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PLANKTON PATCHINESS AND ECOSYSTEM STABILITY

University of Hawaii PH.D. 1980

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PLANKTON PATCHINESS AND ECOSYSTEM STABILITY

A Dissertation Submitted to the Graduate Division of
The University of Hawaii in Partial Fulfillment
of the Requirements for the Degree of

DOCTOR OF PHILOSOPHY

IN OCEANOGRAPHY

May 1980

By

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ACKNOWLEDGMENTS

The principal source of funding for this project was U.S. Environmental Protection Agency Contract No. R803983, Kaneohe Bay Sewage Relaxation Study. Dr. Stephen V. Smith, Principal Investigator of that project, was extremely helpful in providing support and encouragement during this work. I also thank Dr. Jed Hirota for his interest, support, and helpful suggestions in the beginning phases of my research. During the experimental work Gerald Akiyama, Christine Baer, Douglas Brittain, and Rudd Turner provided invaluable assistance. I thank my wife, Margaret, for her help in early editions of the manuscript, for her encouragement during the writing and editing phases, and for putting up with it all. Finally, I thank my mother, Ruth Kimmerer, for typing the final copy.

ABSTRACT

Spatial variability in the controlling rate functions of planktonic ecosystems has been hypothesized to add stability or persistence of species. I have determined the spatial variability in three measures of rate functions in the Kaneohe Bay planktonic ecosystem, one indirect and two direct. 1) The indirect measure, copepod stage frequency distribution, showed spatial variation which was transient. Temporal variation, however, was greater than spatial variation. 2) Copepod production:biomass (P:B) ratios were surprisingly uniform; in only one case out of three was there significant spatial variability, apparently caused by food limitation at one station. 3) Egg production rate was more variable both in space and in time. As with stage frequency distribution, the variability did not occur in a fixed pattern, and temporal variability was greater. Thus spatial heterogeneity of rate functions does exist in Kaneohe Bay but may not be as important to the ecosystem as temporal heterogeneity.

To examine the effect on simple ecosystems of mixing between patches, I enclosed parcels of Bay water in 1.3 m^3 tanks and exchanged water daily between two of them. In both experiments the plankton populations underwent drastic shifts in composition, with the copepods starving and being replaced by rotifers. The experimental ecosystems bore little resemblance to the Kaneohe Bay planktonic ecosystem after

only two weeks of incubation. Mixing between tanks did not affect either persistence of species or variability in their abundances. It therefore appears that horizontal spatial heterogeneity may not be important to the stability of planktonic ecosystems.

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CHAPTER I

INTRODUCTION

All ecosystems contain populations whose distribution is patchy. Planktonic populations have patchy distribution on scales from millimeters (e.g. Alldredge 1976; Carpenter et al. 1977; Roman 1978) to thousands of kilometers (e.g. McGowan 1974). The review by Haury et al. (1978) summarizes reports on patchiness at intermediate scales.

A feature as intrinsic to ecosystems as patchiness undoubtedly has great significance both to their structure and function and in the lives of individual organisms. Until recently, investigations of this phenomenon were largely descriptive. Now that the ubiquity of patchiness has been demonstrated, investigators are focusing their attention on its causes and consequences. This dissertation is an attempt to determine whether patchiness is important to the stability of ecosystems. The following sections are intended as an introduction to the literature on the causes and consequences of plankton patchiness and on ecosystem stability. I then discuss various hypotheses about the effects of spatial heterogeneity on stability, and how I approached the question experimentally.

Causes of patchiness

Early work on the causes of planktonic patchiness focused on hypothetical meso-scale (i.e. kilometers) patches of passively drifting phytoplankton growing at a fixed exponential rate. Theoretical work

by Skellam (1951) and Kierstead and Slobodkin (1953) developed the concept of a "critical patch size" necessary for the growth of a patch, analogous to the "critical mass" needed for a nuclear chain reaction. This critical size, deduced from assumed exponential growth rates in and diffusion from such a patch, was on the order of 10 km for reasonable parameter values. An extension of the theory by Wroblewski et al. (1974) included the effects of uniformly distributed grazing, which effectively reduced the realized growth rate of the phytoplankton, thus increasing the critical size.

Recent advances in methods for the collection of large amounts of space- or time-series data on in vivo fluorescence have allowed the examination of variability in fluorescence and, implicitly, phytoplankton biomass through spectral analysis. The use of this technique in plankton research was pioneered by Platt (1972), who showed that the spectrum of variance of fluorescence over time at a fixed station varied as the -5/3 power of the frequency. This is the same relationship predicted for the variance of velocity in a turbulent velocity field vs. wavenumber in the inertial subrange (e.g. Batchelor 1951), that is, a range between those wavenumbers where energy is added to the fluid and those where it is dissipated by molecular viscosity. A similar relationship can be expected for the concentration of a passive contaminant being mixed in such a turbulent field. The relationship of velocity (or concentration) to wavenumber can be extended to frequency space under the "frozen field" hypothesis (e.g. Webster 1969), whereby variance of velocity in space is equated to variance in time for a turbulent field being advected past a fixed point. Platt (1972)

hypothesized that the similarity of the -5/3 power relationship of chlorophyll variance to frequency with that predicted for velocity implied that phytoplankton were behaving as a passive contaminant whose concentration was under purely physical control.

The finding of a -5/3 power relationship may have been fortuitous. Slopes of velocity spectra in the ocean can differ from that value, which is an approximation based on the theory of homogeneous isotropic turbulence (Webster 1969). More recent investigations in which fluorescence has been measured from fixed points or moving ships have shown similar relationships of variance to frequency or wavenumber, but the slopes have varied between -1 and -3 (Powell et al. 1975; Fasham and Pugh 1976; Denman 1976; Denman et al. 1977; Horwood 1978; Lekan and Wilson 1978; Demers et al. 1979). Several of these investigators have also determined simultaneous spectra for temperature and in one case salinity (Lekan and Wilson 1978). Although numerous papers have dealt with theoretical aspects of fluorescence spectra, these have been rather narrowly focused. Denman and Platt (1976) developed a theory of the interaction of phytoplankton growth with the transfer of variance from large wavelengths to small. They claimed that above a critical wavelength analogous to the critical patch size of Skellam (1951) and Kierstead and Slobodkin (1953), the chlorophyll spectrum should have a diminished slope of -1. In this range their theory predicts chlorophyll variance to be controlled by growth rate, while at shorter wavelengths the spectrum is dominated by turbulent motion. They estimated this critical wavelength to be on the order of 1 km. Using a somewhat different approach, Denman et al. (1977)

showed that the slope of the spectrum should decrease through -1 at the critical wavelength and then become positive at longer wavelengths.

Although Platt's (1978) review of the available spectral data is optimistic, most of the data do not fit these hypotheses. The group of chlorophyll spectra presented by Denman (1976) appears to show the predicted break in slope (or "knee"), but he does not show that the chlorophyll spectra differ significantly from those for temperature. In fact, six of the ten chlorophyll spectra shown in his figure 4 (lower) appear to be virtually identical to those for temperature. Horwood's (1978) data show one spectrum with the hypothesized shape and eight without. Fasham (1978) pointed out that the theory which predicts the spectral knee applies only to equilibrium conditions. He claimed that few of the published spectra are from areas where equilibrium might prevail, and that most of these did show the break in slope. On the other hand, Star and Mullin (1979) showed spectra from the Central Pacific gyre that were nearly flat up to a wavelength of about 500 m. Clearly more data are needed to determine whether this knee is a common feature. In a study of large-scale variability around Long Island, Lekan and Wilson (1978) showed similarity between chlorophyll, temperature, and salinity spectra at wavelengths of 5-20 km, but a flatter spectrum for chlorophyll above and below this range. Demers et al. (1979) presented spectra for chlorophyll and temperature in the St. Lawrence estuary in which the slopes of the temperature and fluorescence spectra are similar for half of the series but lower for chlorophyll through most of the range of wavelengths for the other half.

Although the data do not unambiguously support the hypothesis of a critical wavelength, some authors maintain (Demers et al. 1979) that a flattening of the slope of the chlorophyll spectrum implies biological control. Several noteworthy problems with the interpretation of spectral data have been ignored in some of these reports. Most of the data come from inshore areas where chlorophyll and temperature variances tend to be high. In these regions, hypotheses about physical or biological control of chlorophyll variance can be as easily substantiated from the raw data as from spectral analysis. For example, Lekan and Wilson (1978) concluded that statistical analysis shows more small-scale structure in chlorophyll and more large-scale structure in temperature and salinity, but the raw data (Fig. 3, Lekan and Wilson 1978) show that very clearly. Powell et al. (1975) presented a spectrum for chlorophyll which has a peak near 100 meters and then rises sharply at long wavelengths. Although the peak is interesting and suggests a source of variance which may not be obvious from the raw data, the higher wavelength portion of the spectrum could have been expected in a lake with stream outlets (i.e. sources of variance) distributed on a scale of kilometers.

In the studies from more open waters, coherence of chlorophyll and temperature are as likely to indicate the presence of internal waves as horizontal variability (Denman 1976; Fasham and Pugh 1976). Denman (1976) examined this problem in detail by using sensors separated vertically by 3-5 meters. By comparing the ratios of horizontal variance to mean vertical gradients for chlorophyll and temperature, he made a convincing argument that on some of the

transects a significant part of the chlorophyll variance was caused by mechanisms other than internal waves, i.e. patchiness.

Another potential problem with the use of spectral analysis of fluorescence data is that it ignores the biology underlying fluorescence measurements. The variance of fluorescence can be expected to be less than the sum of the variances in abundance of individual species if some of them are negatively correlated with each other (Dickie 1973). Furthermore, relationships among fluorescence, chlorophyll, and plant biomass are complex and poorly understood. Of course, the ability to rapidly collect and process fluorescence data using automatic sensors has prompted this increased interest in the application of spectral analysis to chlorophyll distributions.

The theoretical basis of spectral analysis makes it far more satisfying than earlier ways of looking at the effects of turbulent diffusion on plankton. Spectral analysis takes into account the stochastic, length-dependent nature of turbulent diffusion. Theoretical development to date, though, has suffered from adherence to the concept of a critical length scale. The cause of patchiness is assumed to be an excess of growth over diffusion, and the resulting large-scale spatial variance is believed to cascade down through an inertial (i.e. physically controlled) sub-range of wavenumber space. Sources of variance in plankton abundance, however, have been found or reasonably hypothesized at many length scales. Some of these are predominantly physically controlled; for example:

1. Mixing of water masses containing different concentrations of plankton (Harris and Smith 1977; Pingree 1978).

2. Bursts of upwelling either as part of a coastal or equatorial upwelling system (Beers et al. 1971; Walsh 1976), from the interaction of storms and bottom topography (Walsh 1976), or from vertical mixing in oceanic gyres (McGowan and Hayward 1978; Shulenberger 1978).
3. Eddies shed from oceanic currents (Wiebe et al. 1976; Haury et al. 1978).
4. Fronts (Pingree 1978; Bowman and Iverson 1978; Kimmerer et al. 1980).
5. Breaking internal waves (Haury et al. 1978).
6. Point sources of nutrients such as stream or sewage discharges.

Sources of patchiness which are predominantly of biological origin include:

1. Swarming or schooling of plankton (Clutter 1969).
2. Aggregation near objects such as reefs (Emery 1968; Ziemann 1970; Hamner and Carleton 1979) or in areas of high food concentration (Sameoto 1976).
3. Aggregation to large particles such as appendicularian houses (Alldredge 1976) and the creation of microscale patches of nutrients associated with these particles (Shanks and Trent 1979).
4. Transfer of patchiness between trophic levels such as by:
   a. Creation of "holes" in prey distributions in the manner described by Levin and Paine (1974). This has been documented for predation by schools of anchovy on plankton (J. A. Koslow pers. comm.). The patches of

appendicularians followed by Wyatt (1973) may have been changed into rings by the concentration of predators in their centers.

b. Vertical migration of patches of herbivores (Wroblewski 1977).

Several sources of variance can occur because of interactions between physical and biological mechanisms, including:

1. Aggregation of buoyant or upward-swimming organisms in convergences (Ragotzkie and Bryson 1953), Langmuir cells (Stavn 1971), on windward shores (Baker and Baker 1976; Seliger et al. 1970), or in stagnant areas (Alldredge and Hamner 1980).
2. Interactions of vertical migration with current shear (Riley 1976; Evans 1978; Kullenberg 1978) or internal seiches (Kamykowski 1974).
3. Migration into favorable current systems resulting in maintenance of a species within a region (Hirota 1973; Trinast 1975; Peterson et al. 1979).

A possible additional cause of patchiness is based on the theory of diffusive instability in reacting chemical species (Segel and Jackson 1972; Okubo 1974; Levin and Segel 1976; Segel and Levin 1976). The original formulation of the hypothesis used stability analysis of linearized differential equations describing the relationships of two species and their diffusivities. Under certain conditions a predator-prey system which was stable in the uniform state could be destabilized if the predator diffused or dispersed faster than the prey. Extension

of this theory to include nonlinear effects (Segel and Levin 1976) has shown that the outcome of these instabilities could be a steady but spatially inhomogeneous system. The wavelengths at which this would occur are long, perhaps hundreds of meters to kilometers for planktonic systems. The existence of such a mechanism has not been demonstrated, though, and such a demonstration would be difficult.

