring bloom period (see Chapter 4), and could have resulted in significant allometric changes in the feeding apparatus. For example, the seasonal changes in cephalothorax length of females collected in winter and summer were approximately the same relative

percent change in body size calculated between successive developmental stages for both Pseudocalanus ($\bar{x}$ = 17.7%) and Acartia ($\bar{x}$ = 16.6%), suggesting that seasonal variations in copepod size could have as significant an effect on feeding capabilities of these copepods as did the ontogenetic component of growth and development.

Although body size differences were measureable in the present study, the conclusion by Schnack (1982) that it is uncertain at this time whether changes in body size (and therefore in filter mesh size) would confer a competitive advantage to a copepod is appropriate. This is especially true when one considers that (1) variable ingestion responses have been reported for copepods similar in size, (2) intraspecific ingestion responses may vary seasonally (Ellis, unpublished data; Head, unpublished data), and (3) the fact that particle spectra available as a food resource may change quite rapidly with respect to particle size and shape over the lifespan of a grazer. However, assuming an allometric relationship between body size and the size of the feeding apparatus (Frost 1972b), and a high relative abundance of small cells in East Sound during late winter and early spring, one may hypothesize that although the larger animals observed at this time of year had larger filters and greater filtering capabilities, they may have had a narrower range of cells available to them. The smaller animals present in summer may have had both the small particle resource available as food throughout the year, and the larger diatom species which became abundant in late spring and summer. The seasonal differences in ingestion rates which have been measured for both Pseudocalanus and Acartia (O'Connors et al. 1976, Corkett and McLaren 1978) may thus reflect seasonally variable feeding capabilities as well as seasonally variable physiological rates. Low food concentrations in winter may not be a critical factor for either of these species, however, since Acartia may maintain its

population by the production of resting eggs in response to lowered water temperature and salinity, or marginal food conditions (Johnson 1981), and Pseudocalanus may overwinter as a stage CV, or rely on oil and lipid accumulations (Koeller et al. 1979, Harris 1982).

In addition to changes in body size and filter morphology, feeding capabilities may also be affected by physiological responses of copepods. Whether the animals are in a physiological state of hunger or satiation, in an active growth phase or an overwintering state of diapause, or whether as adults, copepods are putting energy into reproduction rather than growth, may all affect the feeding responses observed. Similarly, characteristics of the food, such as particle shape and size, the physiological, growth or nutritional state of the cell, the absolute or relative abundance of different particle types, and the relative availability of each cell type to a particular grazer, all interact to affect the final "decision" made by a copepod. Thus, in the present study, the comparative morphology measurements were used only as a first-order description of the feeding capabilities, and to indicate the types and sizes of particles theoretically available to the different developmental stages of Pseudocalanus and Acartia. This treatment of the data suggested that the ontogeny of feeding structures and allometric changes which may occur due to seasonal variations in body size may equally affect the size of particles available to a copepod.

A final point to consider is the appropriate use of structural characteristics in interpreting the functional grazing responses of copepods. A number of studies have indicated a close relationship between feeding appendage morphology and the sizes of cells eaten by a copepod (Anraku and Omori 1963, Schnack 1975, Sullivan et al. 1976). Boyd (1976) used the morphological measurements of Nival and Nival (1973, 1976) plus calculations of filtration efficiency from their data, to argue that apparent selection

for cells to the right of the modal size class of a given cell distribution (i.e., selection for large particles) would occur if the size of the food particles fell within the sigmoid section of the probability function. Thus, there was no "need to credit the animals with the ability to scan the particle size distribution" (Boyd 1976, pg. 178). Although these calculations and Boyd's interpretation were based on a limited number of measurements, this mechanistic explanation of copepod feeding has been used to explain the apparent selective behaviors shown by a variety of copepods.

As indicated above, the classical view of copepods as passive filterers which strain particles out of vortices of water generated by their feeding appendages (Cannon 1928, Gauld 1966, Marshall 1973), has recently been challenged from a variety of directions (Poulet and Marsot 1978, Alcaraz et al. 1980, Poulet and Marsot 1980, Koehl and Strickler 1981). The microcinematographic observations by Alcaraz et al. (1980), and Koehl and Strickler (1981) would at first appear to refute a basic tenet of copepod feeding, namely the actual filtration of cells. However, direct observations of feeding have only been accomplished with large, omnivorous oceanic copepods which have only limited setular complexity on their second maxillae. Even if the traditional measurements of filtration rate or "volume swept clear" do not accurately describe the act of feeding, they do describe the effect of the feeding activity, and may thus provide an appropriate index for measuring the impact which zooplankton species have on their food resource (Conover and Huntley 1980, Huntley 1982). In fact, the data describe a feeding response that would be appropriate for a large copepod feeding in a dilute food environment (Conover 1966, Strickler 1982). A large copepod with limited setular complexity, as represented by Eucalanus pileatus for example, may encounter cells at a sufficiently low rate that particle-by-particle responses

are an effective mechanism for food capture. In situations where inertial effects in the water are minimal, cells (or the ater containing those cells) stop moving almost immediately after beating of the feeding appendages ceases (Koehl and Strickler 1981). One may thus hypothesize that at low food concentrations, a copepod could have enough time to (1) chemosense the quality of the "volume of odor" (Koehl and Strickler 1981) theoretically exuded by a leaky phytoplankton cell, and interpret the directionality of the signal (which is theoretically preserved where viscous forces dominate, Zaret 1980), (2) orient to the odor signal, and (3) preferentially draw the water containing the food particles into the vicinity of the mouth, where the particles can be removed by squeezing the water through the maxillary filter.

This interpretation of algal manipulation may not be entirely appropriate for small, primarily herbivorous, nearshore to estuarine copepods which have evolved complicated setular patterns on their feeding appendages, and have evolved in an environment that varies considerably in both the quantity and quality of food over the lifetime of a copepod. For a copepod living in high food concentrations (e.g., thousands of cells per ml instead of hundreds of cells per ml), reorienting toward a specific food signal may be unnecessary and a waste of time and energy. Also, the directionality of any one signal may be impossible to discern, assuming a multi-dimensional input of signals from all particles in the copepod's immediate environment. Thus individual cells, or small clusters of cells may not be perceived. However, gross differences in cell quality or quantity may be monitored, as it were, on a mouthful-by-mouthful or gutful-by-gutful basis. One might thus hypothesize the evolution of increased setular complexity in the feeding apparatus of small, herbivorous grazers which experience high particulate abundances, especially where the non-food content of the particle distribution is variable

but high. This situation exists in coastal, nearshore, and estuarine environments. Increased setular complexity could allow differential particle selection by the "combing" of cells from a particular location on the filter, a process suggested by Donaghay (1980b), or it could allow the post-capture rejection of non-food or low quality food particles (Wilson 1973, Donaghay and Small 1979, Donaghay 1980b, Landry 1981, Huntley 1982). Since copepods clearly possess a well-developed chemosensory morphology (Friedman and Strickler 1975, Friedman 1980), and can apparently detect differences in food quality (Poulet and Marsot 1978, Poulet and Marsot 1980), sensing differences in particle quality in a mixed food ration may be another adaptive trait chracteristic of, at least, coastal zooplanktonic grazers. In fact, several coastal copepods appear to be able to "track" temporal changes in the size structure of natural particle spectra, short-term changes in the relative abundance of particles resulting from the ingestion of cells from a succession of particle peaks across a distribution (Richman et al. 1977), as well as adjusting to seasonal variations in particle size and abundance (Poulet 1974, O'Connors et al. 1980).

Thus, even if food particles are not actively sieved from the water by the beating of the feeding appendages, the particles are nevertheless sensed, trapped, and apparently size-graded by the appendages during the feeding process (Conover and Huntley 1980, Donaghay 1980b). Although setules may be hidden in a relatively thick boundary layer such that the setae appear functionally smooth, setule spacing and the pattern of setules across the filter may determine the pattern of water flow around the appendages, and thus affect what size particles bump into the filter, and are retained (Koehl and Strickler 1981). These morphological adaptations for removing particles from the water certainly must interact with chemosensory, physiological, and perhaps behavioral capabilities to produce a variety

of feeding responses which allow planktonic grazers to cope with the rapidly changing food spectrum present in coastal and estuarine waters.

CHAPTER 3

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult).

II. Laboratory Grazing Responses of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult)

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II. Laboratory Grazing Responses of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult)

Introduction

Numerous studies have reported the grazing characteristics and functional responses of copepods feeding on natural particles. However, only a handful of studies have compared the feeding responses of different copepod species under the same experimental conditions, and even fewer have attempted to study developmental stages other than the adult female. This chapter reports the results of laboratory grazing experiments and feeding observations of *Pseudocalanus* sp. and *Acartia clausi* developmental stages. These experiments tested the null hypothesis that no differences in feeding responses should result due to copepod species or developmental stage (= size), or from differences in phytoplankton particle size. It was assumed that the classical functional relationship between ingestion rate and food concentration (Frost 1972b) would be observed at the phytoplankton concentrations used in these experiments. The data were used to study the role of active vs. passive selection in the development of adult feeding responses for the two species and to assess how these components varied between copepod stages and/or with phytoplankton cell characteristics. A discussion of several problems inherent in experiments of this type is presented as a cautionary note regarding the use, analysis, and interpretation of grazing data in understanding the feeding responses of herbivorous marine copepods.

Materials and Methods

Animal Collections

Pseudocalanus sp. and Acartia clausi were collected from two locations off the Oregon-Washington coast. Experiments conducted in 1980 used copepods collected from East Sound, a large embayment in Puget Sound, Washington. These experiments were done at the University of Washington Marine Laboratory, Friday Harbor, Washington. Animals for the experiments conducted in 1981 were collected on an incoming tide at the Oregon State University Marine Science Center dock, at Newport, Oregon. These experiments were conducted at Oregon State University.

Animals were collected using a half-meter net with a 64 um mesh inner lining (500 µm mesh outer protective lining) towed at low speed, or hand-drawn through the water either from a small 26 foot modified Oregon dory, or from dock-side. The net was rinsed down while still in the water. and the cod end placed immediately into a bucket of surface water taken just prior to the tow. The cod end was removed from the net and all contents poured into containers filled with water collected at the surface just prior to the tow. The containers were transported back to the laboratory where the cultures were cleaned of any settled detritus, and put into large glass or polypropylene containers. An ample amount of phytoplankton culture (a mixture of the diatom, Thalassiosira fluviatilis = T. weissflogii, and the flagellate, Isochrysis galbana) was added. This maintenance procedure was used until several hundred animals had been sorted and prepared for an experiment.

Experimental Conditions

All experiments were done under the conditions shown in Table 1. Copepods from a live collection were sorted by species and developmental stage into filtered seawater containing a mix of the two experimental food types at the appropriate concentration for each food type (Level B = 5×10^6 μm^3/ml *T. fluviatilis* and 2.5×10^6 μm^3/ml *I. galbana*, Table 1). Food concentrations in this zooplankton stock culture were monitored twice daily and maintained at the appropriate level during a three day preconditioning period. Cell concentrations were established such that the larger cell (*T. fluviatilis*) was twice as abundant as the smaller cell (*I. galbana*) on a cell volume basis, and the smaller cell was approximately 10 times as abundant as the larger cell on a cell number basis (Table 1).

Just prior to each experiment, copepods in the preconditioning stock culture were again sorted to stage to ensure that only newly-molted animals were used in experiments. Since the process of molting may affect grazing rate, this procedure reduced the chance that molting would occur during an experiment. Depending on the species and developmental stage to be used, 10 to 30 animals were sorted for each experimental flask into small 20 ml containers. These animals were maintained under experimental conditions at the appropriate food level for the short period of time required to establish the experimental food concentrations and take the initial cell counts (15-30 minutes). This procedure did not appear to have any traumatic effect on the copepods. Swimming behavior always appeared normal and deaths during an experiment were always quite low (< 10%).

For each food level (Table 1) two control flasks (phytoplankton only) and two experimental flasks (Phytoplankton with copepods added) were used. Phytoplankton concentrations were chosen to represent the full range of *in situ* concentrations that these nearshore copepods might

Table 3-1 Experimental conditions and design for the developmental stage grazing experiments. For each experiment, two replicate experimental flasks (with copepods) and two control flasks (without copepods) were used at each food level. Copepods were preconditioned for three days prior to the beginning of an experiment at Level B. See text for details.

Experimental Conditions

LIGHT LEVEL: 75 - 100 $\mu E/m^2/sec$

TEMPERATURE: 10° +/- $0.5^{\circ}C$

WATER: 30-32 ppt salinity coastal water filtered through 0.45 µm Millipore filter and autoclaved.

MEDIA: F/2 nutrients + vitamins (Strickland and Parsons 1967)
10 µmoles/liter ammonia added as NH_4NO_3

FOOD TYPES:

DIATOM - *Thalassiosira fluviatilis* = *T. weissflogii*
Cell Characteristics:
1. non-chain forming, doublets sometimes present in cultures
2. cells typically pill-box shape without long spines or processes
3. 8-15 µm equivalent spherical diameter (ESD), 900-1400 μm^3/cell

FLAGELLATE - *Isochrysis galbana*
Cell Characteristics:
1. single cell, nearly spherical
2. 2-5 µm ESD, 45-90 μm^3/cell

Experimental Design

FOOD LEVEL	*T. fluviatilis* (10^6 μm^3/ml)	*I. galbana* (10^6 μm^3/ml)	Total (10^6 μm^3/ml)
A	2.5	1.25	3.75
B	5.0	2.5	7.5
C	7.5	3.75	11.5
D	10.0	5.0	15.0

encounter in the field, and still be within the range of concentrations reliably counted with our Coulter Counter system. In order to establish the four food levels used in each experiment, enough stock culture of the highest phytoplankton concentration (Level D, 4-6 liters) was made so that after the initial counts for that level were taken and all flasks for that level were initiated into an experiment (2 control and 2 grazer flasks per level), the remaining stock culture could be diluted with filtered seawater and the concentration of each cell type adjusted to establish the correct levels for the second food concentration (Level C). This procedure was continued until all four food levels had been established. Vitamins and nutrients were added to each stock culture and to the seawater used to dilute the cultures, so that the concentrations were equivalent at all four food levels. Ten umoles/liter ammonia was added (as NH_4NO_3) to all stock cultures and to the diluting water to negate or at least reduce the effects of ammonia excreted by the copepods in the experimental flasks. Initial cell counts were then taken for level D, and the procedure continued until cell counts for each flask at each food level had been completed. From 300 to 600 mls of food suspension were used in each flask, depending upon the grazer species and developmental stage to be used in an experiment. One cell count (the mean of five replicate subsample counts) for each food type was taken approximately 24 hours later to determine final concentrations in each control and experimental flask.

An acrylic plastic cage lined on the bottom with 64 um mesh was used to contain the grazers in each experimental flask. The cages were connected to a horizontal bar positioned above the flasks which was motor-driven to raise and lower the cages through the water 3-4 times every 15 minutes throughout the duration of an experiment. This motion resulted in a well-mixed phytoplankton suspension and min-

imized sinking of the cells. The cage also made the transfer, sorting and counting of copepods a much easier task, and greatly minimized animal losses during an experiment. Identical cages (without copepods) were added to control flasks to control for any "cage effects" on phytoplankton growth and to ensure similar phytoplankton distributions in the control and experimental flasks. Preliminary tests for this design showed no effect of using the cage. Replication between flasks was enhanced using this method.

All experiments were run at 10°C +/-0.5°C, under constant cool-white fluorescent lighting (75-100 $\mu E/m^2/sec$, constant illumination, Table 1). A flow-through water bath was used for temperature control. All experiments conducted at Oregon State University were done in walk-in coldrooms, so that lighting, and both air and water temperature could be rigidly controlled. For experiments conducted at the Friday Harbor Marine Laboratory, a framework was built to support the same water bath and lighting arrangement. Constant lighting was used in all experiments rather than a light-dark cycle or constant darkness in order to achieve better estimates of exponential cell growth over the 24 hour experimental period. Exponential cell growth was a basic assumption in the algorithm used to calculate grazing removals. Copepods were removed from each experimental flask after the final (24 hour) cell counts for that flask were completed. The animals were rinsed from each cage into a petri dish with filtered seawater, counted (number live + dead, and any molts present were noted), identified to developmental stage, and preserved in 5% buffered formalin. An experimental data set from which all subsequent calculations were made was thus composed of the number of animals and volume of water used in each flask, and the particle counts (cell volume and cell number) for each of the two food types in two control and two experimental flasks at each of the four food levels (16 flasks, 32 counts per experiment).

The system used to count cells and for the particle distribution analyses was a model ZBi Coulter Counter with a P-64 size-class "channelizer". The distributions of each food type were counted with a 70 µm aperture on the sensitivity and threshold settings used to optimize the counting statistics for each food type. The cell distributions were displayed visually on an oscilloscope and plotted on an X-Y plotter. All data were initially expressed on a cell volume basis and recorded by size class. The size-class data were taken digitally by a PDP-8e minicomputer and recorded on paper tape for subsequent analysis. The size-class-specific data were taken over 64 discrete channels (size classes) for each food type. Subsequent analyses excluded data from those channels in which there were obvious effects of detrital formation, particle production, or ammonia effects on the cell distribution. These effects were most often apparent in the first five to ten channels of a distribution (i.e., the smallest particles in a distribution). Data from channels where the counting statistics were poor due to low cell numbers (usually the last 20 channels of a distribution) were also excluded. The remaining data from approximately 30 channels for each food type were then used to calculate the grazing functions for each experiment.

In order to relate the grazing data directly to the morphological measurements taken in the comparative morphology study (Chapter 2),the size-class-specific grazing data were grouped into size categories which represented cell size intervals of 1 µm equivalent spherical diameter (ESD), based on the mathematical conversion from cell volume in each channel to ESD of a cell. Grazing functions for the 1 um size categories across the total cell spectrum (2-15 µm ESD) were examined.

Data Analyses

The equations used to calculate the basic grazing functions are listed in Table 2. These equations are derived from the basic production equation (Steele and Frost 1978, Kremer and Nixon 1978):

$$1/N\ dN/dt = a-r-e-w-g-s,$$

where N = phytoplankton population number (cell number), t = time, a = assimilation or gross primary production, r = respiration, e = excretion, w = dilution (advection + diffusion losses), g = grazing, and s = sinking, all expressed as rates. In a laboratory grazing experiment, advection and diffusion losses do not occur, and sinking losses are minimized. The (a-r-e) portion of the equation may thus be set equal to K, the observed phytoplankton growth rate. The notation used here is Kc, representing the growth rate of phytoplankton in the control vessel without copepods present (Output Equation 1, Table 2). The change in cell number with time, $1/N\ dN/dt$, was measured in the grazer flask as the observed or apparent growth rate of the phytoplankton, Ka, which included both phytoplankton growth and grazing losses (Output Equation 2, Table 2). The difference between the growth rate measurements in the control and the experimental flasks represented the estimate for grazing rate, Kg (where $Kg = Kc-Ka$, Output Equation 3, Table 2), over the specified period of time. These equations assumed that both phytoplankton growth and copepod grazing removal were exponential processes. The assumption of exponentiality was considered valid under the experimental conditions of (1) constant illumination at intermediate (non-saturating) light levels, (2) the use of healthy, laboratory-grown (constant light-entrained) phytoplankton cultures in log-phase, with adequate nutrient availability, and (3) the use of animals which were preconditioned to a desired food level and cell

Table 3-2 Grazing functions calculated for each grazing experiment.

Function	Symbol	Calculation	Dimensions
INPUT:			
1. Control Final Concentration	CF	Coulter Counter Output to PDP-8e	um^3/ml, cells/ml
2. Control Initial Concentration	CI		um^3/ml, cells/ml
3. Grazer Final Concentration	GF		um^3/ml, cells/ml
4. Grazer Initial Concentration	GI		um^3/ml, cells/ml
5. Final Control Time	TF_c	Julian Date + Computer Time	day
6. Initial Control Time	TO_c		day
7. Final Grazer Time	TF_g		day
8. Initial Grazer Time	TO_g		day
9. Vessel Volume	V_O		ml
10. Animal number per flask	A		no. animals/flask
OUTPUT:			
1. Control Growth Rate	K_c	$\ln (CF-CI)/TF_c-TO_c$	day^{-1}
2. Apparent Growth Rate	K_a	$\ln (GF-GI)/TF_g-TO_g^c$	day^{-1}
3. Grazing Rate	Kg	$Kc-Ka$	day^{-1}
4. 24 hr-adjusted CF	CI(24)	$(CI)\ e^{Kc}$	um^3/ml, cells/ml
5. 24 hr-adjusted GF	GF(24)	$(CI)\ e^{Ka}$	um^3/ml, cells/ml
6. Exponential Mean Cell Number	EMN	$(CI)\ e^{Ka(T-TO_g)}$	cells/ml
or Biomass	EMB		um^3/ml
7. Grazing Flux Loss	GFL	Kg (EMN or EMB) Vo	um^3/ml, cells/ml
8. Ingestion Rate	IR	GFL/A	um^3/animal/day
9. Apparent Filtration Rate	FRa	IR/(EMN or EMB)	ml/animal/day
10. Capture Rate	CR	GFL/A	cells/animal/day
11. Encounter Rate	ER	*(Fmax) (EMN)	cells/animal/day
12. Retention Rate	RR	**(ERi) (ei)	cells/animal/day
13. Effective Cell Availability	Ae	(EMN) (ei)	cells/ml

* Fmax = Maximum Filtration Rate ** ei = Retention Efficiency for cell size i

type, and otherwise acclimated to the experimental conditions (temperature, salinity, light) for several days prior to the beginning of an experiment.

Grazing estimates on a 24 hour basis (Output Equation 4 and 5, Table 2) were calculated assuming an exponential growth rate equivalent to that actually measured over the experimental time period. Thus, initial and final counts did not have to be taken exactly 24 hours apart during a given experiment in order to calculate the grazing functions on a 24 hour basis. In practice, the flasks for each food level were terminated within +/- 4 hours of a 24 hour experimental period. The 24 hour-based computed data were used in all subsequent calculations (Output Equations 6-13, Table 2).

All cell count measurements and initial calculations were based on changes in cell volume. This procedure was initially imposed by the use of the Coulter Counter, which assessed particle concentrations by monitoring the interruption of an electrical current conducted through the seawater medium, and thus measured particle volume displacement. Particle number was simultaneously recorded as the number of discrete pulses measured in a given volume of water. Particle sizes were thus determined by conversion of the volume of water displaced to an equivalent spherical diameter for each pulse counted, assuming that the particles could be represented as spheres. Mean particle size per channel was calculated as a linear multiple of the channel number and the counter sensitivity, and was based on a calibration curve generated for each aperature size and sensitivity setting.

Cell availability to each copepod developmental stage was first calculated as exponential mean biomass, EMB, or exponential mean cell number, EMN (Output Equation 6, Table 2) on a size-class-specific basis and total food basis, for each food type separately and for both food species combined.

These calculations were used to generate estimates of the total cell volume or cell number removed (grazer flux loss) from a flask (Output Equation 7, Table 2). The channel-specific data for cell availability were then summed, as were the ingestion rate calculations (Output Equation 8, Table 2) for the same set of channels, in order to compare cell availability directly to the amount ingested in each cell size category. Filtration rate was calculated from the channel data, and averaged over the channels for each size category (1 μm ESD intervals) across the full spectrum of cells (Output Equation 9, Table 2). Ingestion (volume basis, μm^3/day) and capture (number basis, cells/day) rates were first calculated on a per animal basis and then converted to a dry weight basis (Output Equation 10, Table 2). For the dry weight determinations (Table 3), 20 to 50 animals of each developmental stage were sorted from laboratory cultures (for Oregon experiments) or from field samples (Washington experiments) onto pre-weighed squares of aluminum foil, dried at 60°C for 3-6 days in a drying oven, and weighed on a Cahn Electrobalance.