All of the actual and possible sources of patchiness would cause peaks and plateaus in a variance spectrum at their respective wave-lengths. Dominant patch sizes in zooplankton have been found on some occasions to be smaller than typical "critical" scales, i.e. tens to hundreds of meters (Fasham et al. 1974; Smith et al. 1976), suggesting small-scale causal mechanisms. The real contribution of spectral analysis is that sources of variance can be identified to a particular length scale and thus possibly to a particular cause. While this has been done in a few cases (Powell et al. 1975; Lekan and Wilson 1978), the search for causes has been sidetracked by a search for confirmation of one theory. Another contribution of spectral analysis is that, by similarity to turbulence theory, hypotheses can be made about the transfer of variance between different length scales. A portion of a fluorescence spectrum with a continuous negative slope around -2 to -3 can be considered an inertial subrange through which variance cascades to very small wavelengths where it is dissipated. Thus one can see that an initial large-scale input of patchiness should result eventually in patchiness at all smaller scales. A predator-prey diffusion-reaction model described by Steele (1974a,b) suggests that variance could also be transferred from smaller to larger scales, thereby flattening the variance spectrum.

Consequences of patchiness

Investigations into the consequences of patchiness have included work on its effects on sampling error and on the uptake rates of individual organisms, and theoretical studies of its effect on ecosystem stability.

The effects of zooplankton patchiness on sampling variability have been investigated in the field by Wiebe and Holland (1968) and Wiebe (1972) and theoretically by Wiebe (1971), although Wiebe's method of determining patch size has been shown to be faulty (Fasham et al. 1974). Venrick (1970) has studied the effect of spatial variability of phytoplankton on sampling error. Wangersky (1974) has shown that variability of particulate organic carbon in bottle samples is increased by occasional trapping of large organic aggregates.

It has been recognized for some time that rates of uptake or feeding on a heterogeneous substrate are not the same as the rates estimated from the average substrate concentration (Williams 1973). Phytoplankton are able to take up nutrients at a rate which greatly exceeds their requirements for those nutrients to sustain maximum growth rate (Caperon 1968; Caperon and Ziemann 1976). Thus they can adjust to time- or space-varying nutrient concentrations and can grow at very low measured concentrations, presumably by taking advantage of short-term or small-scale increases (Caperon and Ziemann 1976). Mean concentrations of food have often been found to be too low to support observed numbers and sizes of feeding organisms (Mullin and Brooks 1970, 1976; Lasker 1975; Brodie et al. 1978), but many such organisms can capitalize on patchiness to enhance their feeding rates.

Whales can apparently detect and feed in patches of zooplankton (Brodie et al. 1978). Lasker (1975) has shown that survival of anchovy larvae depends on their ability to find or remain in chlorophyll maxima. Zooplankton vary in their ability to detect and remain in patches of food (Bainbridge 1953) and to withstand periods of starvation (Mayzaud 1973; Dagg 1977). These abilities may affect their success in a patchy environment (Dagg 1977).

The hypothesis that spatial heterogeneity can stabilize an ecosystem has become a recurring theme in recent literature. Some care is needed to prevent its becoming a dogma filling the niche of the stability-diversity hypothesis. It is nevertheless worth exploring, but some terms require definition first.

Ecosystem stability

The concept of an ecosystem begs an analogy with engineering systems: both have system properties such as capacity (biomass), flux through the system (energy or nutrients), and various kinds of stability. Recent discussion of stability in the ecological literature has been hampered by a lack of consistency of definitions and from carelessness with terms. Stability of an ecosystem has been used to mean: 1) resistance to change (MacArthur 1955); 2) constancy (Holling 1973) or persistence (Smith 1972; Margalef 1969; Hairston et al. 1968); 3) tendency to return or rate of return toward an equilibrium point or trajectory after a small perturbation (May 1973b; Crowley 1977); and even 4) the Shannon-Weaver diversity index (MacArthur 1955).

I will use a set of definitions which closely follows those of Lewontin (1969) and May (1973b). Briefly, there are several distinct kinds of stability, of which I will discuss three:

Structural stability: the ability of the system to withstand changes in parameters such as the number of species. A structurally unstable system when perturbed, as by the addition of a new predator, will collapse into a completely new system.

Neighborhood (also asymptotic, linear, or Lyapunov) stability: the tendency for a system to return toward an equilibrium point when perturbed an arbitrarily small distance away. "Equilibrium" is used here to mean a mathematical steady state in the abundances of interacting elements of the system, rather than a thermodynamic equilibrium.

Global stability: the tendency for a system to remain in a certain region of values of system variables, or to return to a certain trajectory, following a perturbation.

Neighborhood stability is the kind usually referred to in theoretical literature on the stability of ecosystems (e.g. Murdoch and Oaten 1975; Armstrong 1976; Rosenzweig 1971). Stability analyses such as these are interesting theoretically but offer little insight into conditions far from equilibrium. Since ecosystems are away from equilibrium most of the time, neighborhood stability analysis is generally inappropriate (Lewontin 1969). Holling (1973) used the term "resilience" to mean the ability of a system to absorb changes in state variables or forcing functions and still persist. This term

adds no new information, though, provided we use the term "stability" according to the definitions above. For the remainder of this dissertation I will be concerned mainly with global stability, although neighborhood stability analysis will be discussed in connection with some of the theoretical work.

A practical means of measuring the global stability of a real ecosystem has yet to be found. We cannot compare the stability of ecosystems by measuring the variances of their components as, for example, Parsons and Takahashi (1973, p. 132) have done, because the degree of constancy of an ecosystem depends upon its stability, a system property, and the degree of environmental variability, a stochastic forcing function (Crowley 1977). Furthermore, the amplitude and period of fluctuations is a function of the turnover time of the dominant organisms (Davis and van Blaricom 1978). Finally, the degree of variability depends heavily upon whether the measured variable is a species property such as abundance or a community property such as the number of species or diversity (MacArthur and Wilson 1967; C. H. Peterson 1975). Experimentally, the problem of measuring stability is reduced to selection of an appropriate measure of temporal variance or persistence, as an experiment can be so designed that the environmental variability is the same for all treatments.

Ecosystems tend to be persistent; thus we have large-scale biogeographic zones (McGowan 1974) which have persisted for at least as long as people have studied them. The occurrence of many modern planktonic species in Pleistocene sediments (McIntyre and Bé 1967)

implies that some ecosystems may persist over geological time scales. On an ecological time scale, the abundances of organisms averaged over seasonal and other periods tend to remain the same unless system inputs undergo major changes. Such persistence implies that the system's global stability is sufficient to accommodate the normal variability of the environmental forcing functions.

It might be supposed that this sufficient stability of ecosystems arises from the interactions among system components and between these components and external forcing functions. Early attempts to model these interactions mathematically or by experiment, however, led to several anomalous results. First, experiments with predator-prey or competitive interactions in restricted environments often collapsed (Gause 1934; Park 1948; Maly 1975; Luckinbill 1973). Second, mathematical models of species interactions were often unstable (or neutrally stable as in the Lotka-Volterra models) and failed to persist in the presence of added stochasticity (May 1973b; Smith 1972). Finally, the competitive exclusion "principle" became untenable when applied to large groups of apparently resource-limited generalists such as plankton (Hutchinson 1961). This "principle" is really a tautology (Peters 1976) in that the definition of a niche can be expanded until a pair of species no longer competes; thus it is unverifiable. Furthermore, arguments that species do not interfere and therefore do not compete (Hulburt and Horton 1973) are irrelevant for exploitative competition occurring through utilization of a common limiting resource.

Several mechanisms have been identified as potentially destabilizing for ecosystems. Some of these are described below.

Positive feedback of population numbers on growth rate. In the absence of an upper limit such as a carrying capacity, population growth is destabilizing because it is exponential. Thus a population which has invaded a previously open area, grown out of control of a predator, or grown initially faster than a competitor, will continue to grow out of control until some limit is reached (Smith 1972).

Competition. If two species with similar needs for a limiting substrate coexist then the one which has the superior ability to obtain and hold the substrate will eventually drive the other to extinction. Note that no concept of a niche is defined here. The only requirements are that the substrate be limiting and required by both species, that one always be a superior competitor, and that sufficient time be allowed for the interaction to proceed.

Time delays in the response of an organism to changes in its food supply. This can be highly destabilizing in models (Smith 1972; May 1973a) and has been found to operate in simple laboratory systems as well (Caperon 1969; Taylor and Sokal 1976; Maly 1978).

Decreasing feeding or growth efficiency with increasing food concentration. Smith (1972) has shown this to destabilize his models. Although zooplankton apparently do not change their feeding efficiencies (Conover 1968), growth efficiencies of at least some species decrease with increasing food concentration (Harris and Paffenhöfer 1976).

A saturating functional response. Holling (1959) defined the functional response to mean the rate of feeding or nutrient uptake as

a function of food or nutrient concentration. Poulet (1974) and Mayzaud and Poulet (1978) have demonstrated a linear relationship between feeding rates and ambient food concentration for several species of copepods. Short-term experiments in which animals are given food concentrations above and below ambient invariably show saturation above some concentration. The disparity between the long-term variation in feeding rates and the short-term functional response occurs because of a rapid response of the digestive enzymes to the feeding rate (Mayzaud and Poulet 1978). The functional response is more than an experimental artifact (Conover 1978), though, and is of greater relevance to stability analysis.

Functional responses generally fall into three categories as defined by Holling (1959). The Type I response consists of two attached straight line segments, one rising from the origin and the other level (e.g. Frost 1972). The Type II response is similar except that it is a continuous curve, either a rectangular hyperbola or a negative exponential (Ivlev 1961). The Type III response is S-shaped, with a reduced feeding rate at low concentrations. This is equivalent to a Type II response which has been shifted to the right by a feeding threshold below which feeding ceases. Murdoch and Oaten (1975) have developed a criterion for determining whether a particular functional response will be a stabilizing or destabilizing influence on a system. If H is the concentration of food items and F is the functional response, then the interaction is stabilizing if:

$$\frac{\partial F}{\partial H} > \frac{F}{H} \qquad (1)$$

The Type I and II responses fail to satisfy this relationship over any part of their ranges. Either of these responses with a threshold, or a Type III response, can satisfy this inequality for low values of H. Ecosystem models can be very sensitive to the choice of functional response. For example, Steele's (1974c) model required a threshold to prevent collapse, although Landry (1976) pointed out that the model could be stabilized by changing the way in which the top trophic level was removed.

Although Holling (1959) called the Type II the "invertebrate" response and the Type III the "vertebrate" response, there has been some debate over that nomenclature. The kind of response determined in an experiment depends a great deal on experimental design (Frost 1975). Furthermore, the choice of models to fit the feeding data can determine whether a threshold is seen (Mullin et al. 1975; Landry 1976). Detection of a threshold requires careful experimental work; the experiments of Frost (1975) and Fernandez (1979) have shown that the threshold exists for some copepods and nauplii. Whether the feeding threshold is a general phenomenon remains to be seen, but the experimental evidence of Mayzaud and Poulet (1978), Richman (1966), Frost (1972), and Heinbokel (1978), for example, suggest that it is not.

Even if one or more of its trophic links consists of a destabilizing functional response, an ecosystem model is not necessarily unstable. The effect of such a response depends on other terms in the model, including limitations on the lower trophic levels (Levin 1977; Armstrong 1976) and the expression used for mortality in the top trophic level (Landry 1976; Steele 1976).

Potentially stabilizing effects in ecosystems or models are described in the following paragraphs.

Connectance between elements in the food web. The idea that diversity or complexity of ecosystems begat stability arose from a tautological argument by MacArthur (1955). After having become almost an axiom it has fallen into disfavor following attacks by May (1973b), who showed theoretically that increasing random connectance between food web elements did not increase stability. Although it has been argued that "biologically reasonable" connecting links instead of randomly chosen ones would increase stability (deAngelis 1975), there has been no theoretical demonstration that complex systems are inherently more stable than simple ones. Limited experimental data have shown no enhancement of persistence of species from the addition of more species (Hairston et al. 1968; Maly 1975). C. H. Peterson (1975) showed that the proportions of various taxa of benthic infauna in a lagoon with low diversity fluctuated to the same degree as the infauna in a lagoon with high diversity. Finally, the size of the numerical response of hayfield fauna to increased nutrient input was greater in old, diverse fields than in young, less diverse fields (Hurd et al. 1971).

Resource limitation. Rosenzweig (1971, 1972) has shown through graphical analysis of simple predator-prey models that resource limitation should enhance stability. The main effect of resource limitation on a prey species is to lower its abundance into the rising part of the predator's functional response curve. This can reduce the destabilizing effect of a Type I or II functional response or reverse

that effect for a Type III response. Luckinbill (1973) has shown that resource limitation extended the persistence of his predator-prey microcosms. McAllister et al. (1972), on the other hand, found that enrichment had no effect on population fluctuations in a small lake.

Flux through the system. A single-species chemostat is a very stable system because of the resource limitation in the inflow and the density-dependent loss rate in the outflow. Few experiments have been done with multiple species in chemostats, but these can also be stable (Chiao et al. 1977).

Many natural systems may behave in a manner analogous to a chemostat. If the rate of input of a limiting substrate is exogenously controlled, then the total amount of this material in the system will be controlled as well. An example is the euphotic zone of the oligotrophic central oceanic gyre. The rate of input of nitrogen is presumably determined by the rate of entrainment or upwelling of deep water, while the loss rate through sinking of particulate matter or transport by vertical migrators is an increasing function of the biomass present. Thus the total quantity of nitrogenous material in the euphotic zone should be quite stable. This says nothing, of course, about how this material is partitioned among trophic levels, and we still have the problem of understanding the stability of those interactions.

Predator switching. It is possible that switching (Murdoch 1969), whereby a predator preferentially attacks the more abundant prey, could add stability, although mathematical proof is lacking. Switching has been observed in some organisms but not in others; a review of

cases from the literature appears in Murdoch and Oaten (1975). This requires a fairly complex behavior pattern which may explain why it has been found in fishes (Murdoch et al. 1975), although in that case the prey were separated spatially. It is probably less likely to occur among planktonic invertebrates. For example, Mullin (1979) found a predatory copepod not to switch between two alternate prey.

Whether switching can stabilize a model depends on how it is written into the model (Oaten and Murdoch 1975; Steele 1974c). It appears that switching could change the functional response from a Type II to a Type III by removing proportional predation on a given prey at low densities. This seems to be the mechanism by which Holling (1959) found a Type III response to a preferred prey when the alternate food was held constant.

Variation in catchability of a prey. If some prey are more easily caught than others, the resulting functional response should be Type III (Smith, 1972). The effect is similar if an age class of prey is invulnerable (e.g. Mech 1966).

Intraspecific interference. This has been shown theoretically (deAngelis et al. 1975) to be a strongly stabilizing influence. Models which employ a second-order self-limitation term are more stable than otherwise (e.g. Landry 1976).

Temporal heterogeneity. While it may seem paradoxical that temporal variability could add stability to a system, it may enable a competing species to coexist by shifting the competitive advantage among two or more species. Hutchinson (1961) advanced this as a hypothesis to explain the "paradox of the plankton," i.e., the

existence of many species of phytoplankton with apparently overlapping requirements. Little experimental or field evidence on this question has been published. Turpin and Harrison (1979) showed that variability in the rate of nutrient supply to a chemostat could permit coexistence of two species. Silver (1975) showed that Salpa fusiformis swarms only when it co-occurs with a restricted assemblage of diatom species, suggesting that it may be adapted to take advantage of temporal variation in food supply. The data presented by Dagg (1977) also suggest that some copepods are more adapted than others to temporal habitat invariability.

Spatial heterogeneity. This has almost replaced diversity as the explanation of the faithful for ecosystem stability and the coexistence of species. It has received a great deal of theoretical and some experimental attention, but because of the complexity of spatially variant models, results have been mixed.

Possible effects of spatial heterogeneity on stability

Numerous simple model studies have shown that spatial heterogeneity can extend the time to extinction of interacting populations, if not actually stabilize them (e.g. Roff 1974; Allen 1975; Hilborn 1975; Hastings 1977; Gurney and Nisbet 1978). This could occur in real ecosystems by mechanisms which fall into two classes: those that involve fixed spatial heterogeneity of the habitat, and those in which the spatial heterogeneity is transient. The latter class can be seen as an interaction between spatial and temporal heterogeneity. Thus the distinction between variability in space and in time is blurred.

For clarity I will refer to the interaction term as time-varying, transient, or ephemeral spatial heterogeneity, and use "temporal heterogeneity" to mean spatially uniform change in time.

One mechanism by which fixed spatial heterogeneity could stabilize an ecosystem is by smoothing out environmental fluctuations which are uncorrelated in space (Crowley 1977). This model is similar to Margalef's (1967) conceptual model in which plankton patches are likened to gaming tables. The probability of extinction is supposed to be reduced through spreading of the risk, although this would not occur in a truly random environment.

The most obvious and best understood mechanism by which spatial heterogeneity can add stability is the existence of a prey refuge unavailable to predators. In some of the earliest experiments on predator-prey systems, refuges were found to extend the life of an interaction which otherwise collapsed very rapidly (Gause 1934). It also appears to be important in many natural predator-prey systems (e.g. Paine 1974). This mechanism is probably the closest thing to a "carrying capacity" in the sense of the logistic equation model which exists in nature. Sale (1978) has shown that the abundance of reef fish is controlled by the availability of space on the reef. Once a fish has settled into a space its vulnerability to predation becomes very small. Presumably the metamorphosing larvae that cannot find suitable space succumb to predation.

Much of the theoretical and experimental work has concerned dispersal in predator-prey or insect host-parasite systems. The first experimental work to show that dispersal through a complex habitat

would decrease time to extinction of a predator-prey pair was Huffaker's (1958) experiments with mites. Increasing heterogeneity of the habitat increased the time to extinction. Maly (1978) showed that physical complexity of the environment also increased the time to extinction of a ciliate predator and its prey.

Even in a physically homogeneous environment, time to extinction can be increased by enlarging the system relative to the dispersal abilities of the experimental organisms. Luckinbill (1973) showed that the use of a viscous medium increased the time to extinction of the same ciliate predator-prey pair used by Maly. Later experiments with the same organisms showed that increasing container size also prolonged the interaction (Luckinbill 1974). The effect of the volume increase was to slow the rate of decline of prey, as well as to reduce the concentration represented by the last prey individual. Apparently as prey became scarce they also became increasingly difficult for the predators to find or capture.

Theoretical work on dispersal in predator-prey systems has had mixed results, principally because of the variety of ways in which the interaction and the dispersal have been modeled. Allen (1975) has shown that although dispersal or diffusion can extend the duration of such a system, it does not necessarily confer mathematical stability that was otherwise lacking. Huffaker (1958) surmised that the superior dispersal ability of the prey caused the extended persistence in his complex systems. Hilborn (1975) has shown through a simple model that dispersal could be stabilizing but that it did not depend on differential dispersal abilities.

Related to these predator-prey dispersal models is the theory of island biogeography (MacArthur and Wilson 1967). This theory holds that the number of species on an island has a stable equilibrium value that is a function of the extinction rate, which depends on island area, and the immigration rate, a function of distance from other islands and the mainland. The number of individuals of a given species may be highly variable, and it may become extinct on a particular island, but the total number of species remains near the equilibrium value. Although the influence of island area on extinction rate has not been conclusively demonstrated in the field, a number of investigators have supported the theory by showing the influence of island area and distance to other islands on the existing, presumably near equilibrium, numbers of species (e.g. Simberloff 1976). A number of ecological analogs to islands have been found, including flowers (Seifert, 1975), mountaintops (Brown 1971), caves (Culver 1970), and reefs (Brock et al. 1979). In pelagic ecosystems organic aggregates (Alldredge 1976) may function as ecological islands.

Levin and Paine (1974) discussed the role of disturbance in creating spatial heterogeneity. They hypothesized that, in ecosystems such as the rocky intertidal, "holes" are created by the disruption of organisms covering the substratum. These holes permit colonization by other than the dominant competitors. Holes could be created by physical damage from logs or waves (Dayton 1971) or through predation (Paine 1974). This model could be applied to forest fires (Taylor 1973) or to outbreaks of Acanthaster on coral reefs.

Spatial heterogeneity in a planktonic ecosystem could incorporate a combination of these mechanisms, although there is no analog to a fixed refuge in the pelagic ocean. There is variation in the suitability of habitat, particularly in the vertical direction. Animals may use vertical migration to take advantage of this variation by seeking areas of high food concentration at night (Conover, 1968) and low predator abundance by day (Pearre 1973). In the horizontal direction animals may aggregate to convergences such as Langmuir cells (Stavn 1971), where food concentrations are higher than in the surrounding water (Sutcliffe et al. 1971).

In an environment without fixed zones of favorable or unfavorable habitat it would still be possible for heterogeneity to stabilize the system. Richerson et al. (1970) proposed the somewhat misleading term "contemporaneous disequilibrium" to mean spatial variability in rates of growth of phytoplankton species. They suggested, as did Margalef (1967), that this variability could enable many species to coexist by varying their relative rates of success over space. This hypothesis could be extended to include zooplankton. Smith (1972) has suggested that spatial heterogeneity could allow numerous different feeding strategies to meet with spatially varying degrees of success. Thus herbivores feeding by different mechanisms on the same spatially heterogeneous particulate matter would be able to coexist because they would respond differently to the heterogeneity.

Several authors have pointed out that spatial heterogeneity in food supply can have the same effect as a feeding threshold (Landry 1976; Mullin and Brooks 1976). If an animal stays in one area or at

one depth when food is plentiful and moves away when it is scarce, the effect will be an accelerating functional response which satisfies the inequality (equation 1) at low concentrations.

The hypothesis that spatial heterogeneity could stabilize planktonic ecosystems is by no means universally accepted (Steele 1974a,b), and there has been no evidence from the field to support it. The hypothesis of contemporaneous disequilibrium has received some support from Platt and Filion (1973) and Therriault et al. (1978), who showed that phytoplankton productivity indices were spatially variable and that this variability was ephemeral. Landenberger (cited in Murdoch and Oaten 1975) showed that a population of mussels on the pilings of a California pier was maintained by contemporaneous disequilibrium. The mussels on a given piling would go through successional stages of settlement, growth, and eventual destruction by predators or waves. The clumps were all out of phase with one another, so presumably some larvae were available continually.

Obviously more field and experimental evidence is needed. Additional modeling and simulation may continue to shed light on the question of whether spatial heterogeneity can stabilize planktonic ecosystems, but such models have limitations. With a few exceptions (e.g. Segel and Levin 1976; Steele 1976), most ecosystem models which have explicitly pursued questions of stability and spatial variability have used neighborhood stability analysis and therefore linear approximations. Even simple predator-prey models tend to be unstable asymptotically but to exhibit stable limit cycles (May 1972). More complex models may exhibit analogous behavior. They may have "domains

of attraction" (Holling 1973) where the system is globally stable but may not have asymptotically stable equilibria. The most difficult aspect of an ecosystem to model may be the way in which individuals of the top trophic level are removed. For most planktonic ecosystems we do not know the principal predators on the larger zooplankton, their feeding rates, or their numerical responses to changes in food concentration. We also know less than we need for effective modeling of the limitations on the phytoplankton, yet it has been shown that models are very sensitive to that term.

Additional evidence from the field and the laboratory are needed to show:

1. Whether "contemporaneous disequilibrium" is a general phenomenon. The observed patchiness in plankton suggests that rate functions might also be variable, but this might not be so if the plankton are merely passive contaminants undergoing mixing (Platt 1972).
2. Whether spatial heterogeneity arises from small-scale processes within the system or is a result of transfer of variance from longer wavelengths.
3. Whether variability in rate functions can influence the stability of ecosystems as suggested by Margalef (1967) and Richerson et al. (1970).

This research is an attempt to provide partial answers to these questions.

Scope of this research

The planktonic ecosystem of south Kaneohe Bay was chosen as the subject of this research partly for convenience and partly because it has been studied by several previous investigators (e.g. Piyakarnchana 1965; Caperon et al. 1971; Clutter 1973; Krasnick 1973; Bartholomew 1973; W. T. Peterson 1975; Szyper 1978; Szyper et al. 1976; Hirota and Szyper 1976; Smith 1977; Smith et al. 1980). For the duration of this study Kaneohe Bay was the subject of a major research project on the effects of termination of sewage discharge into its southern end. The zooplankton community of south Kaneohe Bay is well defined and has low diversity. The common holoplanktonic metazoa include the chaetognath Sagitta enflata (Piyakarnchana 1976; Szyper 1978) and the appendicularian Oikopleura longicauda (Peterson 1975), and four common microcopepod species (in order of relative abundance): Oithona simplex, Acrocalanus inermis, Oithona nana, and Euterpina acutifrons (Bartholomew 1973). Much of this study concentrated on Acrocalanus inermis, a small (0.7 mm total length) calanoid copepod; the cyclopoid Oithona simplex was also used in some of the studies. Bartholomew (1973) studied the production of A. inermis (he mistakenly identified it as Paracalanus sp.). This species completes its life cycle in about a week.

The hypotheses which this research attempted to test were: 1) that "contemporaneous disequilibrium" is a common phenomenon in Kaneohe Bay; 2) that spatial heterogeneity can arise from small-scale processes within the planktonic ecosystem; 3) that isolated, thoroughly mixed subsamples of the ecosystem possess inherent stability; and

4) that mixing between subsamples of the ecosystem can enhance their stability. The first hypothesis was approached through examination of three measures of system rate functions: a) life stage frequency distribution, an indirect indicator of several rate functions; b) copepod production:biomass or P:B ratios; and c) egg production rates. All three were limited to variability in the horizontal direction only, although it is acknowledged that vertical variability may be much larger. It was expected that in a shallow, usually weakly stratified bay, the horizontal variation would assume greater importance. The rate function preferred for study was P:B. Since this ratio is in part a function of the relative frequencies of development stages, spatial variability in these stage frequencies should give an indirect measure of P:B variation. The stage frequency distributions, however, are also a function of the recent histories of stage-specific growth and mortality rates. Thus a better reason to look at stage frequency distributions is that spatial variability in these distributions implies spatial variability in the stage-specific rates. This is done in the next chapter, using A. inermis and O. simplex.