Encounter rates for each cell type were calculated as the product of the exponential mean cell number for each size category times the maximum filtration rate calculated for that experimental flask (Output Equation 11, Table 2). Encounter rates thus represented the number of cells in each size category theoretically encountered by a copepod in a given amount of time, assuming a constant grazing (and filtration) rate over a 24 hour period. Retention rates were then calculated to represent the number of cells of each type theoretically encountered by an animal and retained on the filter (Output Equation 12, Table 2). The theoretical retention rate for each cell size category was calculated as the encounter rate for than cell size times the retention efficiency for a cell of that size. The total number of cells encountered and theoretically retained on the filter was used to estimate the effective

availability of a cell to each developmental stage (Output Equation 13, Table 2).

Table 3-3 Dry weight measurements (µg/copepod) for each developmental stage of *Pseudocalanus* sp. and *Acartia clausi*. The mean of the two stage-specific weights was used for experiments where stages were combined. The weight estimate used in a given experiment was appropriate for the time of year and location from which the animals were collected.

Stage	Pseudocalanus	Acartia
CI + CII	1.2	0.8
CIII + CIV	3.3	2.5
CV	8.6	8.9
Female	11.4	13.1

Results

Ingestion and Capture Rates

Ingestion rates for the developmental stages of Pseudocalanus and Acartia clausi were calculated on a cell volume basis (μm^3/day). Capture rates were calculated on a cell number basis (cells/day). Removal rates were first calculated on a per animal basis (Fig. 1 and 2), and then converted to a weight-specific basis (Fig. 3 and 4) to adjust for seasonal changes in copepod body size and weight observed during the period of time over which experiments were conducted. For this analysis, the data were combined for the stages CI-CII, CIII-CIV,and CV-female, because no differences in the maximum rates between stages were observed ($p<.05$) on either a per animal or on a weight-specific basis. The data for Acartia CIII-CIV, and the CI-CII stages of both species were treated together in all subsequent analyses because these stages were difficult to sort and were not consistently separated in the laboratory grazing experiments. Animal weights for the combined stages were adjusted for the number of animals of each stage used in a given treatment. Because the animals may have been feeding on the two food types using different feeding mechanisms, the data for the two foods were analysed separately.

The ingestion and capture rate functions for feeding on Thalassiosira were defined by a curvilinear equation for the younger copepodites of both species. Feeding on Isochrysis by all stages and feeding on Thalassiosira in the oldest stages indicated a linear relationship between ingestion or capture rate and food concentration. These rates calculated on a per animal basis (Fig. 1,2) generally increased with increasing developmental stage; rates calculated on a weight-specific basis decreased with developmental stage (Fig. 3,4). Different patterns were ob-

Figure 3-1 Stage-specific ingestion rate (10^6 μm^3/animal/day) for the combined developmental stages of Pseudocalanus sp. (●) and Acartia clausi (O). Rates were calculated for each food separately. Lines shown indicate the best fit of the data to a linear ($Y = aX + b$) or curvilinear function. Curvilinear equations, indicated by an asterisk, were calculated from the linear form of an Ivlev function, $I = Imax\ [1-\exp(-\alpha P)]$, such that $Y = \ln(Imax - I)$, $b = \ln(Imax)$, $a = \alpha$, and X = food concentration (P). See text for details.

Figure 3-1

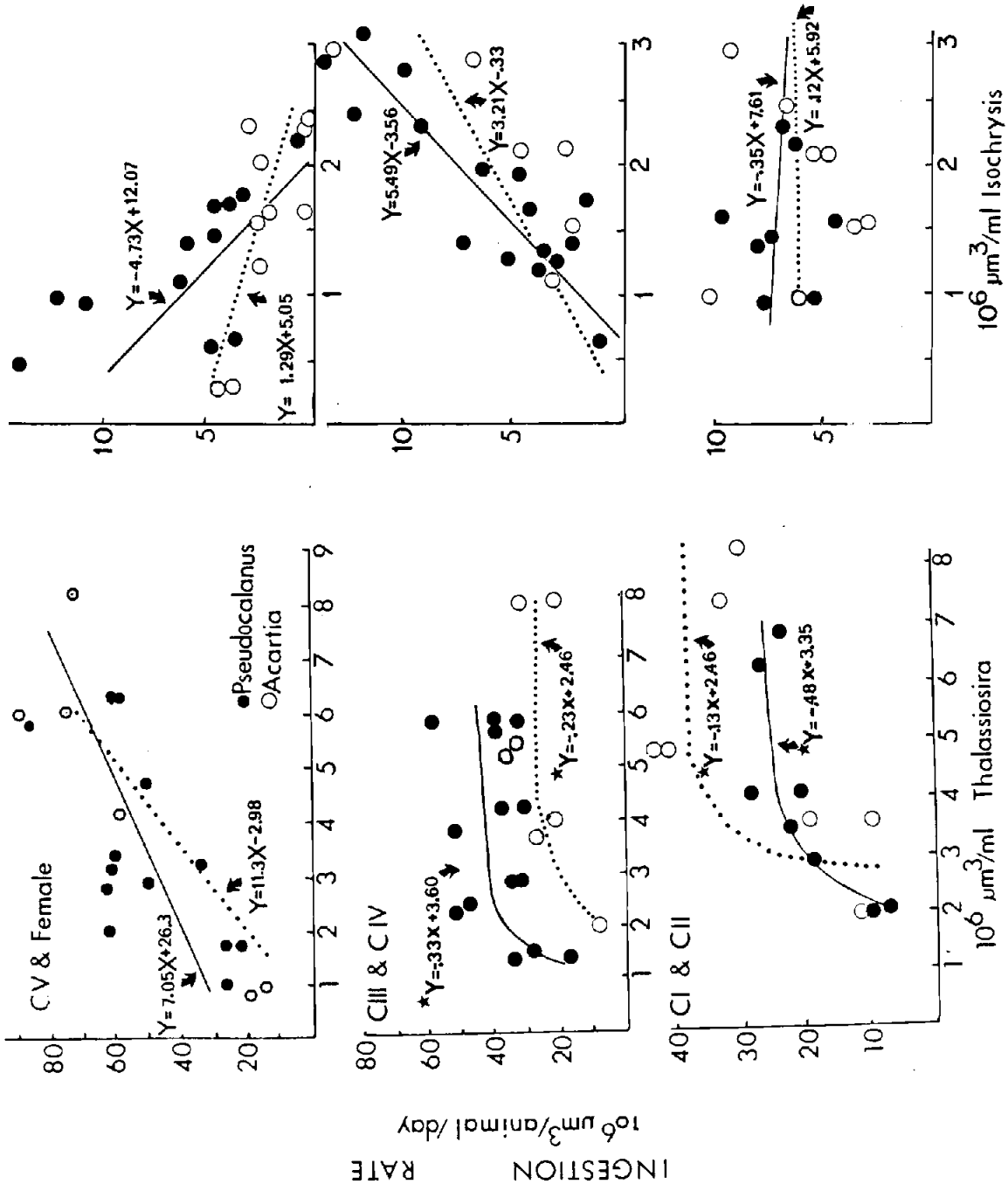

INGESTION RATE
10⁶ µm³/animal /day
CV & Female
Y=7.05X+26.3
Y=11.3X-2.98
●Pseudocalanus
○Acartia
CIII & CIV
Y=.33X+3.60
Y=.23X+2.46
CI & CII
Y=.13X+2.46
Y=.48X+3.35
10⁶ µm³/ml Thalassiosira
Y=-4.73X+12.07
Y= 1.29X+5.05
Y=5.49X-3.56
Y=3.21X-.33
Y=.35X+7.61
Y=.12X+5.92
10⁶ µm³/ml Isochrysis

Figure 3-2 Stage-specific capture rate (10^3 cells/animal/day) for the combined developmental stages of Pseudocalanus (●) and Acartia clausi (O). Equations calculated as in Fig. 1.

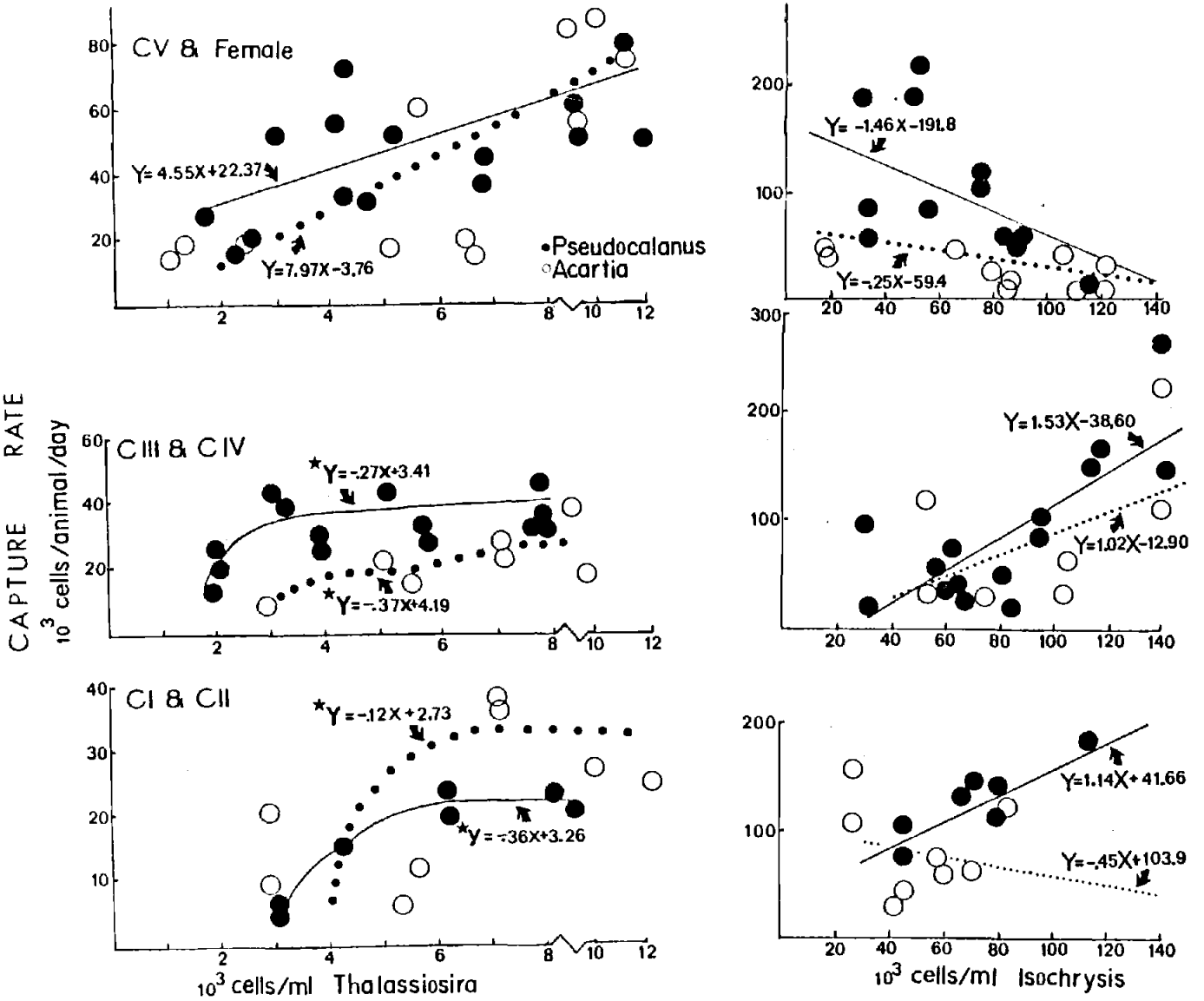

CV & Female
Y= 4.55X+22.37
Y=7.97X-3.76
•Pseudocalanus
○Acartia
Y= -1.46X-191.8
Y=-.25X-59.4
CAPTURE RATE
10^3 cells/animal/day
CIII & CIV
*Y=-.27X+3.41
*Y=-.37X+4.19
Y=1.53X-38.60
Y=1.02X-12.90
CI & CII
*Y=-.12X+2.73
*y=-.36X+3.26
Y=1.14X+41.66
Y=-.45X+103.9
10^3 cells/ml Thalassiosira
10^3 cells/ml Isochrysis

Figure 3-2

Figure 3-3 Weight-specific ingestion rate (10^6 $\mu m^3/\mu g$ copepod dry weight/day) for the combined developmental stages of Pseudocalanus (●) and Acartia clausi (O). Equations calculated as in Fig. 1.

Figure 3-3

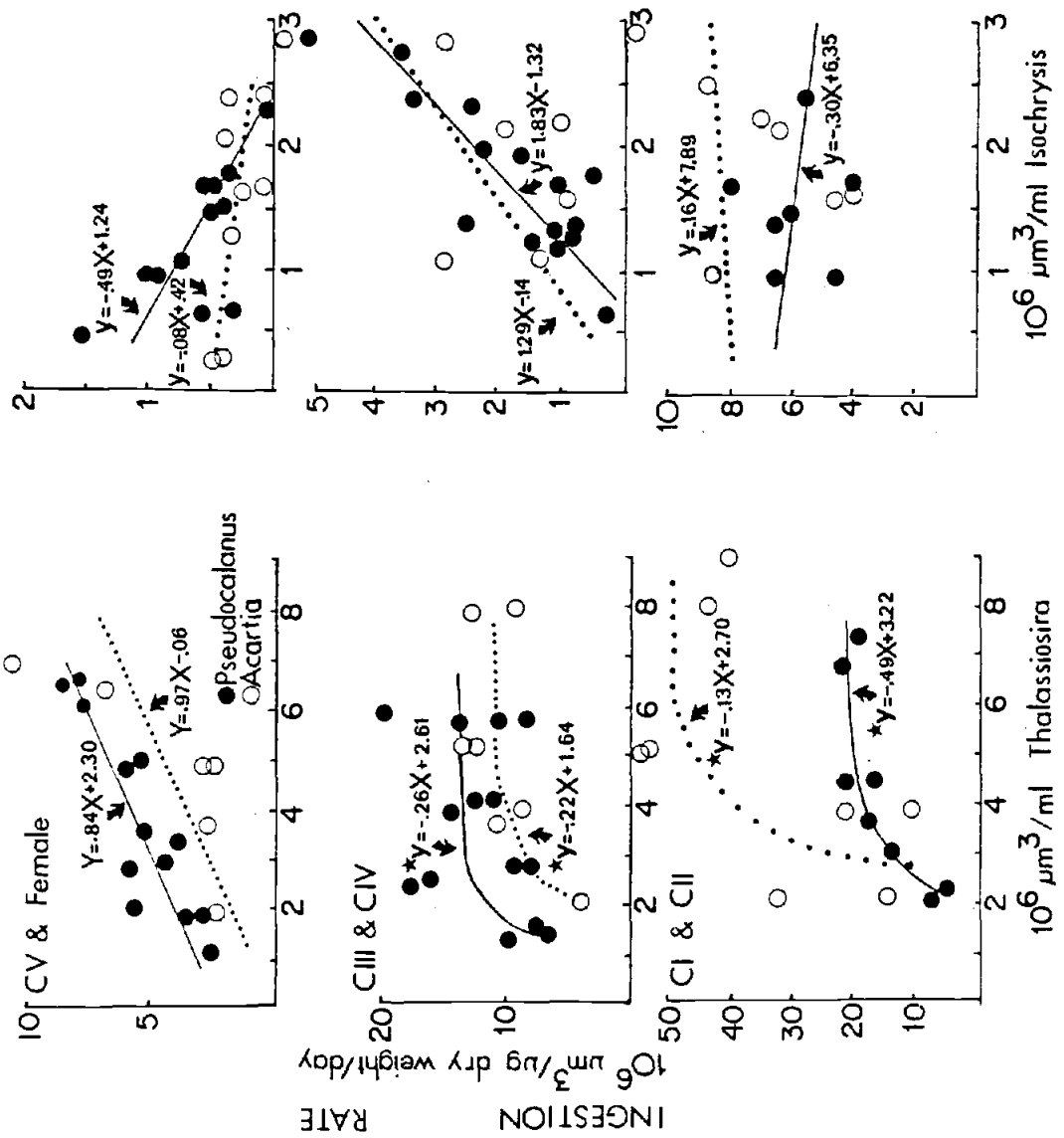
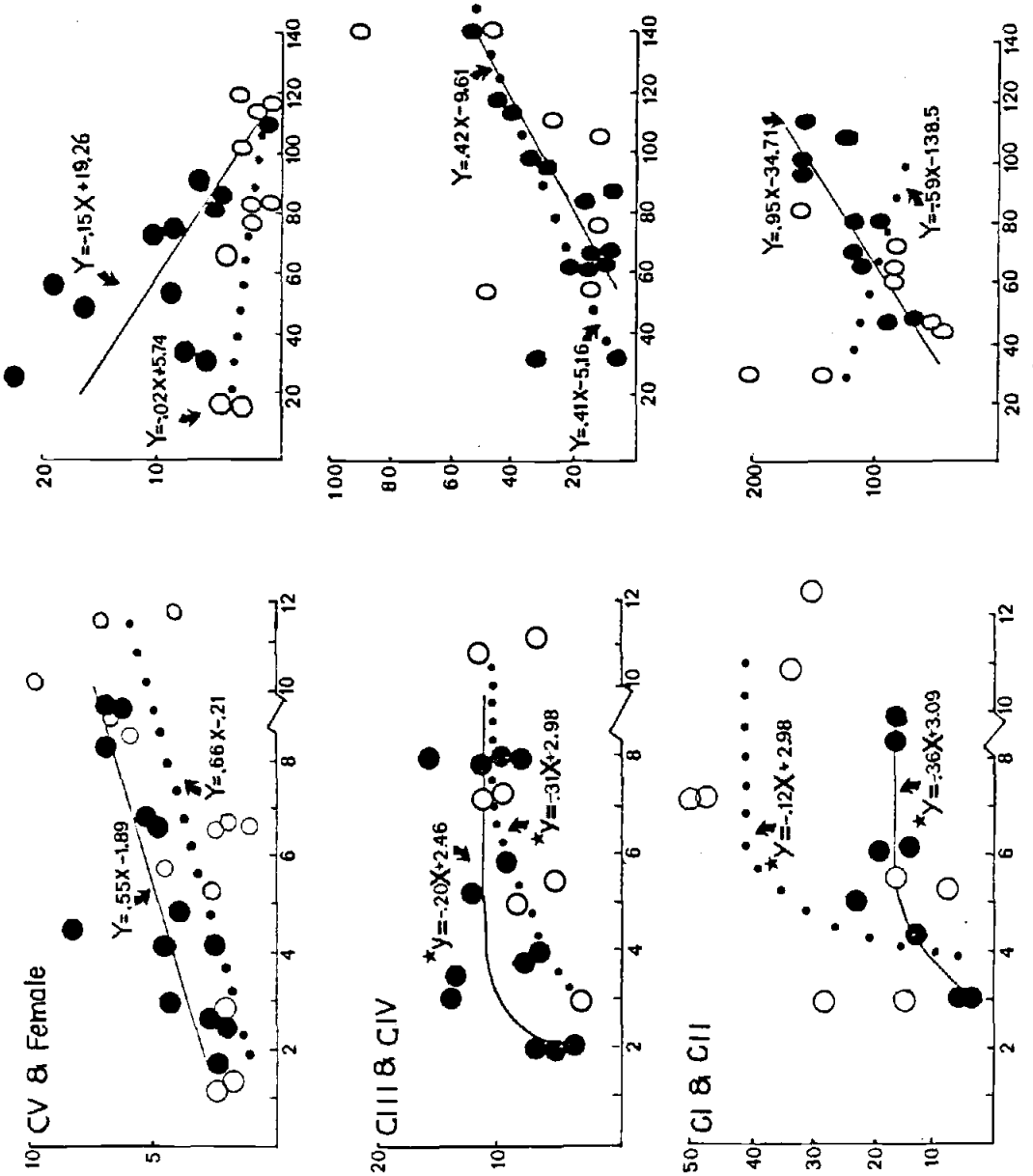

CV & Female
Y=.84X+2.30
Y=.97X-.06
Pseudocalanus
Acartia
CIII & CIV
y=-.26X+2.61
y=-.22X+1.64
CI & CII
y=-.13X+2.70
y=-.49X+3.22
Thalassiosira
y=-.49X+1.24
y=-.08X+.42
y=1.29X-.14
y=1.83X-1.32
y=.16X+7.89
y=-.30X+6.35
Isochrysis
RATE
INGESTION
10^6 µm^3/µg dry weight/day
10^6 µm^3/ml
10^6 µm^3/ml

Figure 3-4 Weight-specific capture rate (10^3 cells/µg copepod dry weight/day) for the combined developmental stages of Pseudocalanus (●) and Acartia clausi (O). Equations calculated as in Fig. 1.

Figure 3-4


CV & Female
Y=.55X-1.89
Y=.66X-.21
CIII & CIV
Y=-.20X+2.46
Y=-.31X+2.98
CI & CII
Y=-.12X+2.98
Y=-.36X+3.09
Y=-.15X+19.26
Y=-.02X+5.74
Y=.42X-9.61
Y=.41X-5.16
Y=.95X-34.71
Y=.59X-138.5
CAPTURE RATE
10^3 cells/ug dry weight/day
10^3 cells/ml Thalassiosira
10^3 cells/ml Isochrysis

served for the older developmental stages (CV-female)as compared to the younger stages. Ingestion of Isochrysis by CV + females decreased with increasing food concentration, whereas the ingestion rates of stages CIII+CIV increased with increasing food concentration. Ingestion of Isochrysis by the youngest stages (CI+CII) of Pseudocalanus was approximately the same over the four concentrations studied (β not significantly different from zero); Acartia CI+CII had elevated ingestion rates for Isochrysis at the lowest food concentration, although a regression of the data indicated no consistent trend with food concentration (β not significantly different from zero). The maximum daily grazing removal of the youngest copepodites (CI+CII) was 3-5 times that of the adult female on a weight-specific basis for Pseudocalanus, and 5-10 times higher for Acartia on a cell number basis. Maximum ingestion and capture rates for Thalassiosira were generally comparable between the two grazer species, with Acartia CI+CII removing slightly more of the diatom compared to Pseudocalanus CI+CII (Table 4).

Based on the ingestion and capture rate data, the contribution of each food type to the ration ingested at each food level was calculated on a cell number (Table 5) and a cell volume (Table 6) basis. For this analysis, the data were calculated for the combined CI+CII and CIII+CIV stages, and for stage CV and the adult female separately. Although the absolute ingestion and capture rates calculated on a per animal basis for stage CV and the adult female of each species were statistically similar, a different pattern was observed in the percent of each food type removed by these stages, and so the data were treated separately. For Pseudocalanus, the mean percentage of Thalassiosira eaten (mean of two replicate flasks at each food level calculated on a cell number basis) was lowest in the youngest and oldest developmental stages (Table 5). Pseudocalanus CI+CII removed 6-14% ($\bar{x}$ = 10.7%) of their ration as Thalassiosira, and thus close to 90% of the ration was from Isochrysis

Table 3-4 Maximum ingestion and capture rates for *Pseudocalanus* sp. and *Acartia clausi* developmental stages. Data are estimates of the maximum daily grazing removal on a stage-specific (per animal) basis and on a weight-specific (per ug copepod dry weight) basis for each food type separately (*T.f.* = *T. fluviatilis*; *I.g.* = *I. galbana*), and for the two foods combined (Total).

Stage - Specific Rates

Stages	Ingestion Rate 10^6 µm³/animal/day			Capture Rate 10^3 cells/animal/day		
	T.f.	I.g.	Total	T.f.	I.g.	Total
			Pseudocalanus			
CI+CII	25	7	32	20	180	200
CIII+CIV	50	13	63	40	200	240
CV+Female	80	14	94	70	200	270
			Acartia			
CI+CII	37	8	45	35	150	185
CIII+CIV	25	12	37	30	200	230
CV+Female	80	4	84	90	50	140

Weight - Specific Rates

Stages	Ingestion Rate 10^6 µm³/ug/day			Capture Rate 10^3 cells/ug/day		
	T.f.	I.g.	Total	T.f.	I.g.	Total
			Pseudocalanus			
CI+CII	20	7	27	15	150	165
CIII+CIV	15	5	20	12	50	62
CV+Female	7	1.5	8.5	7	20	27
			Acartia			
CI+CII	50	8	58	40	150	190
CIII+CIV	10	5	15	10	50	60
CV+Female	10	0.5	10.5	7	5	12

Table 3-5 Percent of the total ration contributed by Thalassiosira and Isochrysis on a cell number basis. Data are the mean percentage from two replicate flasks at each food level, and the overall mean for each stage. A chi-square (X^2) analysis was used to compare the observed percentage of each food type in the ration to an expected value of 10% for Thalassiosira and 90% for Isochrysis based on the relative percentage of each food type in the particle spectrum. p = Significance level; NS = differences not significant at the .05 level. See text for details.

Table 3-5

Stages	Food Level	% Thalassiosira	% Isochrysis	X^2	p
		Pseudocalanus			
CI+CII	A	6	94	1.78	NS
	B	14	86	1.78	NS
	C	11	89	0.20	NS
	D	12	88	0.44	NS
	Mean	10.7	89.3		NS
CIII+CIV	A	36	64	75.11	.01
	B	44	56	128.44	.01
	C	33	67	58.78	.01
	D	18	82	7.10	.05
	Mean	32.7	67.3		.01
CV	A	17	83	5.40	.05
	B	22	78	16.00	.01
	C	49	51	169.00	.01
	D	67	33	361.00	.01
	Mean	38.7	61.3		.01
Female	A	25	75	25.00	.01
	B	21	79	13.40	.01
	C	27	73	32.11	.01
	D	10	90	0.00	NS
	Mean	20.7	79.3		.01
		Acartia			
CI+CII	A	10	90	0.00	NS
	B	20	80	11.10	.01
	C	37	63	81.00	.01
	D	24	76	21.78	.01
	Mean	22.7	77.3		.01
CIII+CIV	A	6	94	1.78	NS
	B	36	64	75.11	.01
	C	39	61	93.44	.01
	D	14	86	1.78	NS
	Mean	23.7	76.3		.01
CV	A	99	1	880.11	.01
	B	30	70	44.44	.01
	C	27	73	32.11	.01
	D	78	22	513.78	.01
	Mean	58.5	41.5		.01
Female	A	33	67	58.78	.01
	B	15	85	2.78	NS
	C	85	15	625.00	.01
	D	85	15	625.00	.01
	Mean	54.5	45.5		.01

Table 3-6 Percent of the total ration contributed by Thalassiosira and Isochrysis on a cell volume basis. Data are the mean percentage of two replicate flasks at each food level, and the overall mean for each stage. A chi-square (X^2) analysis was used to compare the observed percentage of each food type in the ration to an expected value of 67% for Thalassiosira and 33% for Isochrysis based on the relative percentage of each food type in the particle spectrum. p = significance level; NS = differences not significant at the .05 level. See text for details

Table 3-6

Stages	Food Level	% Thalassiosira	% Isochrysis	X^2	p
		Pseudocalanus			
CI+CII	A	54	46	7.64	.01
	B	72	28	1.13	NS
	C	76	24	3.66	NS
	D	80	20	7.74	.01
	Mean	70.5	29.5		NS
CIII+CIV	A	90	10	23.93	.01
	B	92	8	28.27	.01
	C	84	16	13.07	.01
	D	88	12	19.95	.01
	Mean	88.5	11.5		.01
CV	A	74	26	2.22	NS
	B	76	24	3.66	NS
	C	92	8	28.27	.01
	D	96	4	38.04	.01
	Mean	84.5	15.5		.01
Female	A	88	12	19.95	.01
	B	83	17	11.58	.01
	C	92	8	28.27	.01
	D	72	28	1.13	NS
	Mean	83.8	16.2		.01
		Acartia			
CI+CII	A	67	33	0.00	NS
	B	78	22	5.47	.05
	C	90	10	23.93	.01
	D	79	21	6.51	.05
	Mean	78.5	21.5		.05
CIII+CIV	A	57	43	4.52	.05
	B	88	12	19.95	.01
	C	89	11	21.89	.01
	D	70	30	0.41	NS
	Mean	76	24		NS
CV	A	99	1	46.33	.01
	B	88	12	19.95	.01
	C	81	19	8.86	.01
	D	98	2	43.46	.01
	Mean	91.5	8.5		.01
Female	A	77	23	4.52	.05
	B	65	35	0.04	NS
	C	99	1	46.33	.01
	D	99	1	46.33	.01
	Mean	85	15		.01

over the four food levels. Female Pseudocalanus ate 10-27% Thalassiosira ($\bar{x}$ = 20.7%). The contribution to the ration from the diatom increased with increasing food concentration in the Pseudocalanus CV experiment, from 17% at the lowest food level to 67% at the highest food concentration ($\bar{x}$ = 38.7%). The intermediate developmental stages (CIII+CIV) removed 30% of their ration as Thalassiosira at all but the highest food level ($\bar{x}$ = 32.7%).

For Acartia, the younger stages (CI-CIV) ate less Thalassiosira on a cell number basis than the two older Acartia stages, considering all four food levels together (Table 5). Acartia stages CI+CII ate 10-37% Thalassiosira on a cell number basis ($\bar{x}$ = 22.7%), approximately twice the average ration eaten by Pseudocalanus CI+CII. Acartia CIII+CIV generally ate less of the diatom than Pseudocalanus copepodites at the equivalent stage, ranging from 6 to 39% Thalassiosira in the ration on a cell number basis ($\bar{x}$ = 23.7%). Acartia CV primarily ate Thalassiosira at the lowest and highest food concentrations (78% and 99%, respectively), and almost no Isochrysis was eaten at the lowest food level in this experiment. Acartia females ate the most Thalassiosira at the two highest food levels (85%).

Over all experiments, Thalassiosira averaged 10% of the total number of cells available to the grazers at each food level; Isochrysis averaged 90% relative abundance on a cell number basis. Assuming both cell types were encountered, captured, and ingested in proportion to their numerical abundance, the expected percentages for each cell type in the ration would have been 10% and 90%, respectively. A chi-square analysis of the percentage data (Table 5) indicated that the contribution of Thalassiosira to the ration was consistently greater than the expected 10% value in all experiments except for Pseudocalanus CI+CII. For the older stages, only level D in the adult female experiment was not significantly different from the expected value. For Acartia, 12 out of 16 percentages and the mean percentage

for each experiment were significantly greater than the expected percentages on a cell number basis (Table 5). The chi-square analysis of the percentage data thus indicated that only in the youngest stages of Pseudocalanus (CI+CII) were cells consistently removed in direct proportion to their relative abundance in the food spectrum. A similar chi-square analysis of the raw number data (cells ingested/minute vs. cells encountered/minute) for each food type indicated that more Thalassiosira cells were eaten by all developmental stages of both species than expected based on the theoretical abundance of the diatom in the food spectrum at all food levels ($p<.01$).

The data calculated on a cell number basis (Table 5) may be compared to the contribution of each cell type to the ration calculated on a total cell volume basis (Table 6). Total cell volume of the diatom was twice that of the flagellate in all experiments (Table 1). Assuming now that both cell types were retained by the copepods in proportion to their total cell volume in the water, the expected values for the contribution of each cell type to the ration would be 67% for Thalassiosira and 33% for Isochrysis (i.e., a ratio of 2:1). A chi-square analysis of the percentage data on a volume basis (Table 6) indicated that in 11 out of 16 instances, Pseudocalanus removed more of the diatom than expected on a cell volume basis. The lowest food level in the Pseudocalanus CI+CII experiment was the only case where less of the diatom was eaten than expected. For Pseudocalanus, the level of significance of the chi-square values for data calculated on a volume basis (Table 6) did not always coincide with those calculated on a cell number basis (Table 5). For Acartia, the proportions of each cell type removed were significantly different than the expected volume proportions in all but three out of the 16 comparisons. These treatments also showed no significant difference from expected values calculated on a cell number basis

(Table 5). All mean percentages were greater than the expected volume proportions, but were not statistically significant for Pseudocalanus CI+CII and Acartia CIII+CIV. A chi-square analysis of the raw volume data (μm^3 ingested/minute vs. μm^3 encountered/minute) indicated the same pattern as the analysis of the percentage data (Table 6).

Filtration Rate

An average apparent filtration rate was calculated from the ingestion rate data (Output Equation 9, Table 2) for each cell size category (1 µm ESD intervals) across the complete cell spectrum. The maximum filtration rate calculated from each experimental flask was defined as the highest mean filtration rate calculated for the 13-15 µm ESD cell size categories in the Thalassiosira distribution (i.e., the largest cells). This analysis assumed that (1) filtration rate increased with increasing cell size (Frost 1972b), (2) the largest cells in the distribution were removed with the greatest efficiency, and (3) the larger cell size categories were not affected by any experimental biases (e.g., ammonia excretion-induced swelling of cells, detrital formation, or particle production). The only exception to this procedure was in the adult female Acartia experiment, where maximum ingestion and filtration rates were always observed in the 9 and 10 µm ESD size categories.

Weight-specific ingestion and capture rates were similar for CV and adult females of each species primarily because of the differences in the body weights calculated for these developmental stages. However, the maximum filtration rates calculated for females were 2-3 times higher than the rates calculated for the stage CV of that species. The filtration rate data for these two stages were thus treated separately (Table 7). Pseudocalanus CIII+CIV data were also treated separately, since the estimated maximum filtration rates calculated for these stages were somewhat different. The expected decrease in filtration rate with increasing food concentration was observed in some experiments for each species. Maximum filtration rates for Pseudocalanus were higher, on average, for the older developmental stages. Values ranged from 18.7 (+/-7.4) mls/animal/day for the adult female to 5.5 (+/-1.2) mls/animal/day for stages CI+CII. Acartia females also had a higher

Table 3-7 Maximum filtration rate (mls/animal/day) for the developmental stages of Pseudocalanus and Acartia clausi. The value calculated at each food level was the mean rate from two replicate flasks The mean over all four food levels is also listed for each developmental stage.

Stage	Food Levels A	B	C	D	Mean
Pseudocalanus					
CI+CII	5.4	5.6	6.7	5.5	5.5
CIII	7.2	8.6	5.2	4.4	6.4
CIV	12.2	6.9	4.9	5.0	7.3
CV	18.2	9.6	6.6	7.8	10.6
Female	11.4	25.3	17.6	16.8	18.7
Acartia clausi					
CI+CII	7.3	6.9	12.6	5.1	7.9
CIII+CIV	4.4	7.8	9.4	4.3	6.5
CV	7.7	5.2	5.1	8.5	6.6
Female	18.7	18.6	15.9	13.5	16.4

mean maximum filtration rate than their copepodites, but the relationship between filtration rate and developmental stage was not as pronounced as in the Pseudocalanus data.

Encounter Rate and Retention Rate

The previous analyses of the percent contribution of each cell type to the ration (Table 5 and 6) used the basic assumption that Thalassiosira and Isochrysis cells were encountered and retained by the copepods in direct proportion to their numerical abundance (Table 5) or on a cell volume basis (Table 6). The deviations from the expected proportions that occurred could have resulted from the active selection or rejection of one cell type over the other. However, the apparent selection of a cell type could also have resulted from the variable efficiency with which cells of different sizes were retained on the filter of each species. These results could have been interpreted as supporting either an active or a passive feeding process. An additional analysis of the data was thus necessary in order to determine the degree of apparent selection for cells that occurred strictly due to a passive, mechanistic selection process.

Encounter rates for each cell type (Output Equation 11, Table 2) were calculated to represent the number of cells in each size category (and total number of cells within each cell distribution) theoretically encountered by a copepod. Retention rates were then calculated to represent the number of cells of each type theoretically encountered by an animal and retained on the filter (Output Equation 12, Table 2). The theoretical retention rate for each cell size category was calculated as the encounter rate for that cell size category times the retention efficiency for a cell of that size (Table 8). The retention efficiency for each cell size category was determined from the distribution and rel-

Table 3-8 Retention efficiencies (ei) for the developmental stages of Pseudocalanus and Acartia clausi. Retention efficiencies for the different cell size categories were calculated as the cumulative percent frequency of intersetule spacings on the second maxilla of each developmental stage that theoretically would retain a cell of the equivalent spherical diameter (ESD). Means of stages shown were used in the calculations for grazing experiments where stages were combined. Size categories 1-4 represented cells in the Isochrysis distribution. Size categories 5-11 represented cells in the Thalassiosira distribution.

Size Category	ESD (um)	Retention Efficiency (%) CI	CII	Mean	CIII	CIV	Mean	CV	Female
Pseudocalanus									
	1	8.1	1.3	4.7	2.7	6.2	4.4	3.3	4.0
1	2	51.0	40.5	45.8	45.4	50.8	48.1	39.9	40.7
2	3	77.7	76.1	76.9	78.2	81.3	79.7	76.6	67.9
3	4	87.3	86.5	86.9	89.2	90.1	89.7	87.6	83.6
4	5	94.4	92.3	93.4	96.0	94.8	95.4	91.5	90.0
	6	97.9	96.1	97.0	99.1	97.2	98.2	94.4	92.7
	7	99.6	96.6	98.1	100	99.0	99.5	96.3	94.7
	8	100	97.2	98.6	100	99.7	99.9	97.6	95.5
5	9	100	97.3	98.7	100	99.9	100	98.4	96.0
6	10	100	97.6	98.8	100	100	100	99.0	96.8
7	11	100	100	100	100	100	100	99.4	97.0
8	12	100	100	100	100	100	100	99.7	97.2
9	13	100	100	100	100	100	100	100	97.2
10	14	100	100	100	100	100	100	100	97.2
11	15	100	100	100	100	100	100	100	100
Acartia clausi									
	1	0.6	0.8	0.7	0.8	0.2	0.5	1.1	0.0
1	2	7.3	17.6	12.5	12.2	8.8	10.5	13.8	4.2
2	3	30.1	49.4	39.8	32.5	40.6	36.6	44.3	14.1
3	4	49.7	71.2	60.5	55.6	66.9	61.3	67.7	29.2
4	5	67.6	85.1	76.4	74.1	79.4	76.8	79.7	50.9
	6	81.7	92.4	87.1	88.8	91.9	90.3	88.6	64.3
	7	87.3	95.9	91.6	93.3	98.7	96.0	97.2	70.7
	8	92.8	98.0	95.4	95.2	99.8	97.5	99.1	77.2
5	9	95.6	100	97.8	97.3	100	98.7	100	84.8
6	10	98.6	100	99.0	98.3	100	100	100	92.3
7	11	98.6	100	99.2	99.1	100	100	100	94.9
8	12	98.8	100	99.4	99.3	100	100	100	95.3
9	13	99.6	100	99.6	99.6	100	100	100	100
10	14	99.8	100	99.6	99.6	100	100	100	100
11	15	100	100	100	100	100	100	100	100

Table 3-8

ative abundance of intersetule spacings on the second maxilla of each developmental stage of Pseudocalanus and Acartia (Chapter 2).

From the calculation of capture rate, encounter rate, and retention rate, three efficiency indices were calculated (Table 9). These indices represented the range of efficiencies with which cells theoretically encountered and retained on the filter were eaten by each copepod species, assuming (1) the random encounter of different sized cells on the filter, (2) a slight overlap between the equivalent spherical diameter of a cell and the measured intersetule spacings on the filter (+/- 0.5 µm) to ensure the effective retention of a cell on the filter, and that (3) the distribution of intersetule spacings was critical in determining the passive selection of different sized particles. The three indices were calculated as an average over all size categories within each food type, and on a total food basis.

The first efficiency index, EI(1) = CR/ER (Table 9), represented the mean capture efficiency for cells theoretically encountered by a copepod. Since for this calculation all cells were considered available to a copepod, EI(1) was considered a minimum efficiency estimate as it did not take into account the variable retention efficiency of the copepod filter for cells of different sizes. The second index, EI(2) = CR/RR, represented the mean capture efficiency for cells that were theoretically encountered by an individual, retained on the filter, and subsequently eaten. EI(2) was thus a maximum efficiency estimate, and included a morphological component for cell selection. The third index, EI(3) = RR/ER, represented the theoretical mean retention efficiency for cells based solely on the morphology of the filter. This index represented the mean retention efficiency used to calculate EI(2); thus, EI(2) = EI(1)/EI(3). These efficiency indices were calculated for the CI+CII and adult stages of each species to indicate the range of values for each species. Values for the intermediate developmental

Table 3-9 Efficiency Indices (EI) calculated from replicate flasks for the oldest and youngest stages of Pseudocalanus and Acartia clausi. These indices were calculated as ratios of the estimated capture rate (CR), encounter rate (ER), and retention rate (RR) for each stage. EI(1) = CR/ER; EI(2) = CR/RR; EI(3) = RR/ER for each food type and on a total food basis. See text for details.

Stage	Food Level	Thalassiosira			Isochrysis			Total		
		EI(1)	EI(2)	EI(3)	EI(1)	EI(2)	EI(3)	EI(1)	EI(2)	EI(3)
Pseudocalanus										
CI+CII	D1	.32	.32	.99	.21	.25	.85	.22	.25	.86
	D2	.47	.47	.99	.40	.47	.84	.40	.47	.86
	C1	.40	.40	.99	.14	.17	.85	.16	.19	.86
	C2	.30	.30	.99	.15	.18	.85	.16	.19	.86
	B1	.57	.57	.99	.16	.19	.85	.19	.22	.86
	B2	.57	.57	.99	.28	.33	.85	.29	.34	.86
	A1	.17	.17	.99	.16	.19	.85	.16	.19	.85
	A2	.25	.25	.99	.22	.25	.85	.22	.25	.86
	Mean	.38	.38	.99	.22	.25	.85	.23	.26	.86
Female	D2	.67	.68	.98	.25	.33	.77	.27	.35	.78
	C1	.39	.40	.97	.06	.08	.80	.08	.10	.81
	C2	.43	.44	.97	.06	.07	.80	.08	.10	.81
	B1	.57	.59	.98	.14	.18	.79	.16	.20	.80
	B2	.33	.34	.97	.08	.10	.79	.12	.15	.80
	A2	.90	.93	.97	.15	.19	.81	.20	.24	.82
	Mean	.55	.56	.97	.12	.16	.79	.15	.19	.80
Acartia clausi										
CI+CII	D1	.48	.49	.99	.09	.16	.56	.12	.20	.59
	D2	.22	.22	.99	.23	.44	.51	.23	.38	.59
	C1	.39	.39	.99	.04	.08	.52	.06	.12	.54
	C2	.22	.22	.99	.03	.05	.55	.04	.07	.58
	B1	.13	.13	.99	.05	.10	.55	.06	.10	.58
	B2	.19	.19	.99	.04	.08	.56	.05	.09	.58
	A1	.48	.49	.99	.36	.64	.56	.37	.62	.59
	A2	.50	.50	.99	.24	.42	.56	.25	.43	.59
	Mean	.33	.33	.99	.14	.25	.55	.15	.25	.58
Female	D1	.47	.49	.97	.01	.01	.29	.04	.44	.35
	D2	.42	.44	.95	.02	.07	.27	.06	.17	.34
	C1	.42	.44	.95	.01	.05	.29	.05	.15	.35
	C2	.45	.47	.93	.01	.01	.29	.05	.13	.35
	B1	.41	.43	.95	.14	.51	.28	.25	.74	.34
	A1	.88	.93	.95	.13	.43	.29	.18	.54	.34
	A2	.72	.76	.94	.17	.57	.30	.22	.61	.35
	Mean	.54	.57	.96	.07	.24	.29	.12	.40	.35

Table 3-9

stages were intermediate to the values calculated for the oldest and youngest stages of each species.

Based on the estimates of retention efficiency (EI(3), Table 9), Pseudocalanus and Acartia copepodite stages could retain cells within the Thalassiosira distribution (9-15 um ESD) with equal efficiency; Isochrysis cells were more efficiently retained by Pseudocalanus developmental stages. In both copepod species, cells could theoretically have been retained with the greatest efficiency by the youngest (= smallest) stages, due primarily to the allometric relationship observed between developmental stage (i.e., body size) and the size of pores on the filter (Table 8); smaller individuals of both species, both within and between stages, could theoretically retain smaller cells more efficiently, but could still retain larger cells as efficiently as larger animals.

Values for EI(1) and EI(2) differed only slightly for Thalassiosira due to the high retention efficiency for the larger cells by all copepods. For Isochrysis, values for EI(2) were always higher than efficiency estimates calculated as EI(1) due to the lower retention efficiency calculated for the smaller cell type (Table 8 and 9). This pattern also held for the indicies calculated for the two cell types combined (Totals, Table 9), because of the high numerical abundance of Isochrysis in the food spectrum (89-96% relative abundance on a cell number basis over all experiments).

The adult females of both species were equally efficient at capturing diatom cells (EI(1) = 54-55%, Table 9), as were the youngest developmental stages of both species (33-38%). The older stages of each species were more efficient than the youngest stages of that species. Although the data were variable between food levels, Pseudocalanus copepodites ate a higher percentage of the Isochrysis cells theoretically encountered compared to Acartia copepodites at the equivalent developmental stage (EI(1) for Isochrysis

= 22% vs. 14% for females, 12% vs. 7% for stage CI+CII, Table 9). However, based on the comparison of values calculated for EI(2), Acartia developmental stages were just as efficient as Pseudocalanus in procuring a ration (on a cell number basis) from the Isochrysis distribution (EI(2) = 16-25% for Pseudocalanus, 24-25% for Acartia, Table 9). This result could be attributed to the relatively higher capture rates for Isochrysis cells by Pseudocalanus.

On a total food basis, 78-86% of the cells encountered by Pseudocalanus could have been retained on the filter and eaten (EI(3), Totals, Table 9). Only 34-59% of the cells encountered over the full particle spectrum could theoretically be retained by Acartia. However, Pseudocalanus developmental stages were only slightly more efficient at capturing cells that were theoretically encountered over the total particle spectrum at comparable developmental stages (EI(1), Totals, Table 9), even though a much wider size range of cells was theoretically available to this species and individual capture rates were higher. Overall, the Acartia female was the most efficient in capturing cells available to it within the full particle spectrum; that is, Acartia females removed 40% (EI(2) = .40, Table 9) of the cells theoretically available over the full particle spectrum. A chi-square analysis of the observed percentages of cells removed (EI(1), Table 9) compared to the expected percentages of cells theoretically retained by the filter (EI(3), Table 9) indicated that all comparisons were significantly different ($p < .01$) for both food types, and on a total food basis. This analysis suggested that all copepods were relatively inefficient at removing cells theoretically available to them. A chi-square analysis of the observed percentages for EI(1) compared to an expected value for the capture efficiency of cells assuming 100% retention efficiency (i.e., EI(2) = 1.0) also indicated that all copepods removed cells as if they had a very leaky sieve, or were at least inefficient at eating cells that could be retained on

the filter.