In Chapter III the hypothesis that P:B ratios of A. inermis are spatially variable is tested by direct measurement of this rate function at two stations. Chapter IV reports tests of a similar hypothesis with respect to egg production rate.

In Chapter V, I report on an attempt to use parcels of Kaneohe Bay water isolated in tanks to test hypotheses 2-4. The isolated parcels of water are subsets of the Bay planktonic ecosystem with at least two important differences: turbulent mixing with the rest of the system is prevented, and large predators are excluded.

CHAPTER II

SPATIAL VARIATION IN STAGE FREQUENCY DISTRIBUTIONS

Introduction

One postulate of the contemporaneous disequilibrium hypothesis (Richerson 1970) is that different parts of a planktonic ecosystem are out of phase with each other. That is, specific rate functions such as P:B ratios and growth or mortality rates are spatially variable even aside from variability in biomass or numbers. Unfortunately, most such rate functions are difficult to measure with sufficient precision to allow the detection of small-scale spatial differences. Variability in ratios of photosynthesis to chlorophyll among several stations has been observed by Platt and Filion (1973) and Therriault et al. (1978), but the corresponding variability in P:B can be inferred only if the carbon:chlorophyll ratio is constant.

Zooplankton rate functions are difficult to measure and the standard errors are usually large. A way of avoiding this difficulty is to measure spatial variability in age frequency distributions. The age structure of a population at a particular time is a manifestation of the recent history of age-specific birth, growth, and mortality rates, and exchange with surrounding populations. A single such measurement is of course insufficient to determine the values of these rate functions. Nevertheless, a spatial series of such age distributions can show whether the cumulative result of all of these functions is spatially variable.

Another reason to measure the spatial variability of the age structure is that the P:B ratio of a population is in part a function of age structure (Zaika 1968). Thus spatial variability in the age structure implies a potential for spatial variability in P:B.

The difference in age structure between two stations will depend on the difference in the controlling rate functions and the amount of mixing between the stations over some previous time period. Therefore the difference in age structure is hypothesized to increase with the distance between the stations and to decrease with the amount of mixing between the stations.

I determined the life stage frequencies of the copepods Acrocalanus inermis and Oithona simplex at stations in south Kaneohe Bay separated by various distances, and repeatedly at a pair of stations under various wind conditions. Although life stage frequency is not identical to age frequency, it could easily be converted, and variation in one implies variation in the other.

Methods

Samples for spatial variability were collected on three dates: July 13, 1976 (experiment 1), January 24, 1977 (experiment 2), and May 13, 1977 (experiment 3). Sampling was done by different methods on each date, as described below. Wind speeds are also reported as an indicator of the degree of turbulent mixing; long-term mean wind speed at Coconut Island is about 5 m/sec.

In experiment 1, samples were taken along a transect between stations OF and SC (see Figs. 1 and 2). Distances between stations

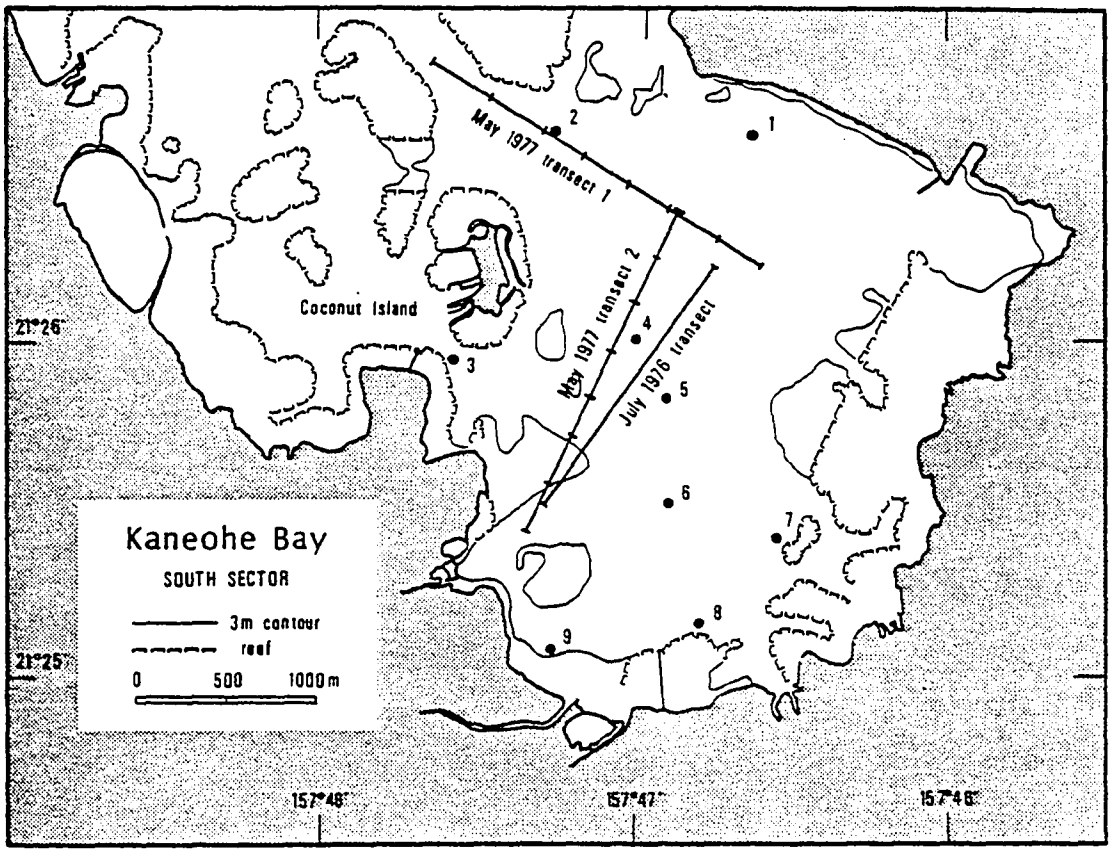


Figure 1. South Kaneohe Bay, showing transects for experiments 1 (July 13, 1976) and 3 (May 13, 1977) and station locations for experiment 2 (January 24, 1977).

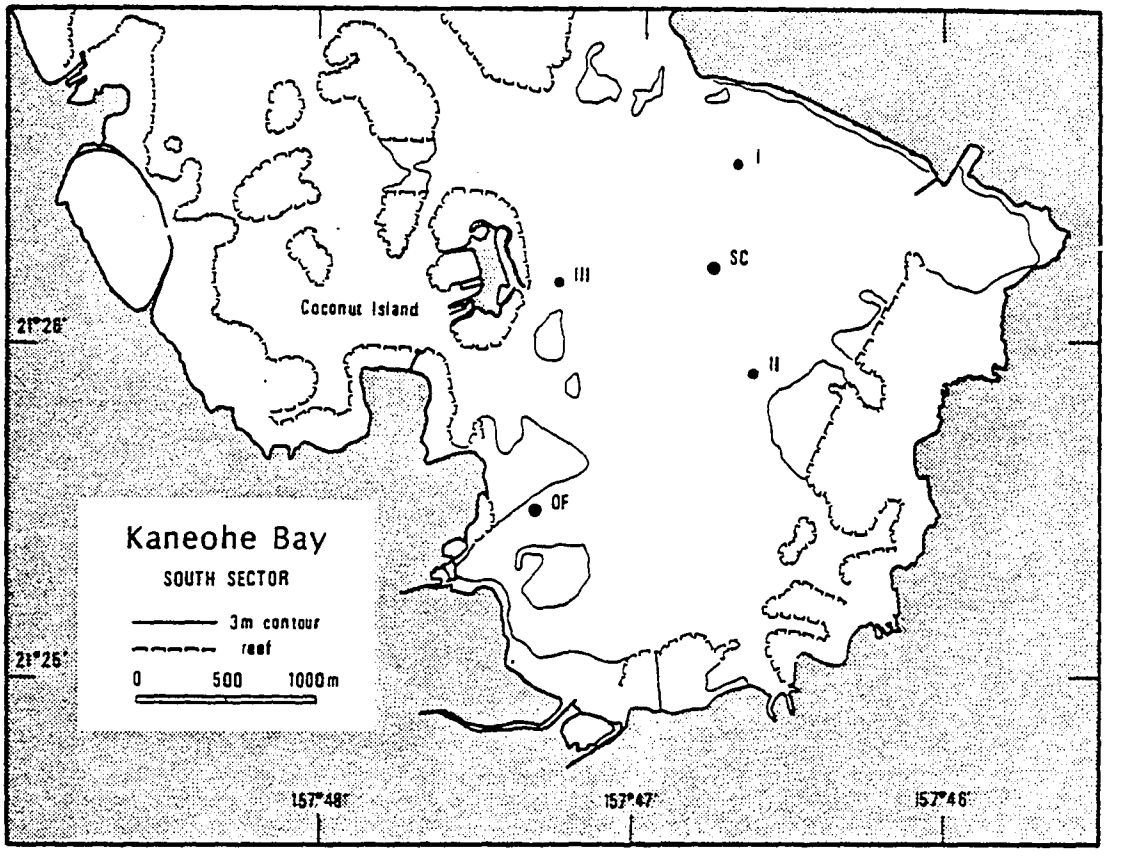


Figure 2. South Kaneohe Bay, showing locations of stations SC and OF and stations I, II, and III used in summer 1979 stage frequency and egg production sampling.

were made approximately equal by running at maximum speed for equal time intervals. Eleven stations at estimated 150 m intervals along the transect were occupied. A submersible bilge pump was used to pump 20-liter water samples from a depth of 3 meters through a 35 μm Nitex screen. The samples were rinsed into vials and placed on ice until arrival at the laboratory, where they were preserved in 2% formalin. The wind on the sampling date was northeast at 7 m/sec.

For experiment 2, nine stations were chosen at random from a grid laid over a chart of the southern Bay (Fig. 1). Positions were determined by using a sextant held horizontally to measure angles between objects of known position. Samples were taken with a 35 μm mesh aperture, 30 cm mouth diameter net towed vertically by hand from 5 meters to the surface, and were preserved immediately in formalin. The wind on that date was southerly at 7 m/sec.

In experiment 3, samples were taken along three transects, two in south Kaneohe Bay (Fig. 1) and one in the central Bay, but samples from the central bay transect had too few animals for adequate stage frequency determination. Positions of the eight stations along each transect were determined with a sextant. Precision of this method of positioning is usually within 20 meters and often as good as 5 meters. Water samples were taken from 2 m depth with a 10 liter Niskin bottle and poured through a 35 μm mesh, the contents of which were preserved immediately. Particle counts on the remaining water were done using a Coulter Counter model TA-II with a 70 μm orifice. The wind was southerly at 4 m/sec.

All samples were stained with Rose Bengal for ease of counting. Copepodite and adult stages of A. inermis and O. simplex, and naupliar stages of A. inermis in experiments 2 and 3, were identified and counted under a dissecting microscope. Because of the similarity of A. inermis naupliar stages NIII-NV, occasional checks on their identification were made by examining them under a compound microscope. A total of 100-600 animals from each sample for each species was counted, usually enough for a mean of 20-60 per stage.

No existing statistical test could be found to test the hypothesis that differences in stage frequencies between stations increase with the distance between stations. Any concordance test would be inapplicable to the data from random stations and would also lose information because it would test only for monotonic increases or decreases in relative abundance of a given stage along a transect. A Monte Carlo or randomization technique was therefore devised.

Counts were first converted to percent frequencies. A dissimilarity index (DI) between each pair of stations was computed as follows:

$$DI_{jk} = \tfrac{1}{2} \sum_{i} (P_{ij} - P_{ik})^2 \quad , j < k$$

where P_{ij} is the percent of stage i in the sample from station j. This is equal to the sum of the variances in the percent frequencies for the two stations. This index was chosen over the usual indices of percent similarity because it emphasizes large differences. Furthermore, the expected value of this index from two samples from the same population is inversely proportional to the total number of animals counted.

The half-matrix of DI_{jk} values was combined with a half-matrix of inter-station distances, and the slope of DI vs. distance was determined by least squares. As the underlying distribution of such a slope was unknown, a Monte Carlo technique was used to test the hypothesis that the slope was greater than 0. Station positions were reassigned in random order and the slope was recalculated for each arrangement. This was repeated at least 1000 times, and the number of these slopes greater than or equal to that from the original data was determined. This was compared with the lower 95% and 99% confidence limits of values for $p = 0.05$ and $p = 0.01$, respectively, determined from the normal approximation to the binomial distribution.

Samples for the effect of mixing on the spatial variability of stage frequency distributions (experiment 4) were taken weekly during the summer of 1979 at test stations separated by 1200 meters (Fig. 2, Stations I and II). A 35 μm mesh, 30 cm mouth diameter net was hauled vertically from 10 m to the surface to collect the samples, which were preserved immediately. A flow meter was used to establish that net efficiency was 68%. Subsamples were taken from a Stempel pipet and stained, and 500-550 A. inermis stages and eggs were counted. Egg counts were not included in the calculations of DI. Wind speeds for the entire period were taken from a WeatherMeasure Model W123-SR-R wind speed and direction recorder located at Coconut Island.

Additional samples were taken semimonthly from February 1976 to August 1978 at stations OF and SC for the Kaneohe Bay sewage diversion study. Vertical tows from 1.5 m off the bottom (i.e. from 12.5 m at station SC and 7.5 m at OF) to the surface were taken with a double

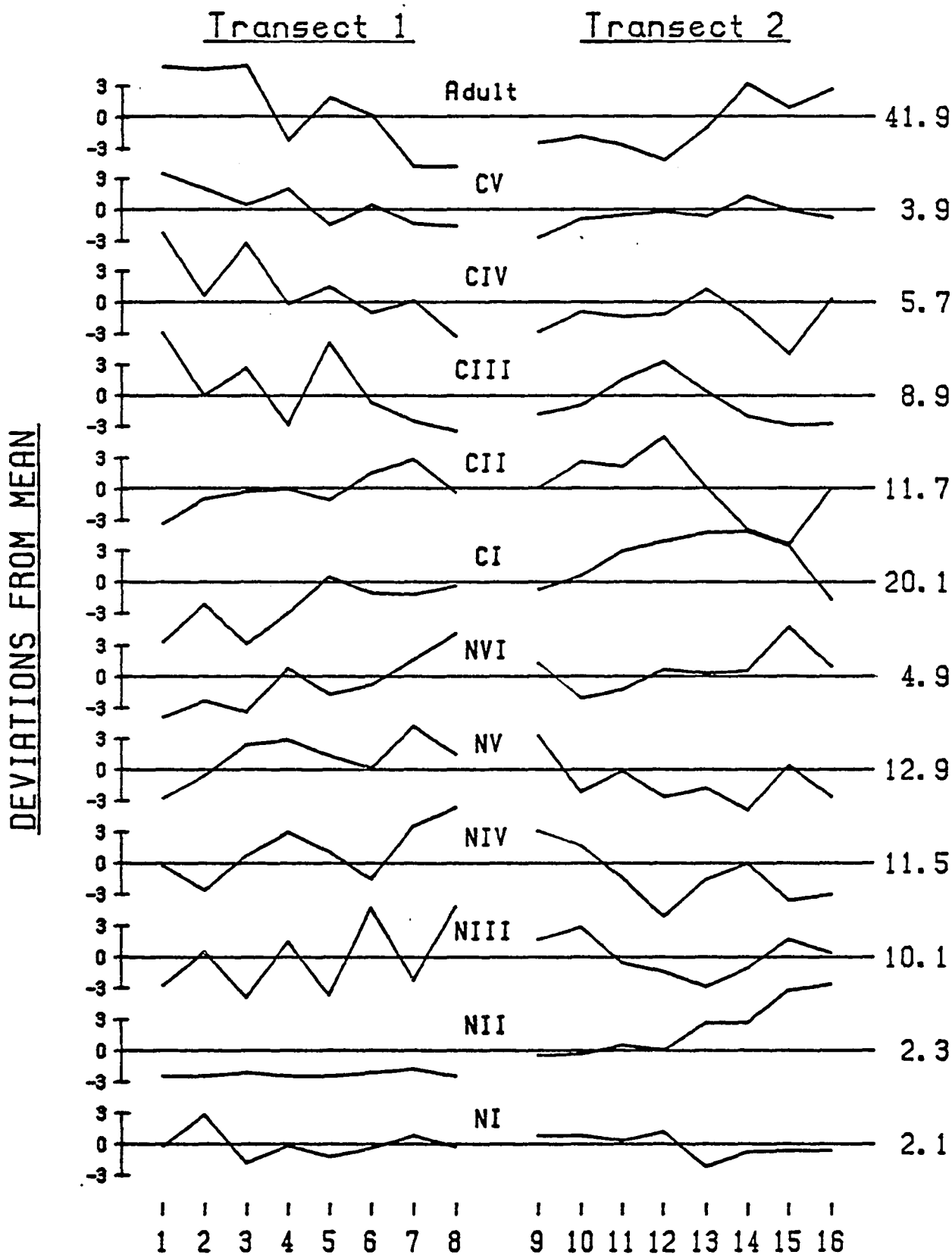
frame net similar to a bongo net (Clutter 1973). One side of the net frame had a 333 μm mesh net attached, while the other side had a 333 μm inner net and a 35 μm outer net. The samples taken with the 35 μm net were subsampled with a plankton splitter and a Stempel pipet. Aliquots were stained and several hundred total zooplankton were counted. The data used for this study consisted of counts of A. inermis and O. simplex divided into early (CI-CII) and late (CIII-CV) copepodite stages and adults.

Results

The percentage abundances of each stage from experiment 3 are shown for A. inermis in Figure 3 and for O. simplex in Figure 4, with the stations ordered from north to south. Trends are apparent for several stages, particularly for the adults and early copepodites of O. simplex. The trends for A. inermis stage I copepodites and adults were similar to those for O. simplex on transect 1 but not on transect 2. Absolute total abundances of both species increased from north to south along transect 1 only. Particle count data (not shown) bore no relationship to either the total abundance or relative abundance of any stage. Percentage frequency data from all sampling dates are shown in Appendix A. North-south trends in relative abundance of O. simplex early copepodites and adults can be seen in the data from experiment 2 but not from experiment 1, and no such trend can be seen in the data for A. inermis from either experiment.

Figures 5 and 6 show the relationship to distance for the transects of experiment 3. As could be expected from the relative abundances, DI increased with distance between stations.

Figure 3. Percentage abundance of A. inermis stages along the two transects in experiment 3. Each value is shown as the deviation from the mean percentage abundance for the two transects. The means are shown at the right of the X axes. Station 1 is the furthest north, and 16 the furthest south.


Transect 1
Transect 2
DEVIATIONS FROM MEAN
Adult
CV
CIV
CIII
CII
CI
NVI
NV
NIV
NIII
NII
NI
3
0
-3
41.9
3.9
5.7
8.9
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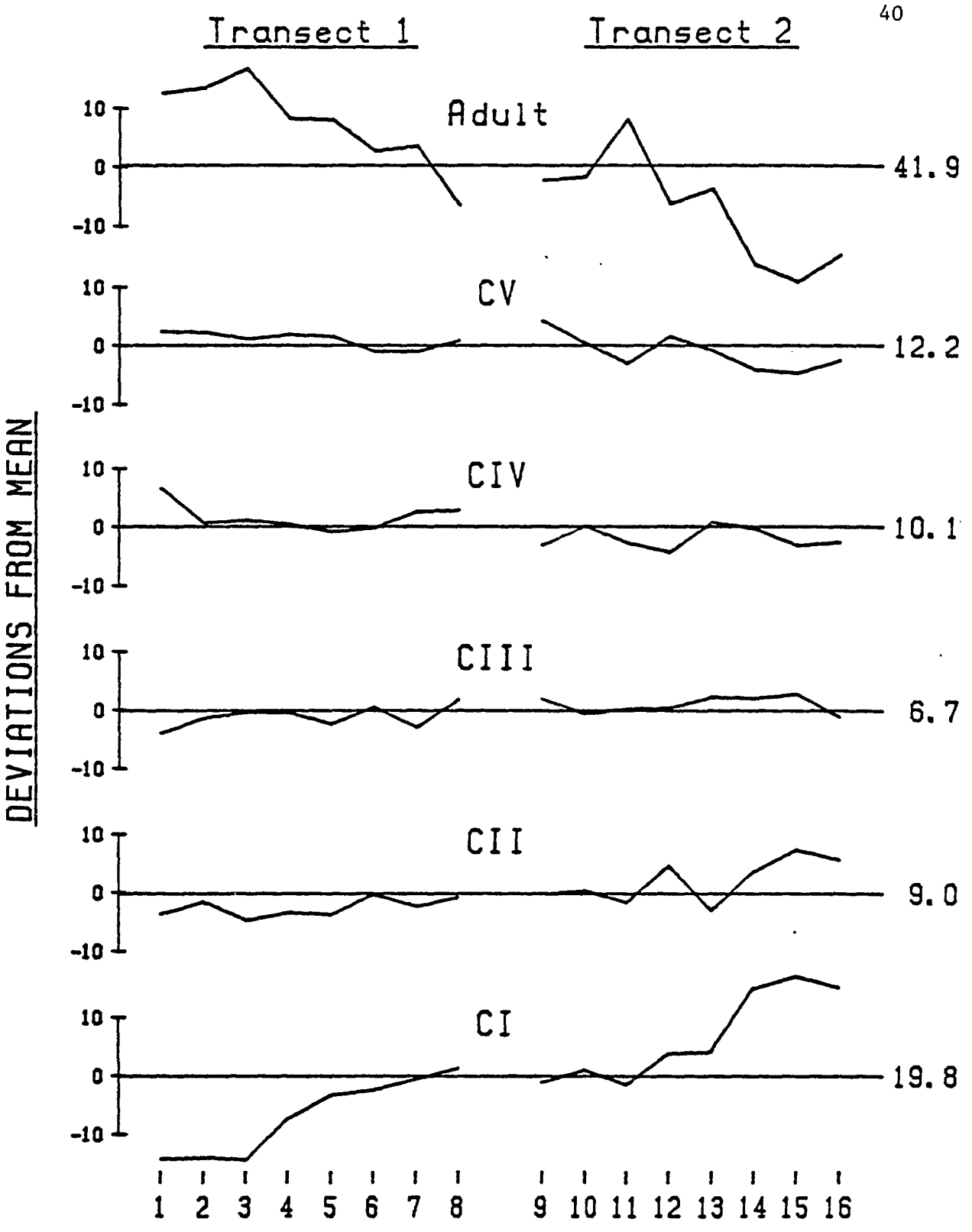


Figure 4. As in Figure 3, but for O. simplex copepodites and adults.

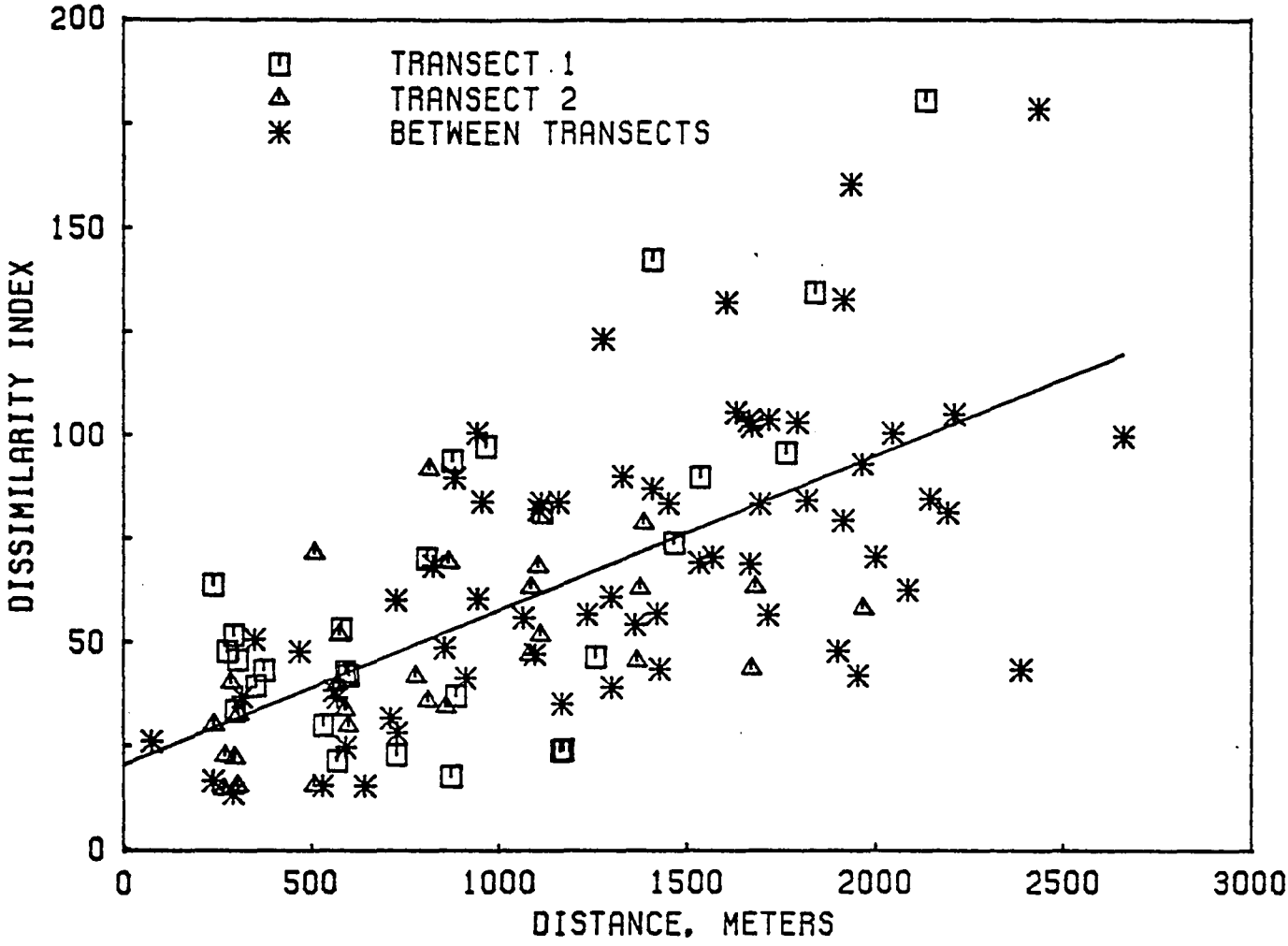


Figure 5. A. inermis dissimilarity index vs. distance between pairs of stations for the data shown in Figure 3. The line, fitted by least squares to all points, has a slope of .037.