Food Ration vs. Effective Food Availability

The number of cells in the daily ration coming from each size category (1 μm ESD) across the particle spectrum was compared to the number of cells from each size category theoretically encountered and available to each grazer. The ration data were first calculated as the number of cells removed from each cell type distribution. These data were compared to the estimates of effective food availability calculated as the number of cells in each size category that were theoretically encountered and retained on the filter (Output Equation 13, Table 2). Differences between the number of cells eaten and the number of cells available within each size category were tested using the Kolmogorov-Smirnov statistic (Sokal and Rolf 1969, Cowles 1979). This statistic tested the level of significance of deviations between an observed frequency distribution (e.g., the number of cells in the ration in each size category within a cell type distribution) and the expected distribution (e.g., the number of cells available in each size category within that distribution) from which the observed distribution was sampled. The relative proportion of cells from each size category in the ration and in the food suspension were also calculated, and differences tested using a chi-square analysis. The Kolmogorov-Smirnov statistical test as applied to the numerical data was considered a more critical analysis than the chi-square test of the proportion data.

All developmental stages of both species ate significantly more Isochrysis than were theoretically encountered and retained on the filter ($p < .05$). For Pseudocalanus feeding on Thalassiosira, in only 7 out of a total of 40 flasks combined over all 5 grazing experiments (17.5%) was there a significant difference between the observed ration and the theoretical number of cells available (Table 10). Only Pseudocalanus CV ate significantly less Thalassiosira

Table 3-10 Results of the Kolmogorov-Smirnov statistical analysis for Pseudocalanus. This analysis tested the significance of the deviations between the observed frequency distributions of the number of cells eaten by a copepod (CR, cells/animal/min) and the expected distribution of cells encountered and theoretically retained on the filter (RR, cells/animal/min) using the estimate of effective availability (Output Equation 13, Table 2) for each developmental stage experiment. All tests were significant at the $p<.01$ level for Isochrysis, and are not included below. Only those tests indicating a significant difference ($p>.05$) between the observed and expected cell frequency distributions for Thalassiosira are listed below. D max = the maximum deviation between the observed and expected number of cells eaten within a distribution from a particular cell size category. N = total number of cells theoretically encountered and retained on the filter (total number of cells/animal/min). Positive values for the maximum deviation between size categories in the two distributions resulted when CR>RR. Negative vaules resulted when RR>CR. See text for details.

Stage	Food Level	D max	N	D max/N	p
CI+CII	D1	8.1	30.8	0.26	.05
	C2	7.3	29.1	0.25	.05
CV	B2	-25.2	36.4	0.69	.01
	A1	7.8	26.8	0.29	.05
	A2	11.6	29.2	0.40	.01
Female	C1	13.1	66.1	0.22	.01
	B2	30.8	73.8	0.42	.01

cells than expected. In the other six cases, more of the diatom was eaten than expected. All other ration distributions were not significantly different from the expected distribution for Thalassiosira ($p < .05$).

For Acartia experiments, in 16 out of 28 flasks (57.1%) the ration distributions were significantly different from the expected distribution for Thalassiosira (Table 11). For the adult female, all tests were significant ($p < .05$) except for one replicate flask at the lowest food level. In only one flask (D1) was less Thalassiosira eaten than expected. All tests indicated no difference between the observed and expected frequency distributions for stage CV. For the younger developmental stages of Acartia, 4 out of 7 tests were significant in the CIII+CIV experiment, and 6 out of 8 tests in the CI+CII experiment (Table 11).

The food ration and effective availability distributions from an adult female experiment (food level A) exemplified the responses typically observed in all Pseudocalanus grazing experiments (Fig.5). For this analysis, the data were expressed as the relative proportion of cells eaten (r) or available (p) in each cell size category across the two cell distribution. (Although plotted on the same axes, the proportions for the two cell distributions were calculated separately.) These data indicated the close relationship between the observed and expected relative frequency distributions for each cell type in the Pseudocalanus experiments. In comparison, Acartia females at the same food level preferentially removed large cells within the Isochrysis distribution and small cells within the Thalassiosira distribution (Fig. 6). This result was indicated by the shift in the ration distribution to the right of the Isochrysis distribution and to the left of the Thalassiosira distribution, and supported the hypothesis of active selection for intermediate-sized cells by Acartia females. In contrast to this apparently active selection event, younger developmental stages of Acartia removed

Table 3-11 Results of the Kolmogorov-Smirnov statistical analysis for *Acartia clausi*. All tests were significant at the $p<.01$ level for *Isochrysis*, but are not listed below. Only those tests which indicated a significant difference ($p<0.05$) between the observed and expected frequency distributions for *Thalassiosira* cells are listed below. Notations as in Table 10. See text for details.

Stage	Food Level	D max	N	D max/N	p
CI+CII	D1	7.7	30.2	.26	.05
	D2	12.2	53.4	.23	.01
	C1	9.9	45.4	.22	.05
	C2	22.8	79.8	.29	.01
	B1	7.5	21.3	.35	.01
	B2	10.1	30.2	.33	.01
CIII+CIV	D2	13.4	42.0	.32	.01
	C1	13.2	50.0	.26	.01
	C2	11.0	44.0	.25	.01
	B1	10.1	35.3	.29	.01
Female	D1	-15.4	92.5	.17	.01
	D2	33.2	162.5	.21	.01
	C1	25.3	141.4	.18	.01
	C2	26.4	120.0	.22	.01
	B1	23.9	101.0	.24	.01
	A1	5.9	21.3	.28	.05

Figure 3-5 Proportion of cells in the ration (r) compared to the proportion of cells theoretically filtered and available (p) to Pseudocalanus adult females (Food Level A, relicate flask 2). Size-class-specific data were grouped into intervals of 1 µm ESD over the full range of cells offered to grazers in each experiment (2-15 µm ESD). The distribution on the left represents Isochrysis cells. The distribution on the right represents Thalassiosira cells.

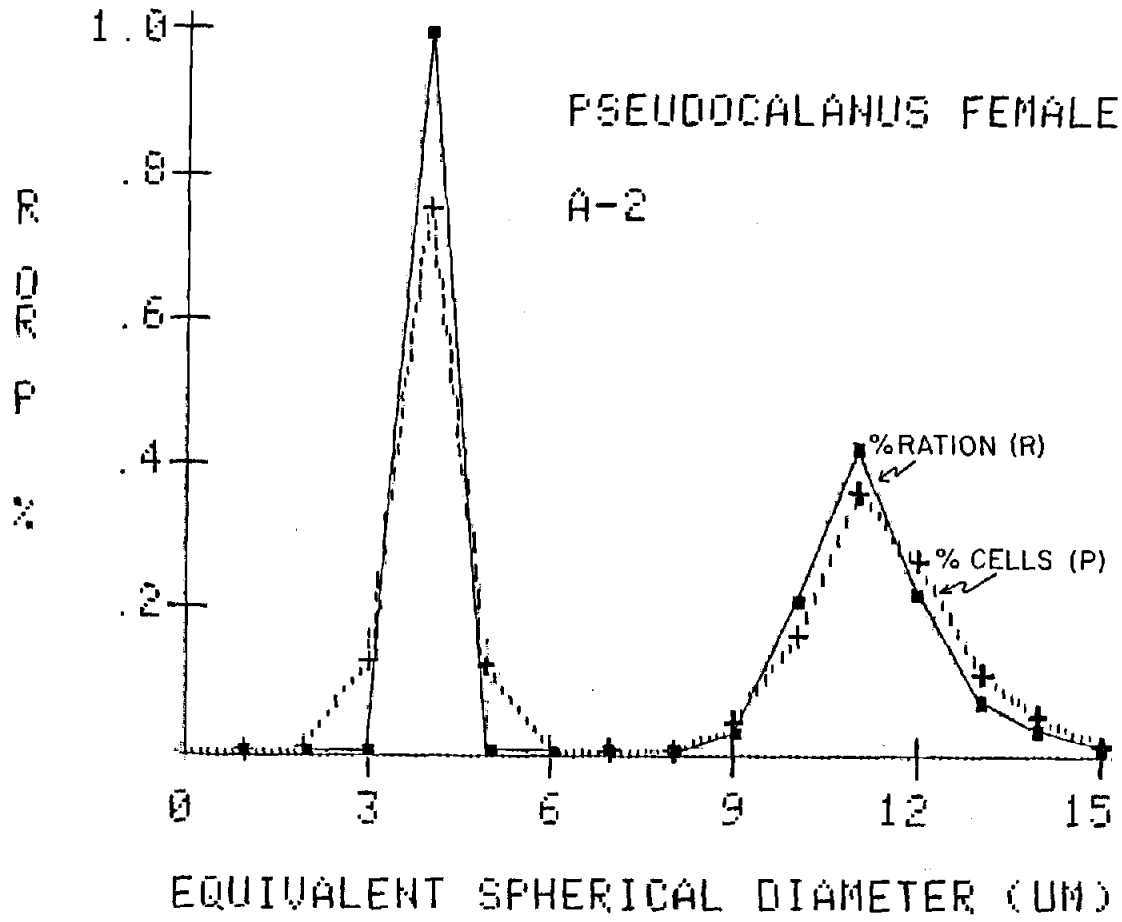

PSEUDOCALANUS FEMALE
A-2
R OR P %
1.0
.8
.6
.4
.2
0
3
6
9
12
15
%RATION (R)
% CELLS (P)
EQUIVALENT SPHERICAL DIAMETER (UM)

Figure 3-5

Figure 3-6 Proportion of cells in the ration (r) compared to the proportion of cells theoretically filtered and available (p) to *Acartia clausi* adult females. Notation as in Fig. 3-5.

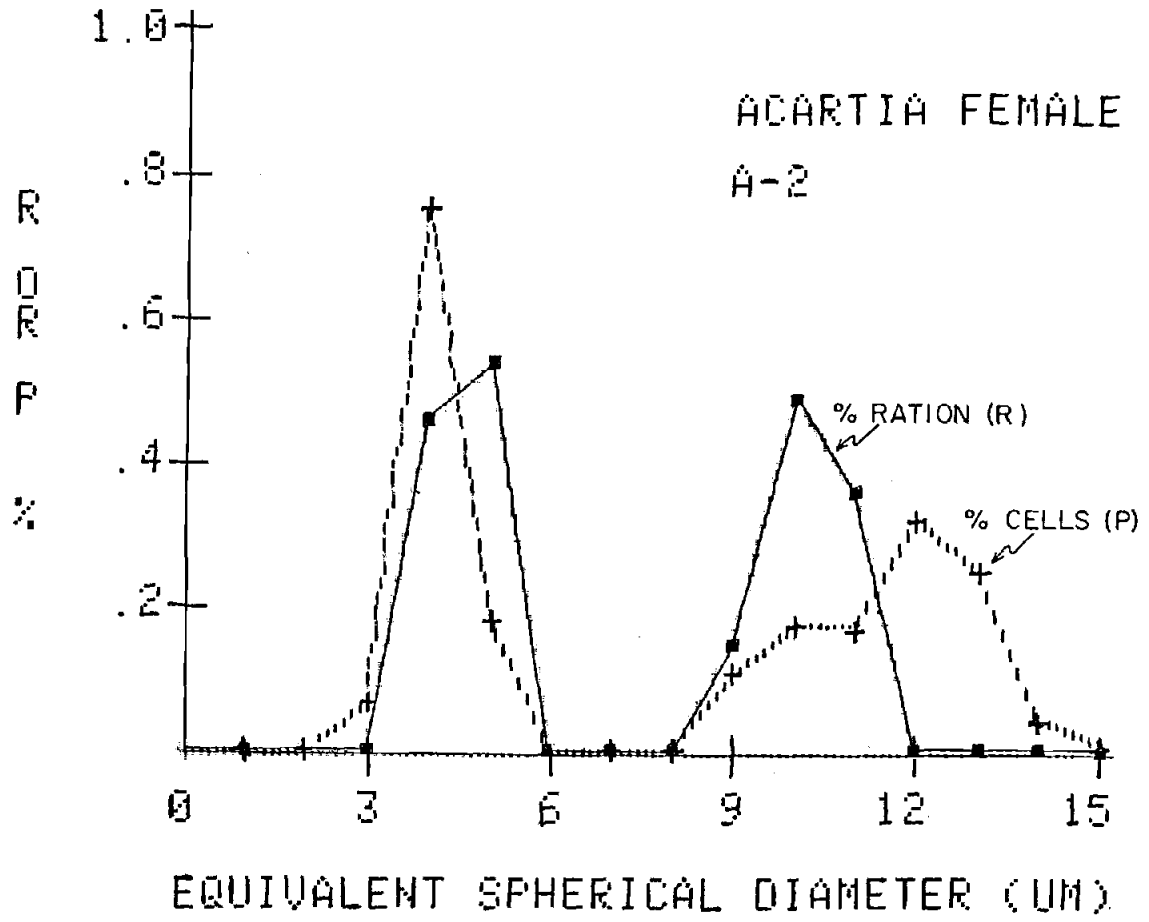
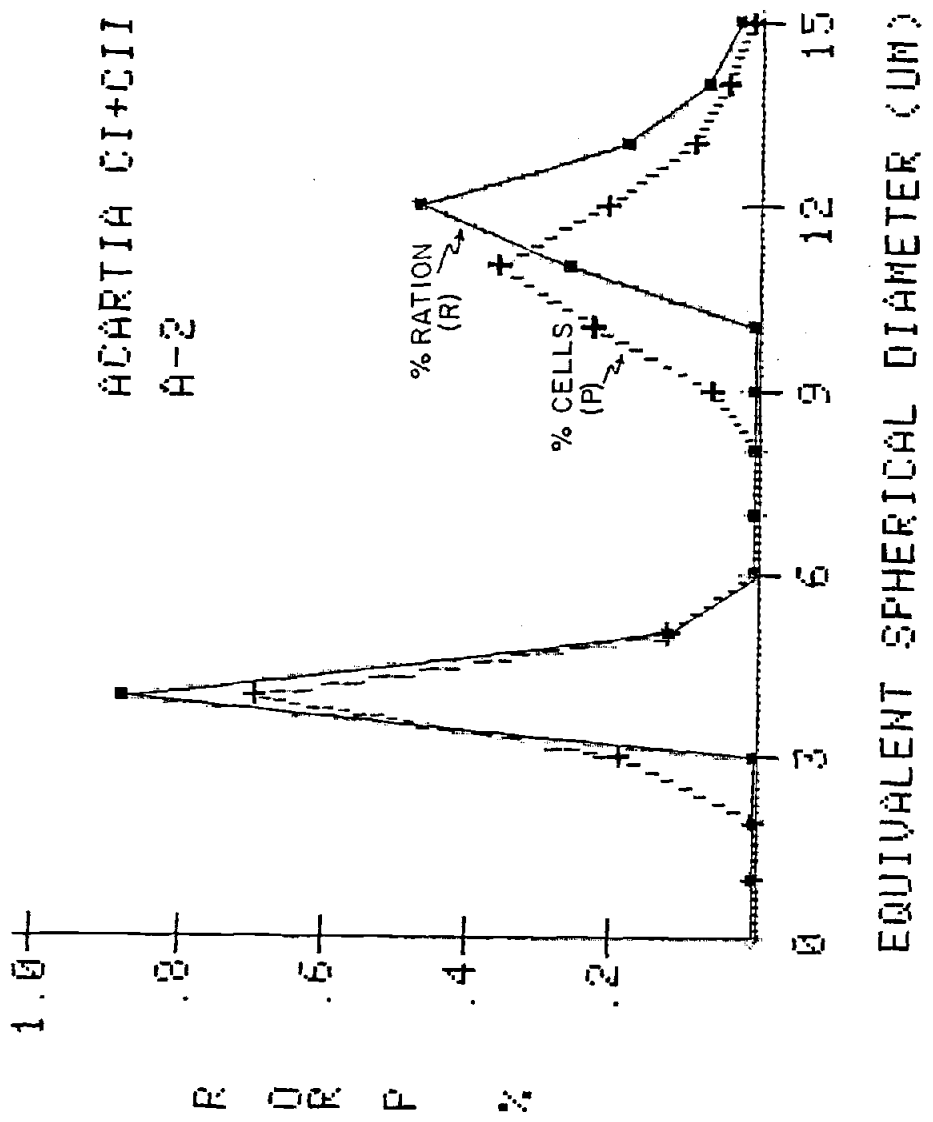

ACARTIA FEMALE
A-2
% RATION (R)
% CELLS (P)
R OR P %
1.0
.8
.6
.4
.2
0
3
6
9
12
15
EQUIVALENT SPHERICAL DIAMETER (UM)

Figure 3-6

Figure 3-7 Proportion of cells in the ration (r) compared to the proportion of cells theoretically filtered and available (p) to Acartia clausi CI+CII. Notation as in Fig. 3-5.

Figure 3-7


ACARTIA CI+CII
A-2
% RATION (R)
% CELLS (P)
EQUIVALENT SPHERICAL DIAMETER (UM)
0
3
6
9
12
15
.2
.4
.6
.8
1.0

Isochrysis cells in proportion to their relative abundance but preferentially ate the larger cells within the Thalassiosira distribution (Fig. 7).

For a final analysis of the grazing data, a Relativized Electivity Index (Vanderploeg and Scavia 1979a,b) was calculated in order to quantify the degree of particle selection observed in the developmental stages of Pseudocalanus and Acartia. This index is analogous to Ivlev's (1961) Electivity Index, but is unaffected by changes in the relative abundances of food types between samples, and may be appropriately used to compare different samples containing the same food types (Lechowicz 1982). For this calculation,

$$E^*i = (Wi - 1/N)/(Wi + 1/N),$$

where Wi = the normalized selectivity coefficient of Vanderploeg and Scavia (1979a), calculated as $(ri/pi)/\sum(ri/pi)$ for each food size category, i, and N = the number of food size categories (N = 4 for Isochrysis; N = 7 for Thalassiosira). The E^*i index varies from +1, indicating maximum positive selection for a food type, to -1, indicating complete rejection of a food type. Random feeding is designated by a value of zero. The mean electivity for each cell size category was calculated for each developmental stage over all food levels from an experiment, using the estimate of effective cell availability for the value of p (Table 12). Selection was considered significantly different from random feeding at $E^*i > +/- 0.55$, because an index of this value or greater was calculated from the original food ration and cell availability proportions when the proportions differed by > 10% in a given cell size category. Although this criterion for judging the level of significance was qualitative, the analysis of the electivity data indicated the same results as the statistical analyses of the cell number data (Table 10 and 11), and was thus considered an appropriate test of the data.

Table 3-12 Mean electivity index for the developmental stages of Pseudocalanus sp. and Acartia clausi. Indices (+/- 1 standard deviation) were calculated for 11 size categories. An electivity value of >+/- 0.55 was considered significantly different from the assumption of random feeding, since only at this level were the ration and cell availability proportions different by more than 10%. Size categories 2-5 represent Isochrysis cells. Size categories 9-15 represent Thalassiosira cells.

Stage	Cell Size Category (ESD in um) 2	3	4	5	9	10	11	12	13	14	15
Pseudocalanus sp.											
CI+CII	-.87 (.34)	-.38 (.61)	-.05 (.31)	.17 (.51)	-1.0 (0.0)	-.91 (.15)	-.25 (.35)	.10 (.13)	.19 (.11)	.09 (.37)	.20 (.41)
CIII		-.95 (.13)	-.29 (.44)	.52 (.08)	-.24 (.53)	-.04 (.41)	-.07 (.15)	-.06 (.08)	-.04 (.11)	-.05 (.14)	.09 (.22)
CIV		-1.0 (0.0)	-.48 (.44)	.55 (.05)	-.45 (.49)	-.08 (.34)	-.05 (.23)	-.12 (.14)	-.01 (.17)	-.13 (.31)	-.06 (.58)
CV	-1.0 (0.0)	-1.0 (0.0)	-.50 (.41)	.60 (.18)	-.93 (.12)	-.45 (.37)	-.23 (.28)	.04 (.14)	.02 (.13)	.13 (.12)	.39 (.12)
Female	-1.0 (0.0)	-1.0 (0.0)	-.54 (.23)	-.25 (.56)	-.69 (.39)	-.33 (.47)	-.22 (.22)	-.07 (.13)	.09 (.15)	.11 (.18)	.23 (.23)
Acartia clausi											
CI+CII	-1.0 (0.0)	-1.0 (0.0)	-.41 (.41)	.54 (.08)	-.79 (.29)	-.87 (.16)	-.54 (.28)	-.13 (.12)	.05 (.17)	.12 (.11)	.48 (.11)
CIII+CIV			-.40 (.53)	.49 (.19)	-1.0 (0.0)	-.89 (.22)	-.41 (.36)	.04 (.22)	.12 (.09)	.09 (.30)	.35 (.28)
CV			-.69 (.48)	.73 (.25)	-1.0 (0.0)	-.86 (.21)	-.27 (.18)	.09 (.07)	.07 (.11)	.16 (.01)	.39 (.12)
Female	-1.0 (0.0)	-1.0 (0.0)	-.50 (.55)	.70 (.30)	.27 (.27)	.19 (.25)	-.17 (.22)	-.62 (.32)	-.72 (29)	-.42 (.58)	-.10 (.57)

Table 3-12

For Pseudocalanus, positive selection for Isochrysis was measured in the 5 µm ESD cell category for the copepodite stages. However, overall, these data were not considered significantly different from random feeding based on the criterion indicated above. Positive selection for Thalassiosira cells of 12-15 µm ESD was also indicated, but the electivities were again all <0.55. This pattern was thus not considered significantly different from random feeding (i.e., $r-p < 0.10$). Cells in the 2 and 3 µm ESD size categories were strongly rejected.

Acartia developmental stages also showed positive selection for 5 µm cells within the Isochrysis distribution, although the pattern was only considered significantly different from random feeding for the older stages (CV+female). Cells in the 2 and 3 µm size categories were strongly rejected. Within the Thalassiosira distribution, 9 and 10 µm cells were apparently rejected by the copepodite stages of Acartia (CI-CV). Positive selection was observed for the larger cells (12-15 µm ESD), but once again the feeding pattern was not considered significantly different from random feeding for these stages. Acartia females apparently rejected 12 and 13 µm cells, and showed weak (but not significant) positive selection for the 9 and 10 µm cells.

Discussion

Feeding Patterns

It has generally been accepted that zooplankton feeding saturates with increasing food concentration according to a rectilinear model (Frost 1972a), a modified Ivlev curve (Parsons *et al.* 1967), or some other curvilinear relationship (Mullin *et al.* 1975). However, in several studies where copepods were fed ambient concentrations of natural food, a linear relationship between ingestion rate and particle concentration has been observed (Poulet 1974, Mayzaud and Poulet 1979), with an inflection in the feeding curve only occurring at or above the ambient concentration of particles that the grazers had been experiencing in the field (Conover 1978). Thus, recent studies have suggested that copepods regularly acclimate to *in situ* concentrations of particles by the induction of substrate-specific digestive enzymes (Mayzaud and Poulet 1979, Cox 1982), and that the saturation-type feeding response observed in laboratory grazing experiments was an artifact resulting from the sudden exposure to high levels of natural particles or artificial foods (laboratory-grown cultures, plastic spheres) which the copepods had not recently been experiencing. In the present study, non-saturating, linear ingestion rates were measured for all the developmental stages of *Pseudocalanus* and *Acartia* feeding on the smaller cell, *Isochrysis*. Linear rates were also measured in experiments with the older stages (CV+females) feeding on either *Isochrysis* or *Thalassiosira*. Only the ingestion functions of the younger developmental stages (CI-CIV) of both species feeding on *Thalassiosira* indicated a curvilinear relationship to increasing food concentration, and only in these experiments was an apparent maximum ingestion rate reached within the range of food concentrations offered.

Although non-saturating feeding curves have generally been observed in natural particle experiments, the data from the present study exemplified a similar acclimation response to the "ambient" food types and cell concentrations offered in the laboratory grazing experiments. By offering relatively high concentrations of the experimental food particles prior to the beginning of a grazing experiment, the three day preconditioning period (at Level B, Table 1) apparently allowed the copepods enough time to physiologically adjust (i.e., enzymatically acclimate) to the experimental food types. Furthermore, the data suggested that the recquisite digestive physiology may have been developed only in the older copepodite stages of both grazer species. Thus, the curvilinear feeding curves indicated in the experiments for stages CI-CIV of both copepod species may have resulted either from the fact that (1) the recquisite digestive physiology had not yet developed in these stages, such that an acclimation response to the experimental food types was not possible (or at least not observable), or (2) the necessary digestive physiology existed but due to their small size, these animals reached their maximum gut capacity and gut passage time at the high concentrations of food offered, and thus a maximum ingestion rate was observed. The fact that a saturation response was observed only in the younger stages feeding on the larger diatom cells also suggested that cells may have been perceived on a cell volume basis. That is, rather than numerical abundance , cell volume may have been the primary characteristic of the phytoplankton that determined its availability to the younger copepodites, either because of their limited gut capacity, or due to their limited morphological and chemosensory capabilities for assessing, capturing, and retaining the smaller cells. Although the feeding rate data were better correlated with food concentration expressed on a volume basis for all but the youngest developmental stages

(Fig.1-4), the analyses of the ration percentages were inconclusive in statistically testing whether cell availability was assessed on a cell volume or a cell number basis.

The linear relationship between ingestion rate and Isochrysis concentration varied between developmental stages. The older copepodites of both species decreased their ingestion rate of Isochrysis with increasing cell concentration, suggesting that at high particle concentrations these copepods became more selective, and preferentially fed on the larger cells. These selective capabilities were not generally apparent in the ingestion responses of the younger developmental stages, however, where a linear increase in ingestion was observed over the increasing Isochrysis concentrations offered: an apparent non-selective, mechanistic response to increasing particle concentration. The three day preconditioning period appeared to be a sufficient amount of time to allow an apparent acclimation to the experimental food types and concentrations, at least in the older developmental stages of Pseudocalanus and Acartia clausi. These data also suggested that an ontogenetic component to the physiological capabilities of copepod grazers may exist. Thus, developmental changes in digestive physiology may be added to the list of factors which interact to produce the variety of feeding responses observed in herbivorous, marine copepods.

The Kolmogorov-Smirnov statistical analyses of the numerical abundance data were first used to indicate the degree of apparent selectivity for particles of different sizes across the two cell distribution. In all cases, the frequency distribution of Isochrysis in the ration was significantly different from the expected frequency distribution for all developmental stages of both species. Only 17.5% (7 out of 40) of the tests for Thalassiosira indicated a significant difference between the frequency distribution of cells in the ration compared to the expected cell distribution for the developmental stages of Pseudocalanus (Table10), suggesting

the passive filtration of diatom cells. For Acartia developmental stages, 57% (16 out of 28) tests indicated a significant difference between the observed and expected frequency distributions, suggesting a greater degree of selection may have been occurring for the developmental stages of Acartia. Negative deviations in the calculation of this statistic were achieved when the number of cells in a particular size category of the observed ration distribution was less than the number of cells theoretically available to the copepod from the expected cell distribution. Negative deviations could have resulted from (1) the inefficiency with which cells were removed from the distribution and eaten, (2) selection against the modal size class in a particle distribution (that is, selection for cells either larger or smaller than the modal size), or (3) could have resulted from such experimental biases as the production of particles due to the breakage of cells during feeding, or changes in cell size or in the shape of the overall particle distribution due to ammonia regeneration in the experimental flasks (see below). The analyses for Isochrysis were significant due primarily to the low efficiency with which the smaller cells within this distribution could be captured and eaten, and because of the high numerical abundance of Isochrysis in the food mix. That is, relatively small maximum deviations (Dmax, Table 10 and 11) from the expected number of cells eaten in a particular size category resulted in highly significant differences between the observed and expected frequency distributions. These deviations resulted primarily from the limitations imposed on feeding by the morphology of the second maxilla for filtering and retaining the smallest cells (Table 8).

The analyses of the numerical data for cells within the Thalassiosira distribution using the Kolmogorov-Smirnov statistic were significant primarily when the modal size class within the distribution of cells in the ration was different from the modal size class in the distribution of

available cells (Table 11, Fig. 6 and 7). Significant differences between the numerical distribution of cells eaten vs. the number of cells encountered and theoretically retained on the filter may have been indicative of active selection for particular particles, or could have reflected the general "leakiness" of the filtering apparatus, or resulted from the fact that the larger cells which could be more efficiently filtered, were not necessarily transferred efficiently to the mandibles for ingestion. Since negative deviations from the Thalassiosira distribution were measured in only one flask for each species, particle production in the intermediate size classes due to "sloppy feeding" and size changes caused by ammonia regeneration were not considered significant problems in the final analyses of the grazing data. Although these analyses allowed a statistical quantification of the differences between the observed and expected frequency distributions, the Kolmogorov-Smirnov statistic only measured the overall difference between the two curves, and did not show where in the particle distribution selection might be occurring. These data were thus used to indicate the apparent "leakiness" of the filtering apparatus of all the copepods, and to suggest that cells were generally removed from the water in accordance with a mechanistic theory of feeding for all the stages of Pseudocalanus, and for the younger stages of Acartia clausi.

Particle selection was studied by calculating an electivity index for each particle size category (Table 12). This analysis indicated that positive selection was significantly different from random feeding only for the 5 μm cells within the Isochrysis distribution for the older stages of Pseudocalanus (CIV-CV), and for CV and female Acartia. The significant negative values for E^*i calculated in the 2 and 3 μm size categories resulted primarily from the morphological limitations of the feeding appendages, as discussed above. These small cells were probably not rejected. They

were simply unavailable to the copepods based on the structural characteristics of the mouthparts. Significant negative values for small cells within the Thalassiosira distribution were calculated for the youngest (CI+CII) and oldest (CV+female) developmental stages of Pseudocalanus, and for all the copepodite stages of Acartia. These cell sizes were theoretically retained by a large number of setule spacings on the second maxillae of all the copepods (Table 8). The significant negative values for E^*i for the small cells within the Thalassiosira distribution may have resulted from a subtle shift in the ration distributions to the left of the cell availability distributions as food concentration decreased. That is, at high food levels the copepods ate slightly larger cells than at the low food concentrations. This trend was observed in the data for both copepod species, although not specifically quantified for the treatment of the data presented here. This pattern of greater selectivity at higher food levels (i.e., the selection of particles at lower relative abundance than the modal size class) was consistent with the hypotheses of optimal foraging theory, but the data are treated elsewhere (Polis and Dexter, in prep.). It is also possible that the elevated ingestion and capture rates on Isochrysis observed in the older stages of both species resulted from this shift in the ration toward the particle peak as total food concentration decreased. The significant shift in the ration of the Acartia female (Table 11, Fig. 6) strongly supported the hypothesis of active selection of intermediate sized cells (or the active rejection of larger cells) within the Isochrysis distribution. The shift in the ration distribution to the right of the cell availability curve observed for the Acartia CI+CII (Fig. 7) may have resulted from the fact that several setae and thus numerous setules were missing on the second maxillae of the youngest developmental stage (Chapter 2, Table 4).

The analysis of the electivity data was interpreted as additional support for the hypothesis that all developmental stages of Pseudocalanus and the younger stages of Acartia (CI-CIV) fed passively. Although some developmental stages of both copepod species showed selection for the 5 μm cells and the larger diatom cells, overall, the hypothesis of active selection was rejected. Only the electivitity results for the adult female Acartia supported the hypothesis of active selection for cells within the Thalassiosira distribution not expected by a mechanistic explanation of feeding.

The results of the grazing analyses thus indicated that the limitations and capabilities imposed upon the developmental stages of Pseudocalanus and Acartia clausi by the morphology of their feeding appendages were important to consider in predicting the feeding responses of these copepods. The smallest cells eaten were approximately 1 μm larger than the width of the smallest pores measured on the second maxillae for the developmental stages of both species. This result supported the idea that some degree of overlap was required for the efficient retention of cells on the filter. The highest percentage of the ration coming from Isochrysis cells (on a cell number basis, Table 5) was observed in the smallest developmental stages of both species, and for the Pseudocalanus adult female. This result may reflect the relative distribution and high frequency of small pores on the filter of the smallest developmental stages, and possibly the ability to manipulate the appendages, vary the rate of filtering, or to close down the setal spaces on the filter of adults. Overall, however, the electivity analyses did not show that Pseudocalanus females could, or would, actively increase their ration coming from the Isochrysis distribution, and ingestion and capture rates on Isochrysis decreased with increasing concentration. Varying the rate of "filtering" or the position of the feeding appendages could have changed the flow of water across or around the mouthparts, and thus have indirectly

affected what cells were trapped by, or bumped into the filter (Koehl and Strickler 1981) without indicating an active selection capability in Pseudocalanus.

Although retention efficiencies for cells in the 2-15 μm ESD range were theoretically higher for Pseudocalanus (Table 8), it was interesting to note that the developmental stages of Acartia were equally efficient at procuring a daily ration (cells ingested per day) from the full distribution of cells offered, both in terms of the number of cells captured vs. the number of cells theoretically encountered, and the number of cells captured vs. the number available to them (Table 9). Thus, populations of the two species may co-occur and be able to maintain equivalent abundances in the field, even though the size range of cells available to the two species directly overlaps, and is theoretically narrower for Acartia. One may thus hypothesize that Pseudocalanus copepodites in particular, and perhaps all small and/or young life cycle stages of herbivorous copepods in general, have the abundant small cell portion of a particle spectrum available to them based on the morphological characteristics of their mouthparts. These copepods may thus not experience food shortages throughout most of the year. Older Acartia stages, which have morphological limitations for specializing on small cells, and/or larger copepods with limited setular complexity, may have instead evolved capabilities which allow them (1) to respond directly to changes in the relative quality and/or quantity of the food resource (e.g., Acartia and other estuarine species, Richman et al. 1977, 1980), or (2) have evolved mechanisms which alleviate the direct dependence on a variable food spectrum (e.g., oil and lipid reserves, seasonal and/or diurnal vertical migrations, and overwintering responses in larger calanoids).

In the present study, for example, the response by Acartia females of preferentially feeding on the intermediate cells in the particle distribution (Fig. 6) could

have resulted from their assessing the high abundance of Isochrysis during the preconditioning period prior to an experiment. The copepods may thus have actively overlapped their setae and subsequently closed down the setule spacings on the filter in order to remove a portion of this known, and very abundant food item. In addition, they may have subsequently had to reject the larger cells within that distribution, or possibly were inefficient in transferring those cells to the mouth.

Although the analyses of the size class-specific data indicated that cell capture rates generally followed the shape of the cell distributions, a qualitative analysis of these data indicated a complicated relationship between phytoplankton growth rates and copepod grazing rates measured within a cell type distribution. Maximum grazing rates were often associated with that portion of a particle spectrum where the growth rate was highest (in both experimental and control flasks). Often, this trend was independent of whether the size class with the highest growth rate represented a large or small cell within the distribution. The trend was observed in experiments for both species at all concentration levels. Higher filtration rates within a particle distribution were thus associated either with the modal size class within the distribution (i.e., the most abundant particle), or with the portion of the distribution having the highest growth rate. In addition, higher grazing and filtration rates were sometimes observed to the far right of the diatom distribution, which may have represented grazing removal of cell doublets. These confounding factors often resulted in tiered filtration rate curves, i.e., curves having several increasing slopes across a particle distribution interrupted by one to several plateaus. These results suggested a response similar to that described by Richman et al. (1977) as "tracking behavior". Since this result was observed in experiments with the youngest copepodites of both species as well as for adults, it is possible

that the basic "tracking" response is a result of the relative availability of cells across a particle spectrum, as forwarded by Poulet (1973, 1974, 1977), rather than due to an active assessment of the size spectra, at least for the younger developmental stages. Thus, the relative availability of different particle types within a natural particle spectrum may be an appropriate measurement to make in order to predict where in the spectrum a copepod's ration will be derived. Beyond this response to relative cell encounter rates, the data also supported the development of additional selection capabilities in the adult female Acartia, and possibly the development of additional physiological capabilities in the older stages of both species. These results fit coherently into the developing hypothesis that at least some estuarine copepods have additional mechanisms by which food quality as well as food quantity may be assessed (Richman et al. 1977, 1980; Donaghay 1980a, 1980b). In the field, the increased availability of a particle type within a spectrum of cells could be due either to a high standing stock of that particle type or due to a high growth rate. Feeding on peaks across a particle spectrum has been noted by a variety of researchers, although the data have been used to support both active (Richman et al. 1977) and passive (Poulet 1974) feeding responses in copepods. Regardless of the feeding mechanism involved, it would appear that preferentially feeding on peaks as they develop temporally across a particle spectrum due to the differential growth rate of cells, could be just as effective a response as feeding on "stable" peaks of high standing stock, and could result in an increased quality of the ration (Raymont 1980).

A final qualitative result of the grazing experiments, discussed briefly above, was that as food concentration decreased, copepodite and adults of both species shifted toward the preferential removal of cells nearer the biomass and abundance peak within both cell distributions. Since at low food concentrations, one may hypothesize a decrease

in selectivity (Conover 1978), the lower food concentrations may have approached the threshold level at which energetic considerations were such that removing the most abundant cells was the most advantageous response (Schoener 1971, Lam and Frost 1976, Lehman 1976).

Experimental Problems

Recent studies have indicated a variety of problems which are typically encountered in conducting laboratory grazing experiments. In addition, the need for caution in interpreting the data in support of active, behavioral selection in copepods has been expressed (Boyd 1976, Deason 1980, Roman and Rublee 1980, Harbison and McAllister 1980). Specifically, the problems of particle production in grazing flasks, differential growth of cells within a particle spectrum, different growth rates between paired control and experimental flasks, and the effects of excreted ammonia on cell size or growth rate, may all contribute to apparent grazing removals. Additional sources of error may be derived directly from the use, and abuse, of data generated from electronic particle counters. Although in the present study, care was taken to remove these biases prior to initiating experiments, often the extent of the problem was not determined until after an experiment had been terminated.

The specific problems encountered in the present study were: (1) ammonia-induced, apparent swelling of small cells (i.e., apparent loss of cells from the first five to ten size classes of a distribution) especially in the flagellate distribution; (2) differential growth rates measured between cell size categories within a distribution; and (3) the formation of doublets in the diatom cultures. All these biases may have interacted to produce the effect of apprently active selection for particular cell types, or may have caused an overestimate of grazing removal, if not specifically accounted for in the analyses of the data. These, and related problems encountered in the laboratory grazing experiments are discussed below.

Increases in cell number or volume as measured by an electronic particle counter may occur during a grazing experiment due to an actual increase in the number of cells in a particular size category, or due to the shifting of

of particles from one size class to a higher size class as individual cells grow (i.e., shifting into a larger equivalent spherical diameter category across the distribution). This apparent loss of cells in the small size classes of a distribution due to growth or swelling will be significant if the cells are not replaced by new cells formed from the division of doublets or cells in the largest size classes of a distribution. Recent studies have indicated the importance of contolling for the excretion of ammonia by copepods during a grazing experiment (Donaghay 1980a, Roman and Rublee 1980, Harbison and McAllister 1980) for a similar reason. Ammonia excretions, along with the addition of dissolved organics from the breakage of cells during feeding, may preferentially stimulate the growth of smaller cells within a culture, resulting, again, in an apparent loss of cells in the small size classes of a distribution. In the present study, ammonia effects in cultures of the larger diatom were minimal, and generally only affected a few size classes at the lower end of the diatom spectrum. These channels were usually excluded from subsequent grazing analyses anyway, due to poor counting statistics, particle production, or detrital formation. The exclusion of cells in these size classes only represented a 1-2% reduction in the total cell number or volume. However, in the distributions of Isochrysis, there was often an apparent loss of cells in the first five to ten channels, even though equal amounts of ammonia were added to control and experimental flasks to specifically control for ammonia excretion by the copepods. Thus, grazing rates on Isochrysis were initially overestimated by a factor of five when ingestion rates were calculated on a total cell volume basis. The channels where these problems visibly occurred were subsequently excluded from all final grazing analyses. This procedure reduced the problem of differential cell growth or swelling, but may have over- or underestimated the actual grazing removal by some unknown amount, since

additional ammonia-induced cell growth may also have been present in size classes to the right of the excluded portion of the distribution. Thus, the two components of "growth" measured by the particle counter, i.e., (1) the real increase in cell numbers, and (2) the shifting of cells into larger size classes, could not be completely differentiated. This effect may have occurred even when ammonia was added equally to control and grazer flasks in amounts presumably sufficient to compensate for any ammonia excreted by the grazers, and in situations where excess ammonia is measurable throughout a grazing experiment. Preliminary calculations indicated that at the higher food levels typically used in laboratory grazing experiments, and especially where small cells are used as a food, the cultures may, in fact, become nitrogen-limited during the course of a 24 hour grazing experiment. It would appear that a better understanding of algal physiology, and the specific cell characteristics for ammonia uptake, must be investigated to a fuller extent in order to appropriately compensate for this effect in future grazing experiments. This problem could be especially important in experiments using natural particle spectra, where flagellates or other small cells are abundant, yet not easily counted by microscope. In these situations, significant biases could be introduced by the interpretation of cell counts generated from an electronic particle counter on a volume basis.

A second problem encountered in the analysis of the grazing data was that growth rates calculated for different cell size categories varied within a single food-type distribution. Increased growth of small cells within a distribution might have been caused by the ammonia additions (Donaghay 1980b). This effect was also enhanced at low food concentrations where relative growth rates were higher. Shading effects at the higher food levels, greater availability of nutrients at lower food levels, and the differential enhancement of cell growth from the release of

dissolved organics into the water from the leaking and breaking of cells during the grazing process itself, may all have contributed to over- or underestimates of grazing due to deviation from the basic assumption of constant, exponential growth inherent in the basic grazing calculations.

A final cautionary note must be made regarding the use of size class analyses in studying selection patterns in copepod feeding responses. In the present study, the larger cell was typically easier to count using an electronic particle counter because detrital interference, particle coincidence, and cell swelling effects were minimal. However, because of the log- base 2 scale used to represent particle diameter, the grouping of the size class-specific data into 1 µm ESD intervals resulted in some categories being represented by only a few size classes. This occurred because the smaller size classes within a distribution are broader compared to those to the right of the distribution peak. Also, the statistics on the last 10 to 30 channels of a distribution (as counted on a 64 channel analyzer) were often insufficient to include the data in subsequent analyses due to the low cell numbers in these channels. Under these conditions, interpreting differences between size classes on a channel by channel basis as indicative of active selection events may be a gross extension of the data. However,expressing grazing removals directly on a total cell basis, without summing the data only from the appropriate size classes, also introduced significant errors. In the present study, all final analyses were thus reported as 1 µm ESD size categories from data summed from the appropriate size classes. The Coulter Counter measures both the displacement of electrical current by a cell (and thus measures cell volume), and records the number of discrete pulses from particles in a given volume of water (and thus the measurement of cell number). However, the apparent swelling of cells from ammonia excretion or due to an

increase in temperature during a count, preferentially biases the estimates of particle concentration when measured on a cell volume basis; however, these problems do not affect the measurement of cell number, since the number of discrete pulses in a given volume of water remains constant regardless of changes in cell volume. Therefore, the data were analysed on a cell number basis primarily, in order to minimize the experimental biases in estimating changes in cell concentration induced by the use of an electronic particle counter.

Conclusions

With these experimental problems in mind as caviats for the analyses presented, the data from the laboratory grazing experiments may be used to support several of the original hypotheses under consideration. Based on these analyses, it would appear that:

(1) all Pseudocalanus developmental stages and the younger stages of Acartia clausi generally removed cells in proportion to the relative effective availability of cells within the particle spectrum. Results supported the hypothesis that the younger developmental stages of both species were feeding passively,

(2) Pseudocalanus developmental stages generally had higher ingestion and capture rates than comparable Acartia stages on a per animal basis, but generally lower rates on a weight-specific basis. Younger developmental stages of both species generally ate more Isochrysis than the older stages, due primarily to the higher efficiency with which small cells were retained on the filter compared to older stages. These results indicated that Pseudocalanus developmental stages and the younger stages of Acartia could effectively specialize on small cells within a particle distribution,

(3) the Acartia female was the only developmental stage

that actively altered its selection of particles away from those expected, based on a mechanistic model of feeding. These results supported the hypothesis that at least the Acartia female may be able to assess the distribution of cells within a particle spectrum, and take advantage of the cells in highest abundance, regardless of particle size,

(4) the lower limit of cells eaten by each species was effectively defined by the smallest pore sizes measured on the main filter setae of the second maxillae. These results were indicative of the importance of incorporating the limitations and capabilities imposed by the morphology of the feeding appendages in predicting the feeding responses of different developmental stages or species,

(5) the non-saturating, linear response in the oldest copepodite stages of both Pseudocalanus and Acartia feeding on both cell types suggested that the ability to adjust physiologically to feeding on introduced particles may only be present in the older copepodite stages. Thus, preconditioning a copepod to a particular food in the laboratory, or an acclimated ingestion response to natural particle spectra in the field, may not be possible for the younger developmental stages of estuarine copepod species.

Clearly, there are sufficient data to say that the limitations and capabilities imposed by the morphology of the mouthparts of copepods plays some role in determining the range and size of particles eaten by copepods. Yet beyond this mechanistic explanation, a variety of studies have indicated that chemosensory, physiological, and possibly behavioral adaptations for assessing changes in a food spectrum which varies considerably in both quality and quantity over the lifetime of an animal may also be quite important, and that these capabilities may vary between copepods adapted to different food environments. In the present study, there was evidence for a physiological acclimation to the experimental food types offered to the older copepodites of both estuarine species, and possibly

an active assessment of the particle spectrum by the Acartia female, and the selection of particles not expected from a passive filtration, mechanistic model of feeding. Although a variety of models have been used to explain specific behaviors observed in copepods (Boyd 1976, Rubenstein and Koehl 1977, Richman et al. 1977, Poulet and Marsot 1980, Landry 1981, Koehl and Strickler 1981, Strickler 1982), perhaps the more parsimonious position would be the interpretation of these various responses by considering both the specific experimental conditions in which the "behavior" was observed, and more importantly, the probable food environment in which the particular animal evolved.

CHAPTER 4

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult).

III. Ecological Applications

Developmental Grazing Capabilities of *Pseudocalanus* sp. and *Acartia clausi* (CI to Adult). III. Ecological Applications

Introduction

Data such as those generated from the comparative morphology study and laboratory grazing experiments can be used to define the feeding capabilities of adult and copepodite stages for locally dominant estuarine and nearshore copepod populations. This information becomes ecologically important when applied to a field situation where a particular species is a dominant member of the zooplankton community, and where the food resource is known and relatively predictable. In such a case, these data may be used to indicate the potential for intraspecific and interspecific competition or partitioning of the food resource, and to assess the grazing impact on, and/or the zooplankton control of the phytoplankton community.

In this regard, selected data from a five month survey (from late March through July, 1980) of an embayment within Puget Sound, Washington (East Sound, Orcas Island), were used to study the grazing impact of a natural zooplankton population. A preliminary analysis of the data indicated that the bay provided for the internal development of the plankton populations within East Sound, without significant influxes of new populations from outside the bay. *Pseudocalanus* sp. and *Acartia clausi* remained the dominant copepods present in the zooplankton community throughout the study period. The data also indicated a reasonably close biological coupling between nutrient concentrations, phytoplankton abundance, and zooplankton abundance, especially during the spring bloom period. This situation provided the appropriate field application for the grazing parameters measured in the laboratory: a known zooplankton population feeding on a known phytoplankton community, without significant influences from outside the area.