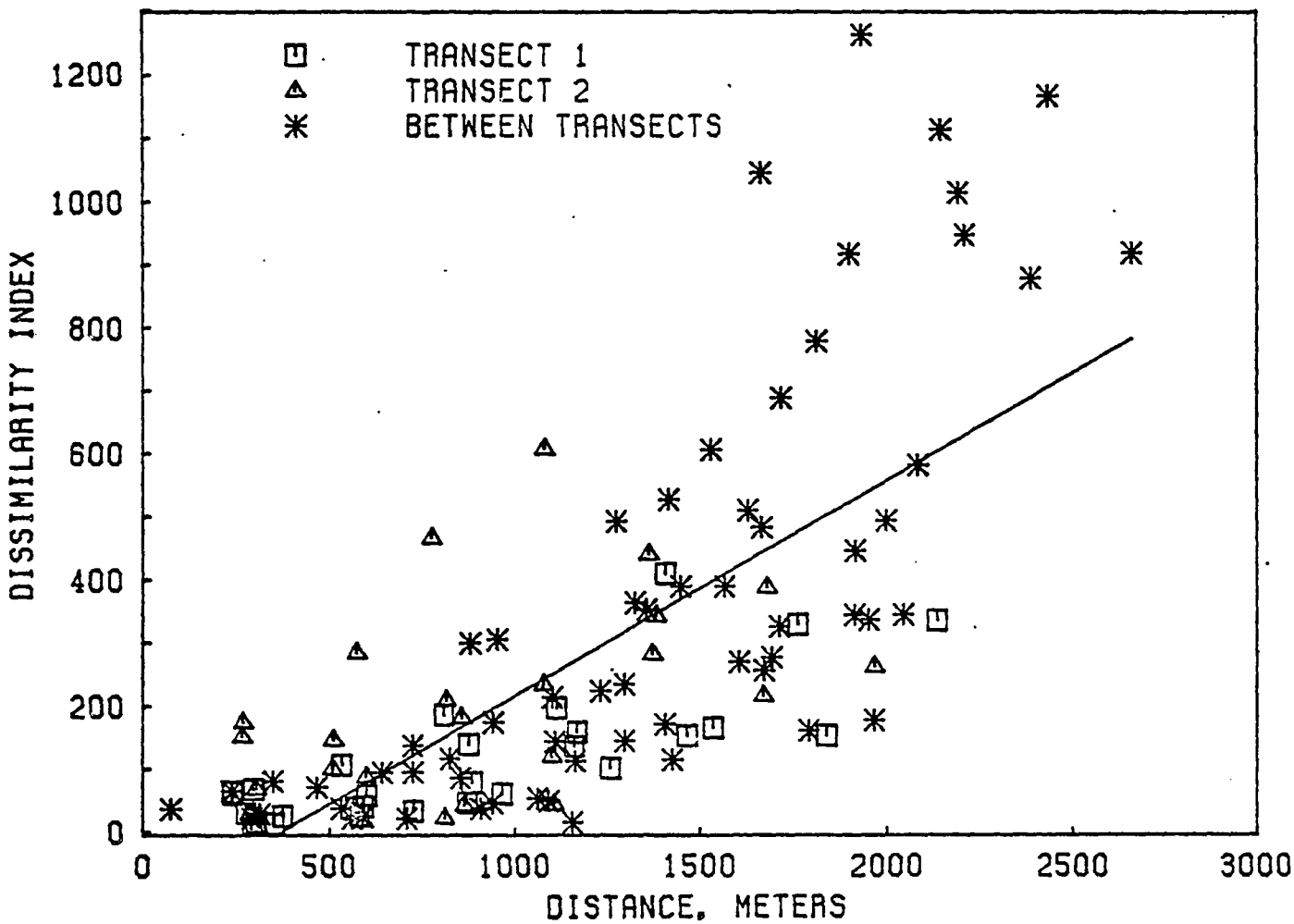


Figure 6. O. simplex dissimilarity index vs. distance between pairs of stations for the data shown in Figure 4. The line, fitted by least squares to all points, has a slope of .342.

An example of the distribution of slopes from random orderings of the stations is shown in Figure 7 for the data for A. inermis in experiment 1. Note that only the copepodite and adult stages were included. All of the distributions had this positively skewed shape. One hundred forty-one of the 3000 slopes, or 4.7%, were at least as great as that determined from the data. For this case the test was repeated to get a total of 6000 random slopes, of which 269 were greater than or equal to the original value. The expected number of values on this tail of the distribution for $p = 0.05$ is 300, with a standard deviation of 17; the lower 95% confidence limit of this value is 272, so the null hypothesis is rejected at $p = 0.05$. Table 1 shows the slopes and the results of all such tests for all sets of samples. The null hypothesis was rejected at $p = 0.05$ or less in every case except for A. inermis in experiment 2.

To determine whether there were any fixed trends in relative abundance of stages, the long-term counts of early and late copepodite and adult stages from stations OF and SC were converted to percentages and the differences between those stations were computed. Only the early copepodites of O. simplex had a significant difference ($p < 0.05$, t-test), and that difference indicated that the early copepodite stages were less abundant at OF than at SC.

From the data of experiment 4 the values of DI for A. inermis were calculated for each date and the correlation coefficient between DI and wind speed was calculated. The correlation with the wind speed on the sampling date was not significant ($p < 0.05$), but DI had a significant

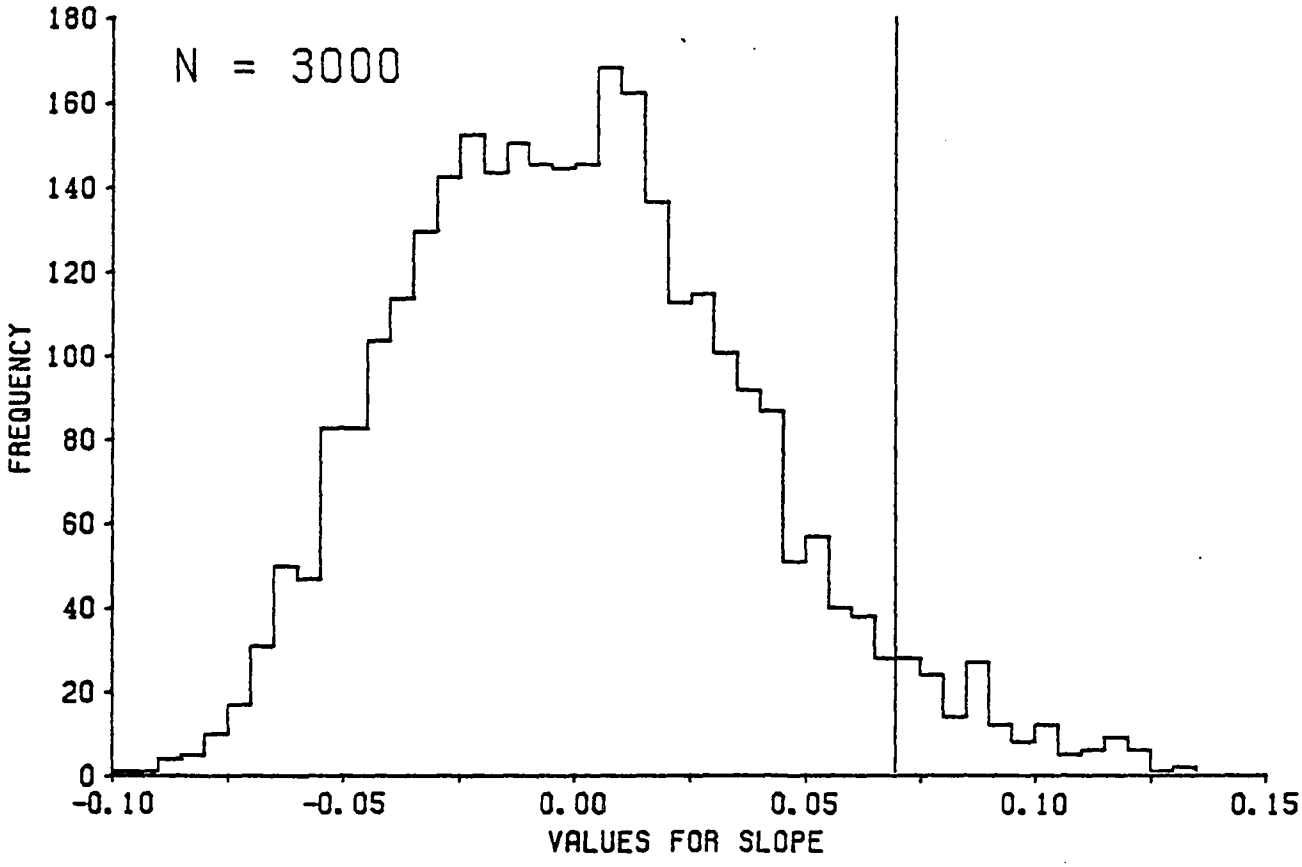


Figure 7. Distribution of 3000 random slopes of DI vs. distance for A. inermis in experiment 1. The vertical line shows the position of the value determined from the original data.

TABLE 1. Results of stage frequency sampling with Monte Carlo simulation tests for significance of slope. Slopes of DI vs. distance for both species and each sampling date are shown with the number of Monte Carlo trials (N), the number of trials in which the observed slope was equaled or exceeded (N≥), and the estimated P value.

Experiment	Date	Species	Slope	N	N≥	p
1	July 13, 1976	A. inermis	0.070	10000	462	<0.05
		O. simplex	.067	1000	13	< .05
2	Jan. 24, 1977	A. inermis	.021	5068	674	> .10
		O. simplex	.291	1000	0	< .01
3	May 13, 1977					
	Transect 1	A. inermis	.053	1700	7	< .01
	Transect 2	A. inermis	.024	2000	8	< .01
	Both transects	A. inermis	.037	1000	0	< .01
	May 13, 1977					
	Transect 1	O. simplex	.155	1000	1	< .01
	Transect 2	O. simplex	.176	2000	44	< .05
	Both transects	O. simplex	0.342	2000	0	<0.01

negative correlation with the wind speeds of the previous two days ($r = -0.59$ for one day lag, -0.58 for two days, $p = 0.02$). Figure 8 shows the relationship of DI to the previous day's wind speed.

Discussion

Several previous authors have documented spatial variability in stage frequencies of copepods. Mullin and Brooks (1976) showed that life stages of *Calanus pacificus* were spatially variable over distances of kilometers, although they did not attempt to relate the differences to the distances between stations. Barlow (1955) and Heinle (1966) showed abundances of *Acartia tonsa* stages in two estuaries to shift toward the adults in samples taken further downstream. Thus recruitment was occurring further upstream in these estuaries, presumably because it was favored by low salinity. A similar situation existed for *O. simplex* on two of the three sampling dates; that is, the adults were relatively more abundant in samples taken away from the sources of fresh water. Kaneohe Bay is, however, a weakly developed estuary with salinities at OF usually only slightly below those at SC (Kimmerer et al. 1980). Furthermore, the longer-term data show that the mean differences in relative abundance of adults between stations OF and SC was not significant. Thus the observed gradients in relative abundance of *O. simplex* adults were transient, and could have been caused in some way by the southerly winds on both of those dates.