A summary of the seasonal biological and physical characteristics of East Sound is presented for winter, the spring bloom transitional period, and summer conditions. Eight dates during the survey period were chosen to represent the different biological situations (i.e., high and low food concentrations, and different relative abundances of phytoplankton and zooplankton) present in East Sound. Using a modified version of the grazing impact model presented by Bartram (1981), grazing estimates for the developmental stages of Pseudocalanus sp. and Acartia clausi were calculated for each of these dates and for the mean conditions during each of the three seasons studied.

Field Site

East Sound is a fjord-like embayment within Puget Sound, Washington, 13 km long, 2 km wide, 18.6 km^2 in area, and 30 meters mean depth in mid-channel (Rattray 1967). The tidal range is approximately 2.4 meters. The bottom bathymetry is flat, shoaling slightly upbay, and the shorelines are quite abrupt. The major bathymetric feature is a large sill extending approximately two-thirds of the distance across the mouth of the bay to within 10 meters of the surface. Exchange of water thus occurs primarily at the surface over the sill, and through a narrow channel located toward the eastern shoreline. Water depth in the channel immediately outside the bay drops to 90 meters or more.

Materials and Methods

Field measurements were taken at four stations every three to five days throughout most of the five month survey period (Fig. 1). Most of the data (Table 1) were generated from water samples pumped from six depths to the surface with a shipboard plankton pumping system (Jabsco gas-driven impellor pump with a three inch diameter intake and outflow hose). At each depth a bucket sample was drawn directly from the outflow hose for water temperature and salinity, particulate carbon and nitrogen (C/N) samples, particulate chlorophyll, and fluorescence. Samples for nutrient analyses were taken directly from the pump outflow and kept on ice during sampling. After transport to the laboratory, the samples were either fun fresh that day, or frozen for processing on the subsequent day. For chlorophyll and C/N samples, 100-200 ml were filtered through a Whatman GFC filter, and the filters kept on ice in a cooler during sampling and transport. In the laboratory, filters were frozen for later processing. Fluorescence determinations were measured on board ship with a Turner Designs or Aminco fluorometer set on discrete mode. The data were recorded manually. A 1 liter sample for phytoplankton species identification and cell enumeration was taken from the pump outflow directly, preserved with 2.5% gluteraldehyde, and transported to the laboratory in a cooler. In the laboratory, a portion of each sample was processed through 1 and 10 um meshes for subsequent size fractionation analyses, and a portion was retained for unfiltered cell counts (Fagerness, in prep.). For counting, 100-200 ml were settled and optically counted with an inverted microscope using the Utermohl method. Zooplankton samples were taken at each depth by pumping directly through a half-meter zooplankton net (64 µm inner mesh with 500 µm mesh outer protective lining). During pumping, the net was suspended overboard from a metal frame which positioned the net collar

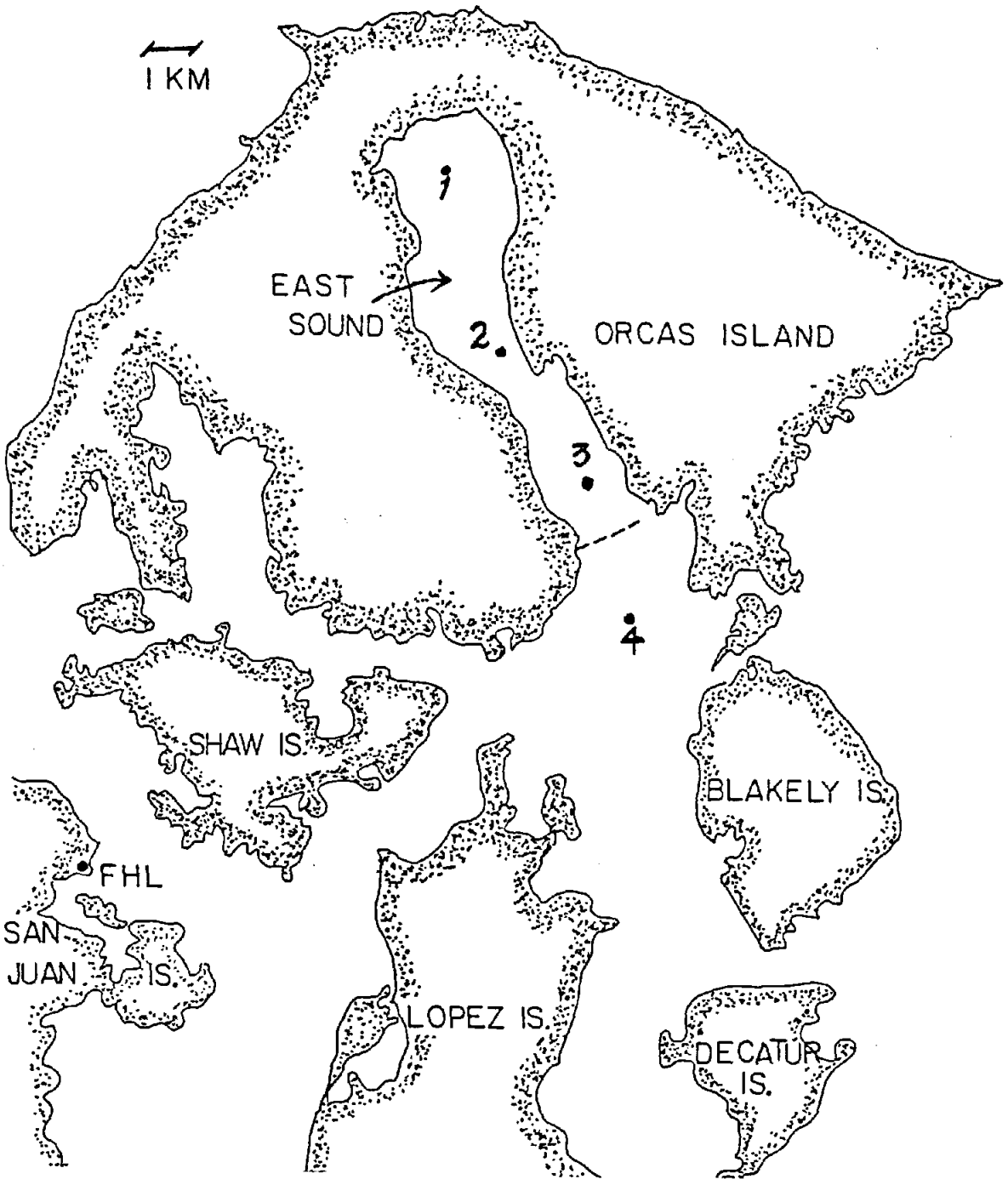


Figure 4-1 A map of East Sound, Washington, showing the four sampling stations used in the field survey. Station 2 was chosen to represent conditions within East Sound, and Station 4 was chosen to represent conditions in channel waters outside the bay.

Table 4-1 Measurements taken during the survey of East Sound, Washington, in 1980.

Parameter	Procedure	Equipment	Dates Samples Taken
1. Temperature	Water bucket sample	YSi T-S probe	April-July
2. Salinity	Water bucket sample	YSi T-S probe	April-July
3. Light	Transmission, Irradiance	Hi-Tech optical Transmissometer	Occasional
4. Nutrients (NO_3+NO_2, SiO_4, PO_4, NH_4)	Pump sample	Technicon Autoanalyser	March-July
5. Fluorescence	Water bucket sample	Turner Designs Flurometer	April-July
	a. w/ and wo/ DCMU		April-July
	b. discrete samples		April-May
	c. continuous flow		May-July
	d. discrete samples	Aminco Fluorometer	June-July
6. Carbon/Nitrogen	Water bucket sample 100-200 ml filtered	CHNO Perkin-Elmer Analyser	May-July
7. Chlorophyll a	Water bucket sample 100-200 ml filtered	Manual, Strickland & Parsons Modified Chlorophyll Analysis	May-June
8. Primary Production	in situ C^{14} incubations	Liquid Scintillation	April-July
9. Phytoplankton	Pump sample unfiltered filtered: 1, 10 µm mesh	Preserved with 2.5% gluteraldehyde	March-July
10. Zooplankton	Pump sample 64 µm mesh plankton net	Preserved with 10% buffered formalin	March-July

and mouth just above the surface of the water during filtering. A 3-5 minute pumping time per sample (at 150-200 gallons/minute) was used so that 1-2 m^3 of water were filtered, except during intense blooms when net clogging was a problem. After pumping each sample, the net mesh was rinsed down into the cod end and the contents of the cod end preserved with 10% buffered formalin. Zooplankton abundance estimates were calculated in the laboratory from microscopic species identification and animal enumeration of several 1 ml subsamples removed from each decanted sample by Stempel pipette. The dominant zooplankton taxa were identified to species and developmental stage using a Wild M-5 binocular microscope. Phytoplankton species identification and cell enumerations were done by V. Fagerness, nutrient analyses by S. Moore, zooplankton identification and enumerations by B. Dexter, chlorophyll analyses by R. Leatham and B. Dexter, C/N and fluorescence determinations by all of the above.

Results

Environmental Conditions in East Sound

The temperatures measured over the study period (March-July, 1980) at 5 and 20 meters for each station indicated that a well-mixed water column was present during winter until May at all stations (Fig. 2). An increasingly homogeneous system was also observed downbay, approaching Station 4 in the channel. Thermal stratification began in late April to early May within the bay and became well established by June or July, especially at the upper two bay stations. By summer, a difference of 4-5°C between 5 and 20 meters was observed at Stations 1 and 2. Winter temperatures at all stations were 7-9°C, and warmed to 14-16°C at the surface by late July.

Nutrient concentrations at all four stations generally decreased from winter to summer (Fig. 3 and 4). Maximum values of 25 µM/l nitrate + nitrite (Fig. 3), and 50 µM/l silicate (Fig. 4) were measured during winter. Nutrient depletion at the surface (and throughout much of the water column) first occurred in May at Stations 1 and 2, with apparent nutrient pulses occurring in mid-May and mid-June. During these pulses, nutrient concentrations within the bay increased to values similar to those measured at Station 4 in the main channel. Surface waters became nutrient-depleted again in July.

Seasonal changes in phytoplankton abundance (Fig. 5) indicated a close correlation between periods of phytoplankton increase and nutrient depletion. Periods of high phytoplankton abundance lagged the nutrient pulses by a week to 10 days. An increase in phytoplankton cell number first occurred in mid-April, which represented a small bloom of silicoflagellates (Dictyoca sp.). The three primary phytoplankton peaks observed during the study period (Fig. 5) resulted from blooms of chain-forming diatoms. The

Figure 4-2 Temperature (°C) in East Sound measured at Station 1-4, for 5 meters and 20 meters from April through July, 1980.

Figure 4-2

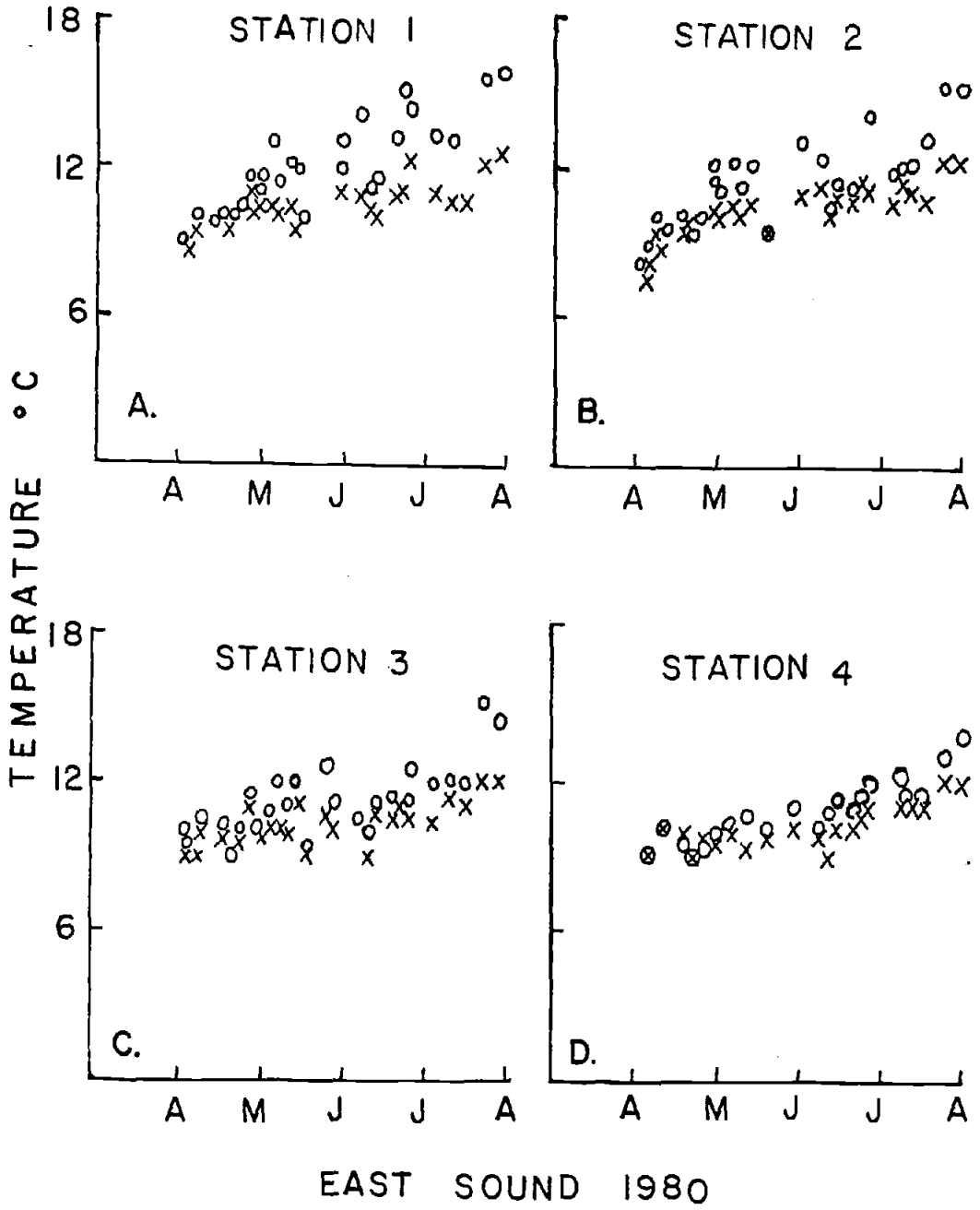

STATION 1
STATION 2
STATION 3
STATION 4
A.
B.
C.
D.
18
12
6
TEMPERATURE °C
A M J J A
EAST SOUND 1980

Figure 4-3 Nitrate + nitrite concentrations (μM/l) at 5 meters in East Sound measured at Station 1-4.

Figure 4-3

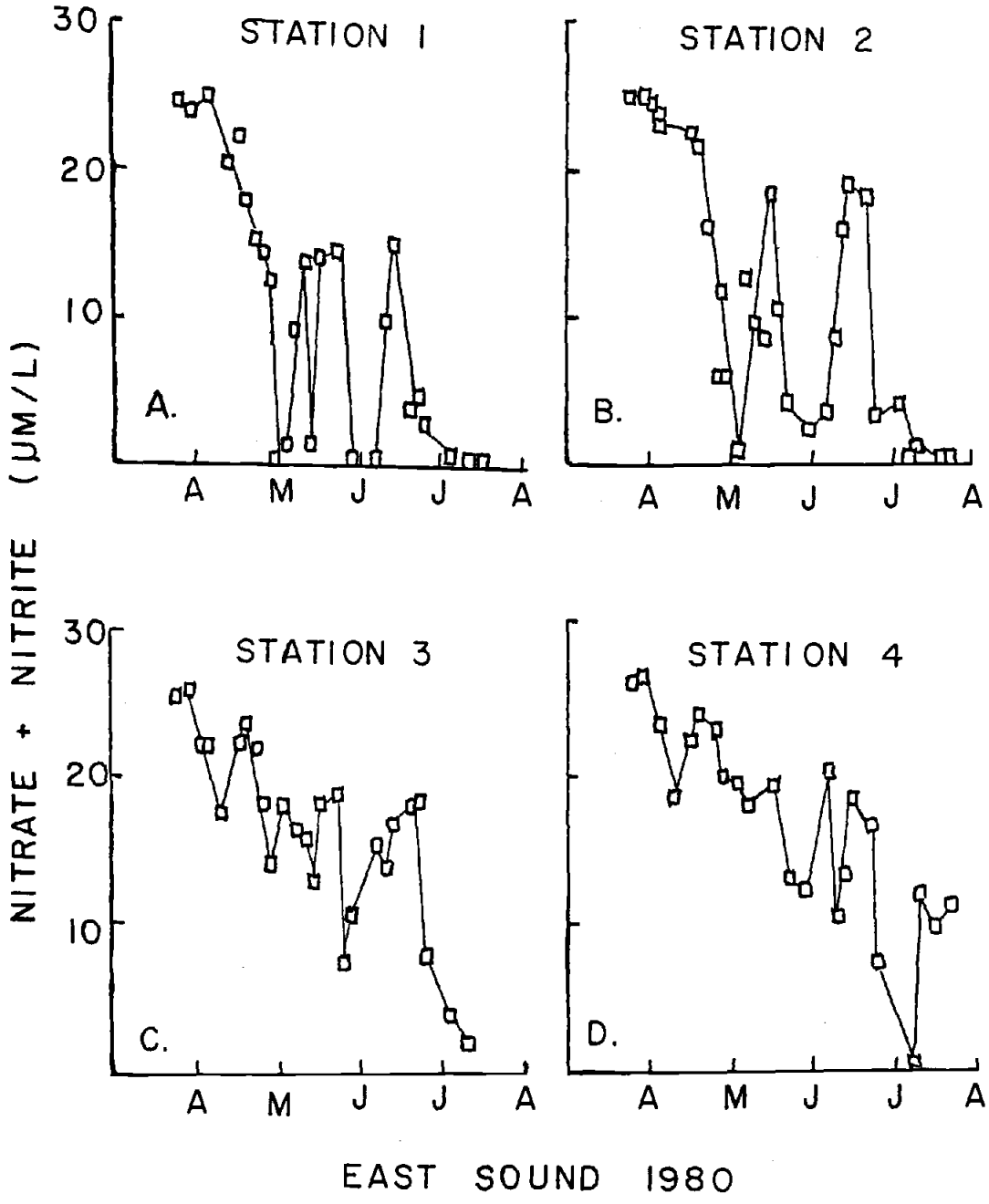

STATION 1
STATION 2
STATION 3
STATION 4
A.
B.
C.
D.
30
20
10
A M J J A
NITRATE + NITRITE (µM/L)
EAST SOUND 1980

Figure 4-4 Silicate concentrations (μM/l) at 5 meters in East Sound measured at Station 1-4.

Figure 4-4

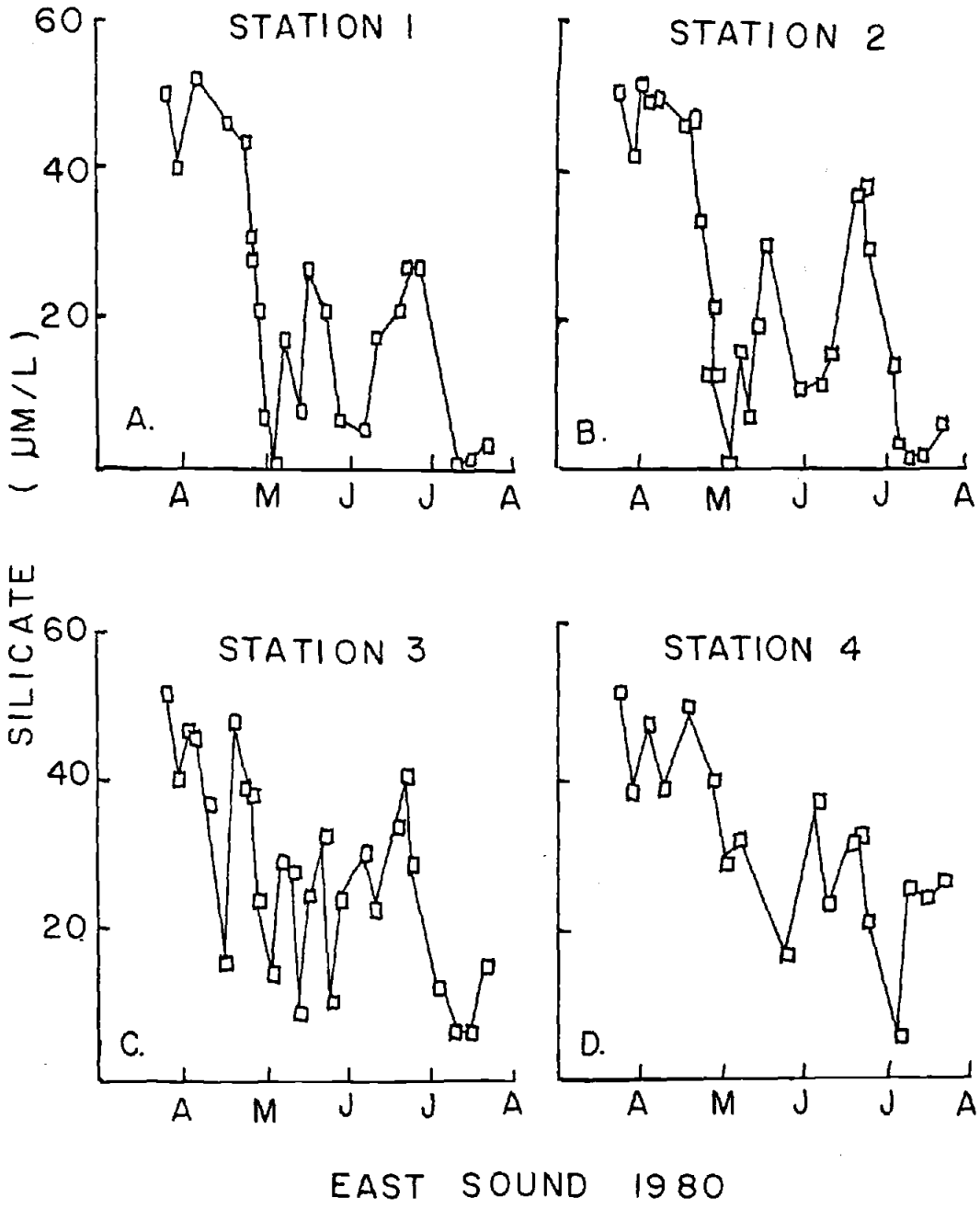
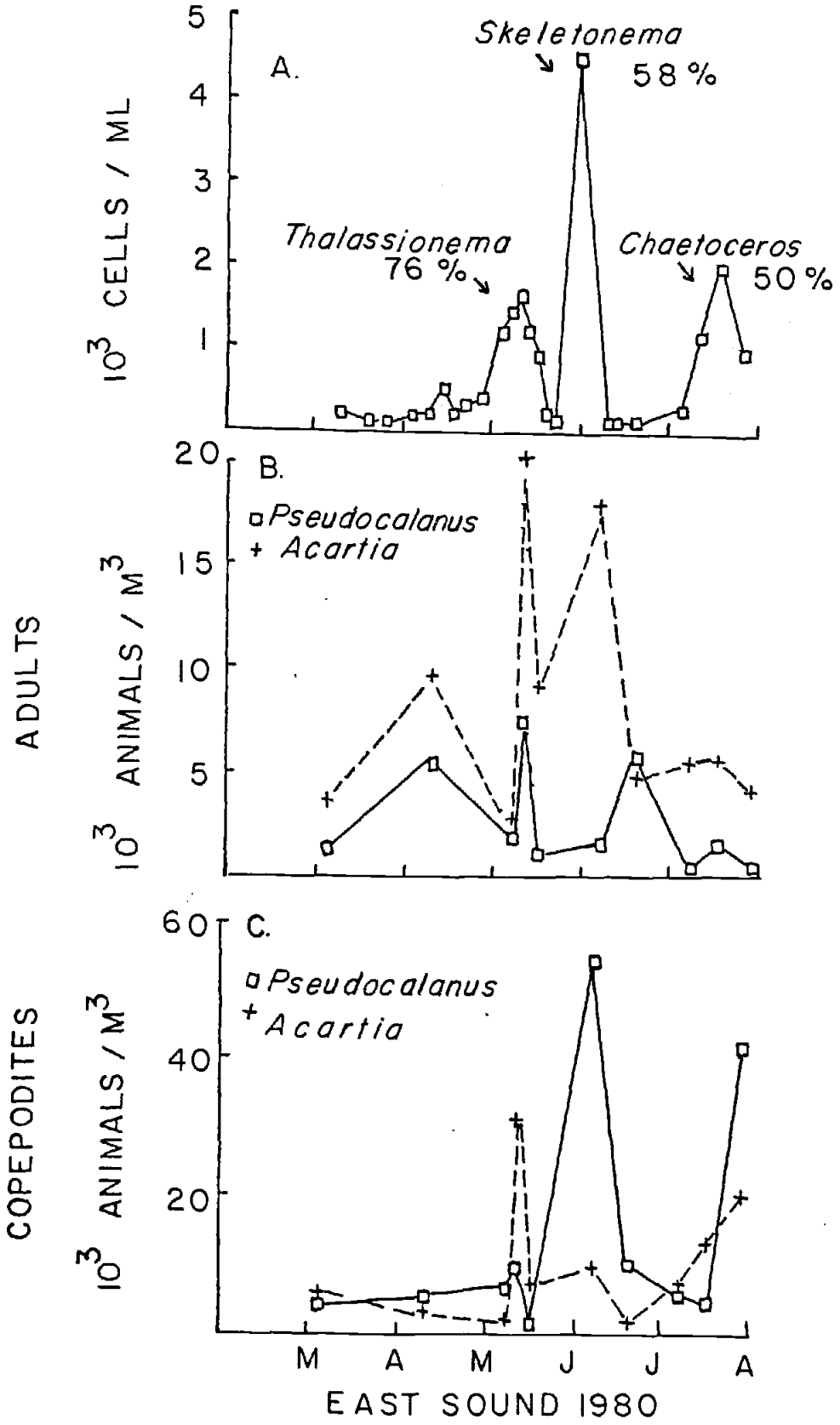

STATION 1
STATION 2
STATION 3
STATION 4
A.
B.
C.
D.
60
40
20
A M J J A
SILICATE (µM/L)
EAST SOUND 1980

Figure 4-5 Seasonal abundance of phytoplankton and zooplankton at 5 meters in East Sound measured at Station 2. (A.) Phytoplankton abundance (cells/ml). (B.) Pseudocalanus (□) and Acartia clausi (+) adults (males + females) abundance (animals/m^3. (C.) Copepodite (CI-CV) abundance for Pseudocalanus and Acartia clausi (animals/m^3).