The apparently increasing slope of DI vs. distance seen in Fig. 6 arises from the use of a second-order dissimilarity measure with the

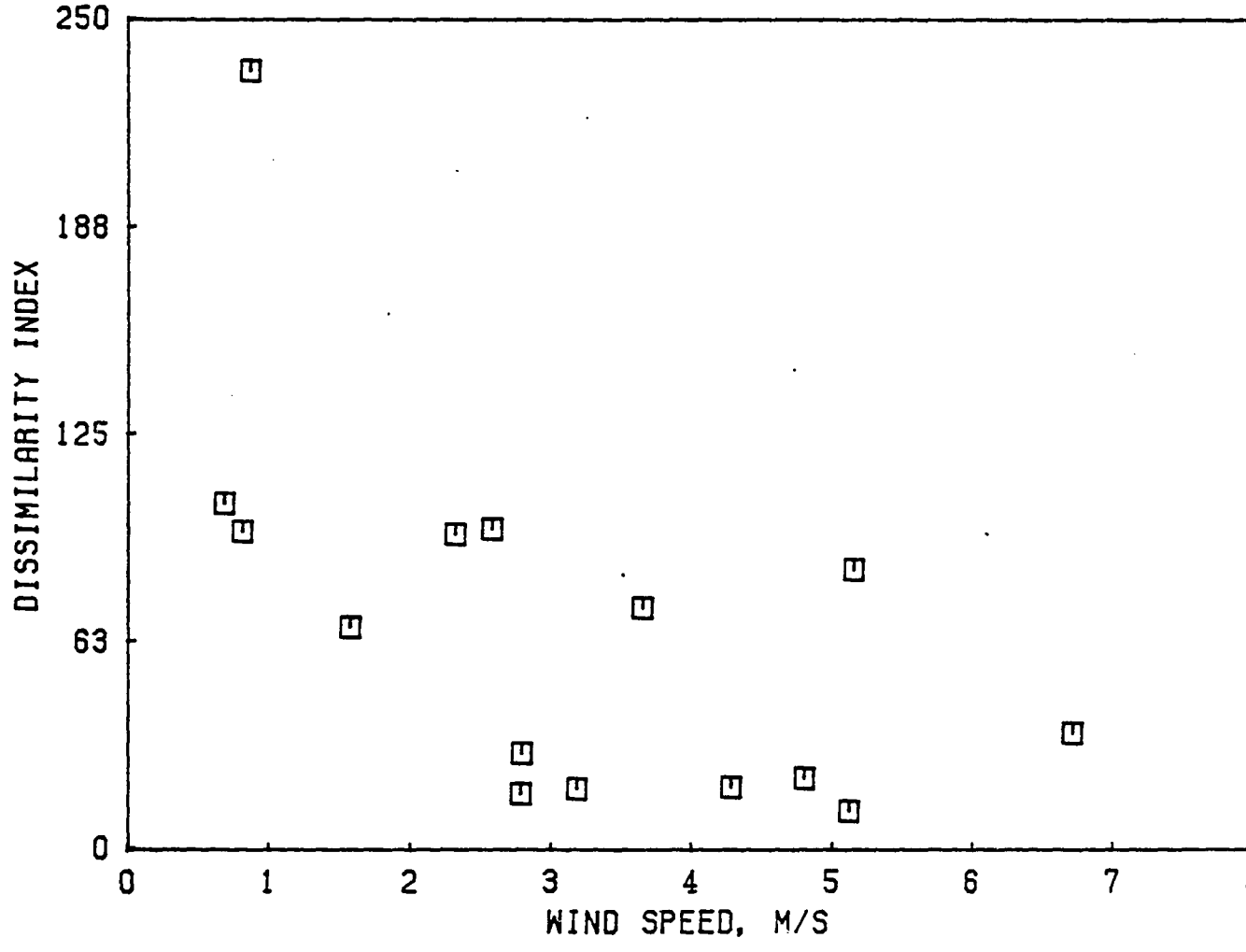


Figure 8. Relationship of DI between stations I and II to previous day's wind speed, for A. inermis, summer 1979.

nearly linear change in relative abundances of the early copepodite and adult stages of O. simplex along the transects (Fig. 4). The calculation of a linear slope of DI vs. distance does not represent the actual relationship, which would have a second-order term in this case. The use of the linear function, though, does not alter the results of the test of significance of the slope.

The significant negative relationship of wind speed over the previous two days to DI suggests that wind-driven mixing acts to remove spatial variability. This was found also to be true for spatial variability in phytoplankton P:B by Therriault et al. (1978). Kullenberg (1978) has stated that the interaction of vertical mixing and wind-driven shear is the predominant mode of horizontal mixing in the ocean for distances up to 10 km. This should be true in Kaneohe Bay, where winds are often strong and the tidal amplitude is only 0.9 m at the most. No effect of variation in tidal amplitude on DI was seen.

There appears to be no critical scale beyond which the stage frequencies diverge from each other, at least in the 150 m to 3 km range observed. This contrasts with the work of Platt and his co-workers (e.g. Platt 1978), who claim that a critical length scale exists below which patchiness is controlled by turbulence and above which it is controlled by biological activity. Although the data on stage frequencies are not directly comparable to data on phytoplankton patchiness, there should be some coupling between the phytoplankton and herbivores. The increase in DI with distance can be interpreted instead as a result of spatial variability in rate functions at all

scales, mitigated by turbulent diffusion. Thus the mosaic of rate functions can be considered analogous to the variability seen in the diversity of the deep-sea benthos (Jumars 1976; Thistle 1976), which occurs at all length scales.

The rate functions controlling stage frequencies are stage-specific birth, growth, and death rates, and possibly the interaction of wind drift with stage-specific depth distributions. These can all be expected to vary spatially. Birth and growth rates depend largely upon the availability and quality of food which in turn depends at least upon nutrient input, light, wind, and consumption by all grazers. Stage-specific death rates depend upon predator abundance, itself a function of the abundance of alternate prey and of higher-order predators. Temporal variability of all of these rate functions is likely to exceed spatial variability, since forcing functions such as wind affect the entire ecosystem. The result of this can be seen in the higher variability of stage frequencies between dates than between stations on the same date. For the summer 1979 data the mean DI between dates was 235 and that between stations only 67.

Spatial variability in rate functions is apparently a transient phenomenon. The long-term data from stations OF and SC showed that only for O. simplex early copepodites was there a fixed difference between these stations. When trade winds are blowing (about 85% of the time) station OF has substantially higher concentrations of particulate matter and chlorophyll than does SC (Kimmerer et al. 1980). This implies that under these conditions, food is not likely to limit the birth and growth rates of these copepods. Food limitation

may occur under calm conditions, though, when the total concentration of particulate matter in the water decreases. In either case, the spatial variability in rate functions is not caused by fixed environmental gradients, and similar variability would be expected in more open bodies of water.

CHAPTER III

SECONDARY PRODUCTION

Introduction

Specific production or P:B ratio of a population is the ratio of biomass produced during an interval to the mean biomass during that interval (Zaika 1973). Production includes biomass gained by the population through somatic growth and reproduction plus biomass gained and then lost to the population through mortality and the production of exuviae.

Zaika (1968) has shown that the P:B ratio of a population of zooplankton is a function of the population's age distribution. A population with mostly younger stages, which grow more rapidly than older animals, can be expected to have a higher P:B ratio than one with an even age distribution or one composed mainly of older stages. As the age distribution of copepods in Kaneohe Bay is spatially variable, we could infer variability in P:B; however, P:B ratio is also a function of food concentration and temperature, so to examine spatial variation in P:B it is preferable to actually measure P:B at two or more locations. The hypothesis tested here is that P:B ratios of populations of the copepod *Acrocalanus inermis* are variable over a distance of about 2 kilometers.

Production in zooplankton is usually estimated through demographic methods. For multivoltine populations with a large size

range such as tropical and subtropical crustaceans, variations on two basic methods are used. The first estimates production as yield to higher trophic levels and decomposers. In this method turnover time, the inverse of P:B, is estimated from instantaneous stage-specific mortality rates; these are calculated from field data on population stage structure and experimental data on development times per stage (e.g. Heinle 1966). Production is calculated as the sum of the stage biomasses divided by the turnover times. The second method estimates production as the sum of stage-specific growth rates. These are determined from biomass per stage and stage development times under various assumptions about rates of mortality and growth between stages (e.g. Mullin and Brooks 1970; Fager 1973). Bartholomew (1973) used a variation on this method to estimate production of A. inermis in Kaneohe Bay, although he used finite growth and mortality rates in his calculations instead of instantaneous rates.

Both of the basic methods require that certain assumptions be met, including balanced gain and loss of stages through advection and turbulent diffusion. Prepas and Rigler (1978) showed that these assumptions are not met in populations of cladocerans in a small lake; in fact, they showed considerable spatial variability in instantaneous mortality rates. Clearly the demographic methods of measuring production are inadequate for detection of spatial variability of P:B ratios in populations whose age structures vary spatially and which are subjected to advection and diffusion.

Several alternative methods of estimating production have appeared in the literature. In one group of methods, which Winberg (1971) calls

the "physiological approach," production is determined from the difference between assimilation and excretion plus respiration. Physiological methods usually involve the use of a constant value for gross growth efficiency and the calculation of metabolic losses from weights per stage. Such methods have been applied to total tropical zooplankton (e.g. Vinogradov et al. 1977, LeBorgne 1977) but are clearly inapplicable to the detection of variation in P:B over short distances.

Another method was used by Barlow (1955) in estimating the rate of production of numbers of the copepod Acartia tonsa in a tidal estuary. He incubated copepods in 20-liter bottles at natural concentrations of all stages for 2-3 days and estimated production from the gain in numbers during the time interval. Although this is production of numbers, not biomass, it could be converted to biomass production by the use of the mean biomass of nauplii and copepodites. Barlow's experimental results compared well with replacement rates needed to balance estimated losses from the estuary through flushing.

The method used here is an extension of that used by Barlow: copepods were incubated in bottles and the production rate was determined as the rate of gain in total biomass. Three experiments, S1 to S3, were conducted to determine spatial variability between two stations. Additional P:B experiments were conducted to assess the method: two were time series incubations (T1 and T2) and two were done to test for effects of crowding and container size (C1 and C2). Several other experiments were done to determine biomass per stage and to validate the method used to determine total A. inermis biomass in the samples.

Methods

Samples were taken at two stations in south Kaneohe Bay (OF and SC in Fig. 2). For preliminary work to develop the method, samples were taken from SC only.

Plankton gauze of several mesh sizes was used to fractionate the samples. These mesh sizes retain experimental animals as shown in Table 2.

TABLE 2. Mesh apertures of plankton gauze used in P:B and egg production experiments, and stages of *A. inermis* retained by each.

Mesh aperture (μm)	Stages retained
333	None
200	Copepodite V-adult
183	Copepodite IV-adult
100	Some nauplius V and VI, most copepodite I, all larger stages
35	Most eggs, nauplius I and II, all larger stages

Animals were collected in surface water dipped up with a bucket and screened through a 333 μm Nitex mesh to remove large predators, notably the abundant chaetognath *Sagitta enflata*. In some experiments animals were concentrated 2- to 4-fold by gently filtering the water with a 35 μm Nitex mesh using upward (reverse) flow to prevent damage to the organisms. Aliquots of 3.8 liters each were poured into 4-liter beakers for zero-time samples and 4-liter bottles for incubation. All glassware had been rinsed with hydrochloric acid

and deionized water, and with experimental water just before being filled. Bottles were suspended about 1 meter below a string of floats on the lee side of Coconut Island for incubation of 22-40 hours.

Biomass of the zero-time samples, and of the experimental samples after incubation, was determined in part by direct measurement of particulate carbon content and in part by counting stages. First each sample was gently concentrated using reverse flow through a 100 μm mesh. After the sample had been rinsed twice with filtered seawater, the larger fraction was placed in a beaker with 500-800 ml of filtered seawater and enough neutral red stain to make the concentration 1-2 mg/l. The stain was added to make the animals more readily visible and so that dead animals could be identified (Crippen and Perrier 1974). The stained animals were incubated for 45 minutes, during which time they received no food and presumably cleared their guts. After incubation, each sample was concentrated to 50-100 ml and refrigerated; in experiments conducted before October 1977 the animals were killed by bubbling carbon dioxide through the sample. Filtrate from all of the screenings was passed through a 35 μm mesh to recover the animals that had passed through the 100 μm mesh. Occasional examinations of the <35 μm filtrate showed that all stages of A. inermis were retained.

On one occasion particle counts were done with a Coulter Counter Model TA-II, using a 70 μm orifice, on the <35 μm water from several bottles. Counts were also done on water from two control bottles which had been screened at 35 μm before incubation.

Chilled samples containing the larger fraction were examined under a dissecting microscope, and post-naupliar stages of A. inermis were removed with a fine-tipped pipet and transferred to a petri dish. All detrital and plant particles and other organisms were removed, and the copepods were transferred to a precombusted glass-fiber filter that had been cut into quarters to reduce the carbon blank. The filter was rinsed with about 1 ml of deionized water, sucked dry, and dried at 60°C for 24-48 hours. Carbon and nitrogen were determined using a Hewlett-Packard Model 185B CHN Analyzer. A master calibration of the instrument was established using 14 blanks and 23 standards (cyclohexanone-2,4-dinitrophenylhydrazone), with most of the standards having carbon contents in the range of values expected from the experimental samples. The calibration was rechecked for every set of samples.

The remaining material in the tray was combined with the smaller fraction of the original sample and preserved for counting; this fraction contained all nauplii and those copepodites and adults which had either passed through the 100 μm mesh, had been missed in the pipeting procedure, or had not taken up the stain. The latter were considered to have died during handling or incubation and were counted separately to enable an estimate of handling mortality to be made. All of the copepodites and adults were counted, along with nauplii in either the entire sample or in a 1/2 or 1/4 aliquot. Estimates of carbon per stage were used to obtain a correction which was added to the carbon from CHN analysis to get total biomass in the sample.

In order to determine carbon per stage of the copepodites and adults, these stages were pipeted out of freshly caught samples of bay plankton. Twenty-five to 300 individuals were concentrated in a drop of filtered seawater, briefly dipped in deionized water, and transferred to an aluminum CHN boat. Carbon per sample was determined as above. Measurements of 10 animals of each stage were made using a dissecting microscope with an ocular micrometer, and volumes were estimated from cephalothorax and abdomen length and width, assuming the shape to be a prolate spheroid and the abdomen to be cylindrical.