Figure 4-5


A.
Skeletonema
58 %
Thalassionema
76 %
Chaetoceros
50 %
10³ CELLS / ML
B.
Pseudocalanus
Acartia
ADULTS
10³ ANIMALS / M³
C.
Pseudocalanus
Acartia
COPEPODITES
10³ ANIMALS / M³
M A M J J A
EAST SOUND 1980

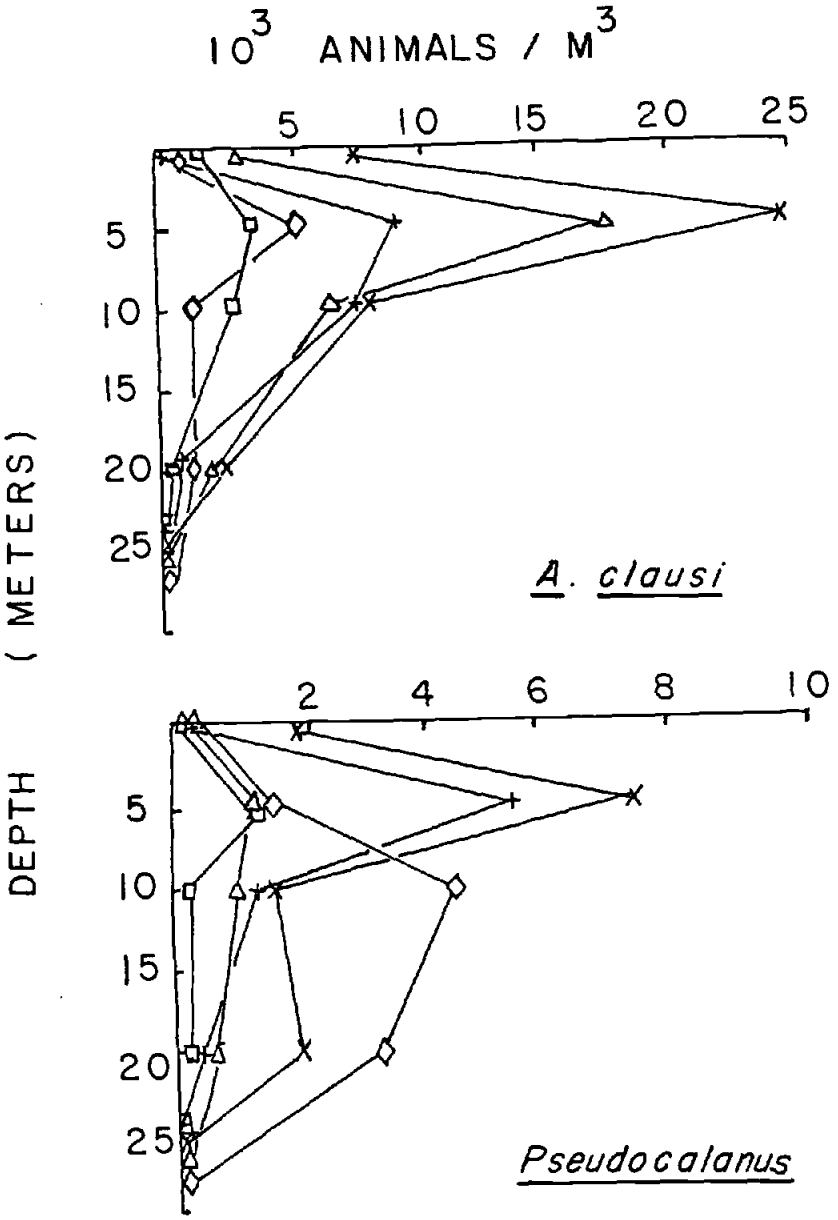
phytoplankton was dominated by Thalassionema nitzschoides in May (76% relative abundance by cell number at 5 meters, Fig. 5), Skeletonema costatum in June (58%), and Chaetoceros spp. in July (50%). The phytoplankton community became increasing diverse through the year, as indicated by the decreasing percent relative abundance for each of the bloom species (Fig. 5). The peaks in phytoplankton cell number at 5 meters were also duplicated in the chlorophyll a and relative fluorescence data (not shown).

Although zooplankton abundances were more variable, the data indicated a good correlation between large increases in phytoplankton cell number and subsequent increases in zooplankton (Fig. 5). At times, copepodite abundances increased by an order of magnitude between sampling dates (e.g., from about 1000/m^3 in May, to 50,000/m^3 Pseudocalanus copepodites in June, Fig. 5). Adult copepods generally remained at lower relative abundances, but were still quite numerous. A small increase in adult copepods was observed at the time of the first silicoflagellate bloom in mid-April. Peak abundances for Pseudocalanus adults coincided with the Thalassionema bloom in early May. Peak abundances for Acartia reached nearly 18,000/m^3 in June (Fig. 5). Acartia copepodites also increased during the May Thalassionema bloom. Pseudocalanus copepodites (and Acartia adults) peaked shortly after the Skeletonema bloom. The abundance of Pseudocalanus adults and Acartia copepodites increased slightly at this time. Copepodites of both species responded to the mid-July Chaetoceros bloom, but the number of adults increased only slightly in July at this station and depth.

Vertical profiles of adult Acartia and Pseudocalanus concentrations indicated the development of an abundance peak at 5 meters within East Sound (Fig. 6). Acartia dominated the zooplankton community during April, May, and June in the upper 10 meters. Pseudocalanus adults reached their abundance peak at 5 meters during April and May; however,

Figure 4-6 Vertical abundance of Pseudocalanus and Acartia clausi adults (animals/m^3) at Station 2. Data are monthly estimates from samples collected on 3 March (□), 11 April (△), 8 May (+), 17 June (×), and 15 July (◇).

Figure 4-6


10^3 ANIMALS / M^3
5
10
15
20
25
DEPTH (METERS)
5
10
15
20
25
A. clausi
2
4
6
8
10
5
10
15
20
25
Pseudocalanus

by July, the depth of peak abundance dropped to 10-20 m. Pseudocalanus adults were not found in surface and 5 meter samples by late July. Zooplankton concentrations at Station 4 were always considerably lower than at Station 2 (not shown), and the zooplankton community at Station 4 typically included many more oceanic species at higher frequencies of occurrence (e.g., eupahusiids, chaetognaths, Calanus, Eucalanus, and Metridia, Table 2 and 3).

In summary, three general sets of conditions existed in East Sound during the study period. The winter period, ending in March-April, was characterized by cold water (less than 10°C), very high nutrient levels (nitrate + nitrite greater than 20 uM/l; silicate greater than 50 uM/l) and low plankton abundances. The spring transition period extended from April through June in 1980. This period was characterized by variable biological and physical conditions: gradually increasing temperature and the onset of a warm surface layer (surface to 10 meters), and two large phytoplankton blooms, with associated decreases in nutrient levels. Pulses of high zooplankton abundance were associated with each of the phytoplankton blooms. There were also appreciable storm-related influxes of channel water at this time of year, resulting in high-nutrient, cold-water plumes extending well into the bay. Summer conditions of warmer water, relatively high plankton abundances, and low nutrient levels began in late June and July. As a strong thermocline was established, the depth of the peak abundance of the adult Pseudocalanus population dropped to 10-20 meters, whereas Acartia adults remained most abundant at 5 meters.

Although advection events clearly occurred during the sampling period, the integrity of the plankton populations within East Sound was retained. Pseudocalanus and Acartia clausi remained the dominant zooplankton species throughout the study period. Zooplankton associated with channel waters that were periodically advected into East Sound generally dissipated from the bay zooplankton sampled within a week

Table 4-2 Frequency of occurrence of the major zooplankton taxa present at Station 2. Common species were present in > 50% of the samples counted for this analysis (N_t=28). Uncommon species were present in 10-50% of the samples. Rare species were present in < 10% of the samples. Taxa are listed by rank order based upon the total number of samples in which taxa were present (in parentheses).

Common		Uncommon		Rare	
Pseudocalanus copepodites	(28)	Appendicularians	(13)	*Eucalanus*	(3)
Acartia clausi adults	(28)	*Tortanus* copepodites	(11)	Chaetognaths	(3)
Acartia copepodites	(28)	*Coryceaus*	(11)	Gastropod eggs	(3)
Oithona	(27)	Crab zoea	(10)	Amphipods	(3)
Copepod nauplii	(27)	*Epilabidocera* copepodites	(10)	Lamellibranch larvae	(3)
Centropages copepodites	(26)	Pteropods	(10)	*Epilabidocera* adults	(2)
Pseudocalanus adults	(23)	Decapod larvae	(9)	Sea cucumber eggs	(1)
Polychaete larvae	(21)	Gastropod larvae	(8)	*Paracalanus*	(1)
Centropages adults	(20)	Harpacticoids	(7)	Euphausiid furcilia	(1)
Oncea	(19)	*Tortanus* adults	(6)		
Barnacle nauplii	(16)	*Calanus*	(6)		
Acartia longiremis	(14)	*Metridia*	(5)		
		Microcalanus	(5)		
		Cladocerans	(4)		

Table 4-3 Frequency of occurrence of the major zooplankton taxa present at Station 4. Notation as in Table 2.

Common		Uncommon		Rare	
Copepod nauplii	(28)	Harpacticoids	(13)	Microcalanus	(3)
Polychaete larvae	(28)	Tortanus copepodites	(12)	Euphausiid calyptopis	(3)
Acartia copepodites	(27)	Barnacle cypris	(11)	Paracalanus	(2)
Pseudocalanus copepodites	(26)	Pteropods	(11)	Isopods	(2)
Oithona	(24)	Cladocerans	(10)	Clausocalanus	(1)
Barnacle nauplii	(24)	Calanus	(9)	Amphipods	(1)
Acartia clausi adults	(23)	Metridia	(9)	Echinoderm larvae	(1)
Appendicularians	(23)	Lamellibranch larvae	(9)		
Centropages copepodites	(22)	Tortanus adults	(8)		
Pseudocalanus adults	(21)	Chaetognaths	(8)		
Oncea	(21)	Gastropod eggs	(8)		
Centropages adults	(16)	Decapod larvae	(7)		
Epilabidocera copepodites	(16)	Euphausiid furcilia	(6)		
Crab Zoea	(15)	Gastropod larvae	(5)		
Acartia longiremis	(14)	Eucalanus	(4)		

of an event. They never replaced the indigenous species in either rank order or relative abundance. The same succession and periodicity of phytoplankton blooms that had occurred in previous years also occurred in 1980, indicating that a relatively predictable food resource existed for the zooplankton of East Sound on a long-term basis. However, the smaller-scale temporal (seasonal) and spatial (vertical) differences in zooplankton and phytoplankton species abundances indicated that several different possible "food environments" could be identified for the dominant copepods of East Sound.

Eight dates during the survey period were selected to represent the nominally different food conditions encountered by Pseudocalanus and Acartia clausi developmental stages within East Sound (Table 5). Phytoplankton concentrations from 31 May and 5 June were both used in conjunction with the zooplankton abundances from 5 June in order to study the impact of the same zooplankton population under conditions of both high (31 May) and low (5June) food concentration (Table 7).

Grazing Impact Model of East Sound

The grazing removal rates for the developmental stages of Pseudocalanus and Acartia clausi were calculated on a stage-specific basis (Is) using an equation modified from Bartram (1981):

$$Is = (Fj)\cdot(Hj)\cdot(E)\cdot(P),$$

where Fj = stage-specific maximum filtration rate (mls/animal/day), Hj = stage-specific grazer concentration (animal/m^3) for each developmental stage, j, E = cell capture efficiency, and P = total phytoplankton concentration (cells/ml). Fj was derived from the laboratory grazing experiments as the mean maximum filtration rate calculated over all four

food levels for each developmental stage (Table 6). E was calculated as the mean capture efficiency empirically derived from the laboratory grazing experiments for each developmental stage (EI (1), Chapter 3, Table 9). This ratio (Capture Rate/Encounter Rate) was considered the best estimate of minimum cell capture efficiency for each species (Table 6). The data were summed over all developmental stages to calculate the grazing removal for the entire population of Pseudocalanus and Acartia clausi separately and for the two grazer populations combined. (Future analyses will incorporate the size class-specific, theoretical retention efficiencies generated in the comparative morphology study in conjunction with the size class analyses of the natural particle spectra in order to generate an efficiency term which is specific for both phytoplankton cell size and copepod developmental stage. This model can be generated once the size-fractionated phytoplankton concentrations have been completed; Fagerness, in prep.).

The field data from East Sound were used to define the average winter, spring, and summer conditions observed over the survey period, and to depict the probable food environments encountered by the dominant copepod grazers at Station 2 (Table 4). The grazing impact of each population was calculated using the phytoplankton and zooplankton concentrations from eight dates during the survey period, and for the mean conditions observed at Station 2. The grazing impact of each population was calculated using the phytoplankton and zooplankton concentrations from eight dates during the survey period, and for the mean conditions observed at Station 2. These dates were chosen to represent (1) bloom conditions, (2) background conditions, when phytoplankton concentrations were low and flagellates dominated, and (3) the seasonal mean conditions observed over the survey period (Table 5). Grazing impact calculations using the empirically-derived maximum filtration rate and minimum capture efficiency estimate were compared to grazing impact calculations using

Table 4-4 Environmental conditions present in East Sound on selected dates during the survey period. Data from these dates were used to calculate the grazing impact of the dominant copepod grazer populations in East Sound during winter, spring, and summer.

Date	Environmental Conditions			
	Phytoplankton Abundance Level (Bloom Species)	Dominant Zooplankton Taxa	Nutrients	Temperature
Winter				
3 March	Background	*Acartia* copepodites	Winter Maximum	Winter Minimum
11 April	Background	*Acartia* adults	Decreasing	Low
Spring				
8 May	Bloom (*Thalassionema*)	*Acartia* copepodites	Surface Depletion	Increasing
16 May	Background	*Acartia* copepodites	Nutrient Pulse	Increasing
31 May	Bloom (*Skeletonema*)	*Pseudocalanus* copepodites	Near Depletion	Increasing
5 June	Background	*Pseudocalanus* copepodites	Near Depletion	Increasing
Summer				
17 June	Background	*Pseudocalanus* copepodites	Nutrient Pulse	Summer Maximum
15 July	Bloom (*Chaetoceros*)	*Pseudocalanus* copepodites	Summer Minimum	Summer Maximum

Table 4-5 Stage-specific abundances for Pseudocalanus and Acartia clausi and the phytoplankton abundances measured at Station 2 (5 meters). These data were used to calculate the stage-specific grazing impact on each data for each species, and for the seasonal mean conditions (Mean), bloom conditions (Bloom), and during periods of low, background level phytoplankton concentrations (Background). Phytoplankton concentrations measured on both 31 May and 5 June were used in conjunction with the zooplankton abundances measured on 5 June to determine the range of values for the grazing impact of the same population during high and low food abundances. The phytoplankton concentration for March was the monthly average.

	3 Mar	11 Apr	8 May	16 May	31 May/ 5 Jun	17 Jun	15 Jul	Mean	Bloom	Bkgrd
10^6cells/m^3:	55.5	330.5	1153.0	175.0	4712/100	50	2502	1135	2789	142
Stage			Zooplankton Abundance (animals/m^3)							
Pseudocalanus sp.										
Female	202	2082	4138	523	2742	1919	524	1733	2468	1182
CV	202	1340	1396	175	3988	5234	673	1858	2019	1737
CIV	327	646	2642	274	5484	2169	449	1713	2858	854
CIII	466	1125	2194	399	16849	1122	1197	3337	6747	778
CII	358	168	1147	573	19840	474	748	3330	7245	393
CI	762	24	349	773	4686	648	673	1131	1903	552
Total	2317	5385	11866	2717	53589	11566	4264	13102	23240	5496
Acartia clausi										
Female	995	2656	12064	2343	6082	1471	7106	4674	8417	1866
CV	824	814	7104	1321	947	598	2618	2032	3556	889
CIV	715	239	6854	748	648	249	1571	1575	3024	488
CIII	591	503	5359	598	1396	75	2618	1591	3124	442
CII	871	646	2792	798	1147	224	2842	1331	2260	635
CI	1042	957	4960	947	1147	798	3665	1931	3257	936
Total	5038	5815	39133	6755	11367	3415	20420	13134	23638	5256

Table 4-6 Input for the stage-specific grazing impact model, which used a stage-specific maximum filtration rate (mean +/- 1 Standard deviation) and a species-specific cell capture efficiency term. Phytoplankton concentrations and zooplankton abundances used in this model are listed in Table 5.

Stage-specific Maximum Filtration Rate (ml/animal/day)

Stage	Pseudocalanus	Acartia
Female	18.67 +/- 7.4	16.39 +/- 2.7
CV	11.09 +/- 5.4	6.67 +/- 2.0
CIV	7.21 +/- 3.6	6.76 +/- 2.9
CIII	6.19 +/- 1.9	6.76 +/- 2.9
CI + CII	5.53 +/- 1.2	7.95 +/- 3.9

Species-specific Cell Capture Efficiency (%)
(Cells Captured/Cells Encountered)

19.36 +/- 8.5	13.53 +/- 10.6

a maximum, theoretical capture efficiency of 1.0, which assumed 100% retention for all cells encountered by the filter, and 100%consumption of those cells retained by the filter.

The stage-specific daily grazing removal rates for the developmental stages of the Pseudocalanus and Acartia populations in East Sound indicated that only during phytoplankton bloom conditions could the dominant grazer populations have removed more than a few percent of the measurable standing stock (Table 7 and 8). Maximum removal rates and the percent of the standing stock theoretically removed by each grazer population occurred on the three designated bloom dates (16 May, 5 June, and 15 July; Table 7). An average of 6.9% of the standing stock was theoretically removed during average bloom conditions for the two species combined (Table 8). Assuming 100% efficiency for cell retention and ingestion, theoretically 43% of the standing stock could have been removed by the combined grazer populations during bloom conditions (Table 8), due both to the high concentration of phytoplankton cells in the water, and the high abundances reached by both grazer populations at this time.

During periods of low phytoplankton abundance, the two copepod populations each removed, on average, less than 2% of the measured standing stock, assuming the minimum estimate for cell capture efficiency, and approximately 5% of the standing stock assuming a maximum efficiency of 100% (Table 8). The Acartia population theoretically could have removed twice the amount of measured, available phytoplankton compared to the Pseudocalanus population (Table 8), even though the effective availability of cells was theoretically less for Acartia developmental stages (Table 6) due to the relative inefficiency with which small cells were retained by the filtering apparatus. On average, the population abundances of the two species were comparable during periods of both high and low cell abundances (Table 5). The stage-

Table 4-7 Stage-specific grazing removal by *Pseudocalanus* and *Acartia* populations on selected dates during winter, spring, and summer in East Sound, Washington. Grazing removals for 5 June were calculated using phytoplankton abundances measured on both 31 May and 5 June for comparison.

	Winter			Spring			Summer	
	3 Mar	11 Apr	8 May	16 May	31 May	5 Jun	17 Jun	15 Jul
Pseudocalanus								
Female	0.07	2.48	17.25	0.33	46.70	0.99	0.35	4.78
CV	0.04	0.95	3.46	0.07	40.35	0.86	0.56	3.65
CIV	0.05	0.30	4.25	0.07	36.07	0.77	0.15	1.58
CIII	0.06	0.44	3.03	0.08	110.82	2.02	0.07	3.62
CII	0.04	0.06	1.42	0.11	112.03	2.12	0.03	2.02
CI	0.03	0.01	0.43	0.14	23.64	0.50	0.03	1.82
Species Total:	0.34	4.24	29.83	0.80	369.61	7.26	0.38	17.47
% Stock Removed:	0.34	1.29	2.59	0.46	7.80	7.30	0.80	2.90
Acartia clausi								
Female	0.22	1.94	30.85	0.91	63.55	1.35	0.16	39.46
CV	0.07	0.24	7.39	0.21	4.03	0.09	0.03	5.91
CIV	0.07	0.07	7.23	0.12	2.79	0.06	0.01	3.60
CIII	0.05	0.15	5.65	0.10	6.02	0.13	0.003	5.99
CII	0.09	0.23	3.46	0.15	5.81	0.12	0.01	7.65
CI	0.11	0.34	6.15	0.18	5.81	0.12	0.04	9.86
Species Total:	0.62	2.98	60.73	1.66	88.01	1.87	0.26	72.44
% Stock Removed:	0.62	0.71	5.27	0.95	1.90	1.80	0.40	0.70
Total Daily Removal for Combined Populations:	0.96	7.22	90.56	2.46	457.62	9.13	0.64	89.91
% Stock Removed by Combined Populations:	0.96	2.20	7.86	1.41	9.70	9.10	1.20	3.59

Table 4-8 Stage-specific grazing removal of Pseudocalanus and Acartia populations for the mean conditions in East Sound. Estimates of the daily grazing removal (10^6 cells removed/stage/m^3/day) were calculated using the data listed in Table 5 and6. The maximum daily grazing removal was calculated for each stage assuming 100% efficiency for cell retention. Minimum estimates of grazing removal were calculated assuming the lowest efficiency calculated from the laboratory grazing experiments. % = percent of the estimated standing stock removed by each stage, each species, and for the two populations combined.

Table 4-8

Daily Grazing Removal

	Mean Conditions		Bloom Conditions		Background Conditions	
	10^6Cells	%	10^6Cells	%	10^6Cells	%
A. Maximum Grazing Impact: assumes 100% efficiency in capturing cells						
Pseudocalanus						
Female	36.72	3.24	128.51	4.61	3.13	2.12
CV	23.38	2.06	62.45	2.24	2.74	1.93
CIV	14.02	1.24	57.47	2.06	0.87	0.62
CIII	23.44	2.07	116.48	4.18	0.68	0.48
CII	20.90	0.18	111.74	4.01	0.31	0.22
CI	7.10	0.63	29.35	1.05	0.43	0.30
Total	125.57	11.06	505.99	18.14	8.17	5.75
Acartia clausi						
Female	86.95	7.66	384.76	13.80	4.34	3.06
CV	19.82	1.75	66.15	2.37	0.13	0.09
CIV	12.08	1.06	57.01	2.04	0.47	0.33
CIII	12.21	1.08	58.90	2.11	0.42	0.30
CII	12.01	1.06	50.11	1.80	0.72	0.50
CI	17.42	1.54	72.22	2.59	1.06	0.74
Total	160.49	14.14	689.14	24.71	7.14	5.02
Combined Total:	286.07	25.20	1195.14	42.85	15.31	10.78
B. Minimum Grazing Impact: assumes lowest species-specific efficiency in capturing cells						
Pseudocalanus						
Female	7.11	0.63	24.88	0.89	0.61	0.43
CV	4.53	0.40	12.09	0.43	0.53	0.37
CIV	2.71	0.24	11.13	0.40	0.17	0.12
CIII	4.54	0.40	22.55	0.81	0.13	0.09
CII	4.05	0.36	21.63	0.78	0.59	0.04
CI	1.37	0.12	5.68	0.20	0.34	0.06
Total	24.31	2.14	97.96	3.51	1.58	1.11
Acartia clausi						
Female	11.74	1.03	51.94	1.86	0.59	0.41
C	2.68	0.24	8.93	0.32	0.17	0.01
CIV	1.63	0.14	7.70	0.28	0.63	0.04
CIII	1.65	0.15	7.95	0.29	0.57	0.04
CII	1.62	0.14	6.76	0.24	0.97	0.07
CI	2.35	0.21	9.75	0.35	0.14	0.10
Total	21.67	1.91	93.03	3.34	0.96	0.68
Combined Total:	45.98	4.05	190.99	6.85	2.54	1.79

specific grazing removals for the female population of each species were always highest. The only exception to this pattern was noted on 17 June, when Pseudocalanus stage CV removed slightly more than the female (Table 7).

The stage-specific grazing removals were used to calculate the grazing impact of each developmental stage on a dry weight basis (Iw), using the equation:

$$Iw = (Fj)\cdot(Hj)\cdot(Ej)\cdot(P)/(Hj)\cdot(Wj),$$

where Fj = stage-specific maximum filtration rate, Hj = copepod developmental stage abundance, Ej = cell capture efficiency, P = total phytoplankton concentration, and Wj = stage-specific copepod dry weight. Thus, the total number of cells theoretically removed by each developmental stage (j) was divided by the total dry weight for that stage, to yield a grazing removal estimate with the dimensions of cells removed/ug dry weight/day. The body weight for each developmental stage was calculated as mean dry weight (ug) from individuals sorted from East Sound preserved plankton samples (Station 2, 5 meters). Groups of animals (n = 50) were transferred to tared pieces of aluminun foil, dried for three to five days at 60°C, and subsequently weighed on a Cahn Electrobalance (Table 9).

Weight-specific removal rates calculated for the mean bloom, mean background, and seasonal mean conditions in East Sound were much higher for Acartia than for Pseudocalanus developmental stages (Table 10). Although stage-specific abundances and grazing removal rates for the two species were generally comparable, the higher weight-specific rates for Acartia were generally due to the relative differences measured for copepod dry weight in comparable developmental stages of the two species. On average, the Acartia population could remove 3.3-3.5 times more cells per ug dry weight than the Pseudocalanus population. There was greater than an order of magnitude range in the estimated number of cells

Table 4-9 Dry weight estimates (µg dry weight/copepod) for the developmental stages of Pseudocalanus and Acartia clausi used as input values for the weight-specific grazing impact model.

	Copepod Body Weight (µg)	
Stage	Pseudocalanus	Acartia
Female*	10.97	4.58
CV	8.6	1.6
CIV	3.7	0.9
CIII	2.9	0.6
CII	1.6	0.4
CI	0.8	0.2

*Seasonal mean weights

Table 4-10 Weight-specific grazing impact for the mean conditions in East Sound, using the maximum and minimum estimates for cell capture efficiency. Dimensions are cells removed/µg copepod dry weight/day.

Table 4-10

Stage	Daily Grazing Removal		
	Mean Conditions	Bloom Conditions	Background Conditions
A. Maximum Grazing Impact: assumes 100% efficiency in capturing cells			
Pseudocalanus sp.			
Female	1932	4747	242
CV	1464	3657	183
CIV	2212	5435	277
CIII	2423	5953	303
CII	3923	9639	491
CI	7844	19284	981
Total	19798	48715	2477
Mean	3300	8119	413
Acartia clausi			
Female	4062	9994	508
CV	6096	11626	89
CIV	8522	20945	1067
CIII	12782	31429	1601
CII	22575	55432	2822
CI	45140	110931	5651
Total	99177	240357	11738
Mean	1653	40060	1956
B. Minimum Grazing Impact: assumes lowest species-specific efficiency for capturing cells			
Pseudocalanus sp.			
Female	374	919	47
CV	283	696	35
CIV	428	1052	54
CIII	469	1153	59
CII	759	1866	95
CI	1519	3733	190
Total	3832	9419	480
Mean	639	1570	80
Acartia clausi			
Female	548	1347	69
CV	823	1569	12
CIV	1151	2828	144
CIII	1726	4243	216
CII	3048	7483	381
CI	6094	14976	763
Total	13390	32446	1585
Mean	2232	5408	264

removed per stage as calculated using the minimum and maximum estimate for capture efficiency.

Since the female stages of both species generally removed the highest percentages of the measurable standing stock (Table 7), a final grazing impact model was calculaed to determine the effect of cnanges in female body size and weight on the grazing removal of females. The cephalothorax length was measured for 50 females sorted from samples taken on nine dates during the survey period at Station 2 (5 m). The mean body length was calculated for the females from each date (Table 11). Estimates for female body weight were then calculated using the equation $Y = 11.48X^{2.88}$ for Pseudocalanus, and $Y = 11.59X^{3.52}$ for Acartia, where Y = copepod dry weight in ug, and X = cephalothorax length in mm. These empirically-derived equations closely approximated the theoretical relationship between copepod body weight and body length ($W = L^3$, Steele and Mullin 1977). The maximum, minimum, and seasonal mean female weight were used in conjunction with the minimum species-specific efficiency estimates (Table 11) to calculate the seasonal range of values for female grazing removal under the mean conditions observed in East Sound over the study period (Table 12).

Estimated female body weight ranged from a summer low of 7.94 ug for Pseudocalanus and 2.79 µg for Acartia, to a winter maximum of 13.21 µg for Pseudocalanus and 5.76 µg for Acartia (Table 11). This represented a 60% decrease in body weight for Pseudocalanus and a 48% decrease for Acartia females from winter to summer. During winter, Acartia females at their maximum weight were 44% of the weight of Pseudocalanus females, and 35% of the Pseudocalanus female weight at their minimum weight estimated in summer (mean = 42%). However, the weight-specific grazing impact calculated for these individuals indicated that Acartia females were theoretically capable of removing 50-80% more phytoplankton per unit dry weight than comparable Pseudocalanus females over

Table 4-11 Cephalothorax length (mm) and estimated dry weight (µg) for females of Pseudocalanus and Acartia clausi from plankton samples collected in East Sound. Dry weights were calculated from the relationship between body length and weight given in the text for each species.

	Pseudocalanus sp.		Acartia clausi	
Date	Body Length	Body Weight	Body Length	Body Weight
3 Mar	1.04	12.85	0.76	4.41
11 Apr	1.05	13.21	0.82	5.76
8 May	1.05	13.21	0.82	5.76
16 May	1.03	12.50	0.82	5.76
31 May	0.98	10.83	0.78	4.83
5 June	0.94	9.61	0.77	4.62
17 June	0.93	9.31	0.74	4.02
15 July	0.93	9.31	0.70	3.30
27 July	0.88	7.94	0.68	2.79
Maximum	1.05	13.21	0.82	5.76
Minimum	0.88	7.94	0.68	2.79
Mean	0.98	10.97	0.76	4.58

the mean bloom, mean background, and seasonal mean conditions (Table 12).

Table 4-12 Effects of seasonal changes in female body weight on the grazing impact of *Pseudocalanus* and *Acartia clausi* for the seasonal mean, mean bloom, and mean background conditions in East Sound. The maximum, minimum, and mean estimates for female body weight were determined from the data in Table 11. Daily removals were calculated using the minimum estimate for capture efficiency and then compared to estimates calculated using the theoretical maximum cell capture efficiency. Results were calculated as cells removed/ µg female dry weight/day.

Female Weight (µg)		Capture Efficiency	Daily Grazing Removal		
			Seasonal Mean	Mean Bloom	Mean Background
Pseudocalanus sp.					
Maximum	13.21	0.1936	311	763	39
		1.0	1604	3942	201
Minimum	7.94	0.1936	517	1270	65
		1.0	2669	6558	334
Mean	10.97	0.1936	374	919	47
		1.0	1932	4747	242
Acartia clausi					
Maximum	5.76	0.1350	436	1071	55
		1.0	3230	7936	404
Minimum	2.79	0.1350	910	2212	113
		1.0	6740	16384	834
Mean	4.58	0.1350	548	1347	69
		1.0	4062	9981	508

Discussion

Physical processes generally control the onset of phytoplankton blooms in temperate marine ecosystems via the advection of a seed population into an area, or due to increases in nutrient concentrations (Parsons and Takahashi 1973, Ramont 1980). However, grazers may play an important role in the duration and extent of a phytoplankton bloom (Parsons and Takahashi 1973, Bougis 1976, Walsh 1976, Raymont 1980). Grazing has thus generally been included as an important loss term for the phytoplankton in marine ecosystem models (Steele 1974, Steele and Mullin 1977, Steele and Frost 1978). In East Sound, both physical and biological processes were important in determining the dynamics of the plankton community. The physical data indicated that intrusions of nutrient-rich water occurred prior to each of the primary increases in phytoplankton concentration. Except for this input of new nutrients, presumably from outside the bay, nutrient depletion occurred seasonally, and primarily in surface (0-10 meters) water. The most probable cause for these nutrient pulses was from the advection of channel water into East Sound at the surface due to two extensive storm systems which dominated the local weather patterns at those times. Prevailing winds in the area (generally in an upbay direction from personal observations, and Rattray 1967) were such that significant advection over the sill always accompanied the large storms passing through the area, especially during the spring transition period. These storm-induced intrusions of high nutrient water probably established the conditions necessary for subsequent phytoplankton blooms to develop.

The calculations of stage-specific grazing impact (Table 7 and 8) indicated that, in all cases, the combined removal of cells by the younger developmental stages of Pseudocalanus was theoretically greater than the cell removal by adult females. Grazing removals for the combined copepodite stages (CI-CV) ranged from 1.6 to 2.9 (mean conditions =

2.4) times the removal of the female population during low and high level food conditions, respectively. For Acartia, however, the female population removal was 0.6 to 0.8 (mean conditions = 0.85) times greater than the combined removal of all the copepodite stages. Although at times the relative abundance of the female stages was low, their grazing removal was generally the highest stage-specific rate calculated for both species. On a weight basis, the theoretical maximum grazing removal for Pseudocalanus copepodites was consistently 9.2-9.3 times the daily mean female removal (cells removed/ug dry weight/day). Acartia copepodites theoretically removed 22.1-23.1 times the weight-specific removal of the mean female Acartia. The population of smaller females observed in summer theoretically could have removed twice the number of cells per unit dry weight than the larger individuals present in winter, due both to the seasonal decrease in weight for adult grazers and the increase in average cell concentration. However, this calculation assumed that the maximum filtration rates derived from the laboratory grazing experiments were valid estimates for all sizes of females.

Based on the results from laboratory grazing experiments, the size range of cells available to individuals of these two species overlapped considerably. A lower cell size limit of approximately 2-3 um was apparent for the copepodite stages of Pseudocalanus. Acartia developmental stages effectively grazed the 3-4 or 5 um particles. Acartia individuals also appeared to be slightly more efficient in capturing, or preferred to eat, the larger cells in the diatom distribution as young copepodites. However, Acartia females showed an apparently active selection for intermediate sized cells, possibly reflecting the preconditioning influence of a particle spectrum composed of very abundant but small particles. In this regard, including the size class analyses of the particle spectra of East Sound (Fagerness, in prep.) in the calculation of effective availability

for different cell types will be an important parameter to consider in future analyses of relative grazing impact.

Although the effective availability of small cells to the developmental stages of Acartia was theoretically lower than for Pseudocalanus, the Acartia population maintained itself at equivalent levels during periods of both low (background) and high (bloom) phytoplankton abundances within East Sound. Theoretically, the Acartia population removed a higher percentage of the available standing stock compared to the Pseudocalanus population during bloom conditions, assuming 100% efficiency for cell retention and ingestion, and amounts equivalent to the Pseudocalanus population using the minimum estimate for cell capture efficiency (Table 8). Individual cells of all the major bloom species were within the size range and type of cells eaten by both species. It was also interesting to note that the phytoplankton species succession and monthly periodicity of blooms observed in 1980 were the same patterns recorded 50 years earlier specifically for the phytoplankton in East Sound, and for the Puget Sound region in general (Gran and Thompson 1931, Phifer 1934b).

The smaller developmental stages theoretically might have had difficulty handling the spined diatoms (Chaetoceros) or longer chains (both Thalassionema and Skeletonema) due to the increase in the effective cell size caused by the spines and by chain formation (Schnack 1979, Gifford et al. 1981) relative to the small size of their feeding appendages. The high abundances of Acartia clausi developmental stages present throughout the study period, may be indicative of the development of additional particle selection capabilities observed for females of this species in the present study. That is, the ability to assess differential food quality, and the equivalent efficiency with which a ration was procured over the same size range of cells available to Pseudocalanus, could have allowed Acartia to effectively compete with Pseudocalanus developmental stages. Assuming an allometric

relationship between body size (or weight) and the size and dimensions of the feeding structures (Frost 1972b, Schnack 1982), it is also possible that the smaller animals observed in summer effectively had a wider range (as well as a greater abundance) of cells available to them. These animals may have been able to take advantage of the small cell resource typically abundant as a component in particulate "background" levels, as well as being capable of eating the larger diatom cells. The decrease in body size from winter to summer, and the increase in the number of younger copepodite stages during late spring and summer for both species, may also suggest an increasingly efficient use of the small cell portion of the particle spectrum by the populations of both species.

The populations of Pseudocalanus and Acartia dominated the zooplankton community in East Sound throughout the survey period (83.8% of the total number of calanoid copepods estimated at Station 2 during periods of both high and low phytoplankton abundance). Although not directly measured, differential predation on the zooplankton probably was not a factor in creating the measurable differences in copepod species composition and abundance observed inside and outside the bay. The primary predation pressure from schools of herring and "blooms" of jellyfish and other gelatinous zooplankton which were periodically observed in the bay, occurred at the same time and to the same apparent degree as in channel waters outside East Sound, and throughout much of the Puget Sound region.

The range of values calculated for the grazing impact of these populations indicated that they could have had a significant effect in decimating (using the estimates for maximum grazing removal), or at least modifying the phytoplankton standing stock (using the minimum estimate for grazing removal), although they were probably never in a situation of food limitation. The rate calculations assuming 100% efficiency for cell capture, retention, and ingestion

were probably unrealistically high, since the efficiency estimates calculated from the actual removal of cells in the laboratory grazing experiments (i.e., the species-specific values for EI (1)) were relatively low for both species. The removal rates calculated using the minimum efficiency estimates for cell retention and ingestion indicated the importance of including both the effects of numerically abundant, younger developmental stages, and the effect of seasonal variations in the mean size of grazers, in estimating the full impact of a grazer population on their food resource.

Clearly there are limitations in a study of this kind. one must always be careful when using laboratory-derived estimates for grazing removal to predict the interaction of grazer populations in the field. In this regard, the study must be considered a theoretical treatment of the data. However, recent studies have indicated that ingestion rates in the field may approximate the maximum rates obtained from laboratory grazing experiments during bloom conditions (Poulet 1974, Landry 1981), or when non-food particle interference occurs (Huntley 1982). Also, at this point, data from only a limited number of dates was available for analysis, and thus only the seasonal mean conditions in East Sound could be effectively treated. Although primary production estimates, rather than measurements of standing stock, would have been the more appropriate and perhaps more interesting comparison to make in predicting the dynamic impact of these grazer populations on the phytoplankton community of East Sound, estimates of standing stock have been used in the literature (e.g., Poulet 1974) to indicate the balance between production and consumption in the field. This relationship may be used most appropriately where phytoplankton and zooplankton populations develop together (Raymont 1980). Additional data from gut contents analyses (e.g., Schnack 1975, 1981) would also have been useful in determining the exact nature of the dietary overlap between the different

species and developmental stages, since the presence of a large standing stock for a particular food species may indicate that it is not being eaten.

Since the range of particle sizes eaten by marine copepods is considered to be quite narrow (Raymont 1980), the potential exists for considerable overlap in diets (Mullin 1966, Frost 1972b, Poulet 1974) consumed by animals of very different sizes (Harris 1982). This overlap may result in both intraspecific and interspecific competition for the planktonic food resource, especially during periods of low food abundance, or when the particle spectrum varies rapidly in time or space. Recent models of the dynamics of planktonic systems (e.g., Steele and Frost 1977) have been based upon the assumption that there was a correlation between copepod size and the size of the particles eaten. Traditionally, it has been hypothesized that larger copepods feed more efficiently on larger cells, if for no other reason than the morphological limitations of their feeding apparatus (Parsons et al. 1969, Parsons and LeBrasseur 1970, Frost 1972b, Bougis 1976, Harris 1982).

The basic controversy regarding size selection was addressed by Frost (1972b) in a comparison of the more general, theoretical considerations of Schoener (1971) and the classical theory of size-selection efficiency forwarded by Brooks and Dodson (1967) for freshwater copepods. As applied to copepods, Schoener hypothesized that all grazers were equally specialized (i.e., equally efficient) in capturing cells and attaining a ration from a particular portion of a natural particle spectrum, but that different grazers have become more efficient (i.e., specialized) on different regions of the particle spectrum. Thus, he hypothesized that direct competition for the food resource should only occur at low food densities. Small grazers could outcompete larger grazers under these conditions since the portion of the food spectrum composed of small cells, which numerically dominate the particle spectra of marine systems, would be available to

them. Brooks and Dodson (1967) hypothesized the opposite result of competition at low food densities. Since small cells were equally available to large and small herbivores alike, they hypothesized that the higher ingestion rates and larger size of the feeding appendages characteristic of large herbivores would allow them to be more efficient at procuring a ration from larger cells in the distribution, as well as having small cells available to them as food.

For marine copepods, Parsons et al. (1969) suggested that Calanus growth in the Straits of Georgia was limited by an inadequate food supply during times of low phytoplankton abundance (i.e., below feeding threshold levels, Frost 1972a), and when u-flagellates dominated the particle spectrum, whereas smaller cells were effectively used by Pseudocalanus. Similar results were reported for Pseudocalanus in Saanich Inlet, where it dominated the zooplankton biomass throughout the year (Koeller et al. 1979). Harris (1982) specifically tested the size-efficiency hypothesis for these two species under natural but enclosed conditions (a CEPEX experiment). Although the shapes of the ingestion curves varied between experiments, Harris concluded that even though the body sizes of Pseudocalanus and Calanus differed by an order of magnitude, the range of particles eaten was quite similar. Similar conclusions have been drawn by Richman et al. (1977), Poulet (1978), Gamble (1978), and Cowles (1979), for a variety of marine copepods from coastal to estuarine environments.

In the present study, Pseudocalanus, the larger copepod at all developmental stages, had smaller setule spacings dominating the filter, was able to eat cells of a slightly smaller size in a laboratory mix of particles, and had a higher percent of the total ration coming from the flagellate distribution at all developmental stages, compared to Acartia. However, the Acartia female preferentially selected small cells within the diatom distribution. In addition, the appropriate morphology exists for the capture of individual

particles, as well as for filtering cells, in both species (Conover 1956, Marshall 1973, Corkett and McLaren 1978). The piercing and sucking of very large cells, and the eating of chains in a spaghetti-like motion are apparently capabilities which a variety of copepods have (Conover 1956, Poulet 1974, Alcaraz et al. 1980, Koehl and Strickler 1981). Thus, similar abilities may exist for ingesting very large particles and/or particle chains. These data would suggest that body size does not necessarily correctly predict the size range of types of particles eaten by marine herbivorous copepods.

Temperate marine and coastal environments may be characterized by a variable food resource in both space and time, and with respect to the size, composition and concentration of food particles available to grazers (Sheldon et al. 1972, Poulet 1973, Poulet 1974, Landry 1981). Switching the grazing pressure between peaks of varying relative abundance (Poulet 1974, Richman et al. 1977), or switching between different types of prey (Landry 1981) as they grow and change seasonally (or on shorter time scales, e.g., during bloom conditions), would be an effective mechanism by which an herbivore could maintain a varied food resource (Hilbert et al. 1981, Harris 1982). Whether this response occurs as the result of an active process (Richman et al. 1977, Donaghay 1980b) or is based on as simple an assumption as the differential relative availability of different types or sizes of particles (Poulet 1974, Poulet and Marsot 1980), the effect would appear to be an adaptive response for a grazer living in a food environment which is quasi-unpredictable on a short term basis, but which may be characterized by generally high food abundance on longer time scales.

No single, overiding paradigm for phytoplankton- zooplankton grazing interactions has yet been developed to coherently explain or interpret the massive amount of data regarding the extent of selection capabilities in marine

copepods. The data suggest that a variety of responses exist. It would appear, however, that we have arrived at the point where a synthesis of those data is necessary. We can no longer run laboratory grazing experiments without having a field application in mind. And we can no longer promote the study of copepod feeding behavior without considering at the same time an ecological and evolutionary perspective. Should some brave soul attempt the feat, the overiding consideration should, of course, be that the individual organisms involved in primary and secondary production are inherently co-adapted, just as has been proposed for benthic grazers (Lubchenco and Gaines 1980), and for nutrient-phytoplankton interactions in the sea (Peterson 1975, Walsh 1976, Brand 1981). Marine copepods do behave in the sense that they are able to respond to both physical and biological variables in their environment in more than just a passive manner, and thus remain inordinately attuned to the vagaries of a planktonic existence. We need now only to understand the level of interaction of those variables, at the appropriate time and space scales on which they operate with respect to the lifespan of an individual grazer, in order to synthesize the data into an evolutionary perspective for marine phytoplankton-zooplankton interactions.

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