Several samples of nauplius stages IV to VI and one sample of 1200 nauplius stage I, obtained by raising them from eggs, were treated as above for CHN analysis. Volumes of naupliar stages III-VI were determined on lab-reared animals by the use of a Coulter Counter Model TA-II with a 400 μm orifice. Animal volume was determined from the calibration setting needed to make equal numbers of nauplii fall into adjacent channels. The volume of nauplius stage I was estimated by measuring the dimensions using a compound microscope with an ocular micrometer, assuming its shape to be an oblate spheroid. Carbon content of each naupliar stage was determined by use of the carbon/-volume ratio obtained for stages IV to VI. Carbon content was assumed to be constant during development from egg to NII. Microscopic examination of these naupliar stages revealed no evidence of feeding appendages or guts in these stages so it is assumed that they do not feed; the first two stages of some other calanoids also do not feed (Mullin and Brooks 1970).

Specific production was calculated as the rate of increase of ln(B), where B is the total A. inermis biomass per liter. The production lost as molts was neglected. For most experiments the specific production was calculated as the slope of a straight line fitted by least squares to the data of ln(B) vs. time. For experiments designed to test the effects of container size (see Results) the specific production was calculated as

$$\ln(B/B_0)/\Delta t$$

where B_0 was the mean of 2 or 3 initial samples, and B the biomass of each sample after incubation.

Results

Copepodite and adult body carbon content was related to cephalothorax length through a power function with an exponent of 3.4 for the females (Fig. 9). This is greater than 3 because the earlier stages have a lower ratio of width to length. A comparison of body carbon with volume estimated from the dimensions of the cephalothorax (Table 3) shows that the ratio of carbon to volume has a median of 0.12, and a range of 0.09-0.14 μg $C/10^6$ μm^3.

The volume and carbon content of the sixth naupliar stage (NVI) overlapped with those of the first copepodite stage (CI). Carbon per unit volume measured for stages NV and NVI was 0.12 μg $C/10^6$ μm^3, the same as the median of the copepodite stages, while in stage NIV it was 0.09. Carbon per unit volume measured for NI was 0.16 μg $C/10^6$ μm^3. Eggs of the closely related Paracalanus parvus contain 0.022 μg C in a diameter of 74 μm (D. Checkley pers. comm.); the resulting carbon

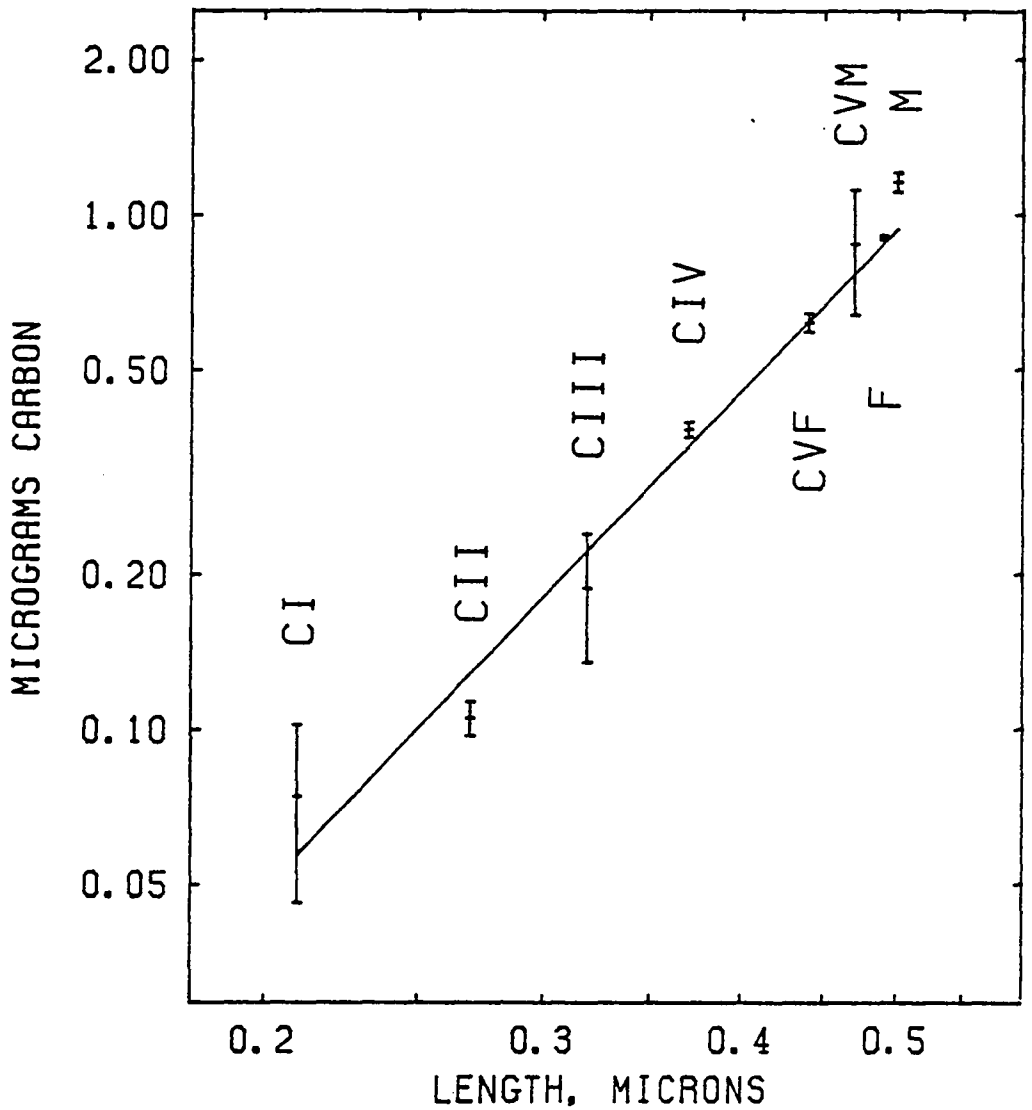


Figure 9. Relationship of body carbon to cephalothorax length for A. inermis post-naupliar stages. Line fitted by least squares.

TABLE 3. Estimates of volume and carbon per stage for copepodites and adults of A. inermis. Each value for length and width is a mean of 5-10 individuals. Carbon values are means of at least 3 samples.

Stage	Length (μm)	Width (μm)	Volume ($10^6 \mu m^3$)	Carbon (μg)	Carbon / volume
CI	220	70	0.56	0.07	0.13
CII	268	85	1.01	0.10	.10
CIII	316	92	1.40	0.19	.14
CIV	365	121	2.80	0.38	.14
CVF	436	142	4.60	0.62	.13
CVM	471	178	7.81	0.88	.11
F	492	192	9.50	0.90	.09
M	492	192	9.50	1.14	0.12

per unit volume is 0.10. A value of 0.12 μg C/10^6 μm^3 was used as the best estimate of carbon per unit volume; the measured values, volumes, and resulting calculated values are shown in Table 4.

The time between initial refrigeration and filtering and drying of animals was several hours and occasionally up to 8 hours. To determine whether storage of this duration had any effect on estimates of carbon content, several aliquots of net-caught plankton were placed in petri dishes and refrigerated for up to 31 hours. At intervals during that time, 3 sets of 12 female A. inermis were removed from one of the petri dishes and analyzed for body carbon. Figure 10 shows that decay could be detected at 25 hours but not at 5 hours. If the rate of loss of carbon is assumed to be linear over the time interval, the loss in 8 hours would be about 5%. It is assumed that specific rates of loss of body carbon would be the same in copepodite stages and males as in females. Because most of the samples were processed in less than 8 hours, this source of error has been neglected.

The effects of the addition of stain and carbon dioxide on the measured carbon content of the animals were determined in a two-way factorial experiment. Groups of 25 females picked from a fresh plankton catch were assigned to one of four treatments: stained or unstained, and killed with CO_2 or not killed. Except for the addition of stain and CO_2, handling was identical for all groups. Three or four replicates in each treatment were used. Analysis of variance revealed no significant effect of either stain or CO_2. A second experiment was then conducted using the stain only, and using both males and females. The results of this experiment (Table 5) show

TABLE 4. Volumes and body carbon of nauplii of A. inermis. Volumes are means of two estimates. Measured carbon values are single determinations; estimated values are based on a carbon/volume ratio of 0.12 μg C/10^6μm^3.

Stage	Volume (10^6μm^3)	C measured (μg)	C estimated (μg)
NI	0.12	0.019	0.015
NII	--	--	0.015
NIII	0.14	--	0.02
NIV	0.32	0.030	0.035
NV	0.52	0.061	0.06
NVI	0.60	0.072	0.07
NVI		0.069	

TABLE 5. Comparison of biomass carbon of stained and unstained adult A. inermis. Each value represents μg C per animal based on measurements of carbon in 25 animals.

Female		Male	
Stain	No stain	Stain	No stain
1.02	0.96	1.35	1.19
0.98	0.94	1.33	1.15
0.96	0.93	1.23	1.13
0.94	0.89	1.21	1.11
0.92	0.89	1.14	1.10
0.91	0.88	1.12	1.09
0.90	0.87	1.10	1.09
0.90	0.82	1.05	
0.89	0.80		
	0.79		
Mean:			
0.94	0.88	1.19	1.12

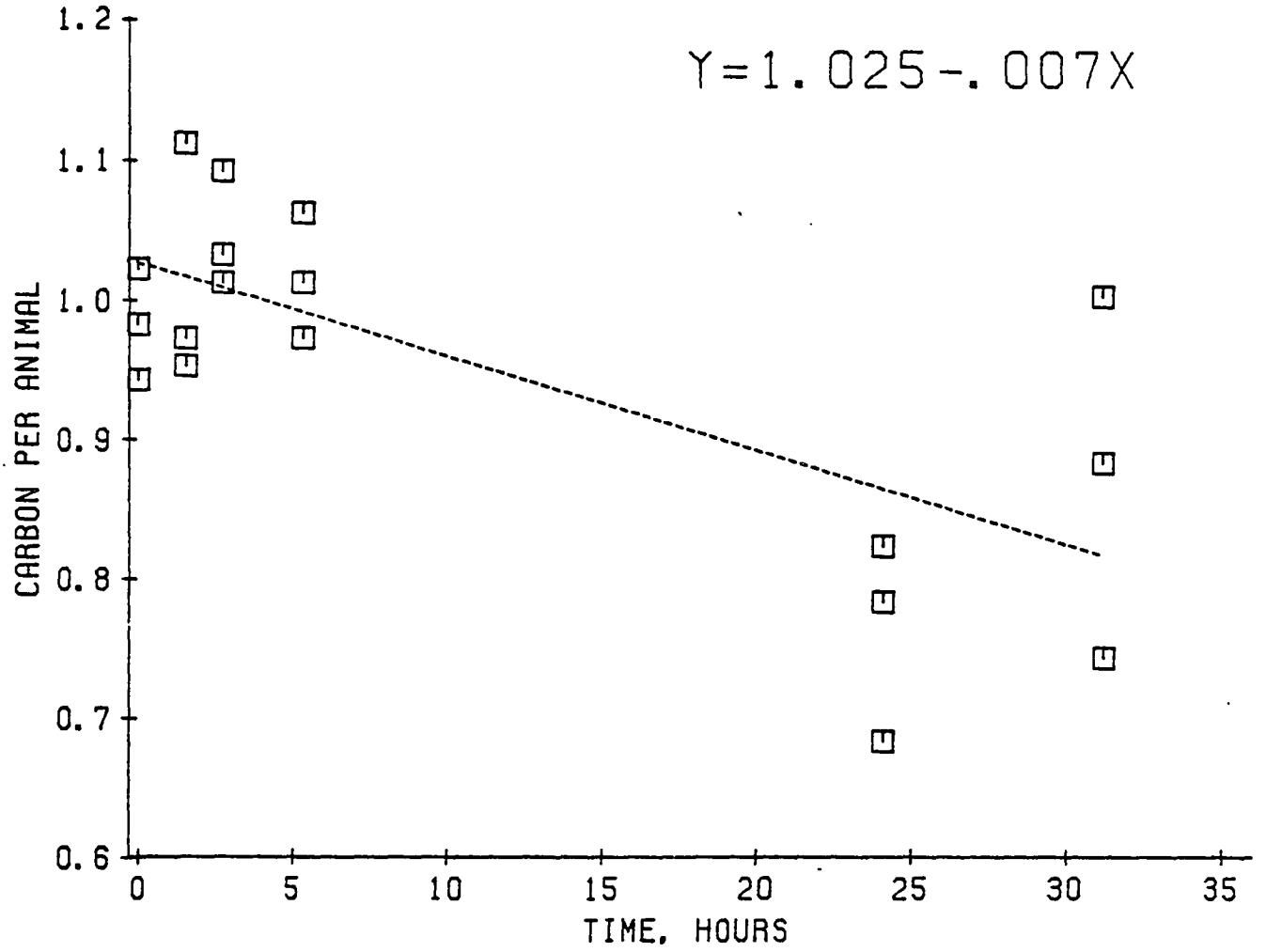


Figure 10. Loss of body carbon content in female A. inermis refrigerated for up to 31 hours.

that the carbon content of the stained animals was lower by about 6%; this difference was the same for both males and females but significant only for the females. Because all of the biomass measures were made on stained animals, this source of error was not corrected for; obviously it would have no effect on the P:B ratios.

Table 6 is a summary of data from each of the P:B experiments described below. Data presented are the temperatures, initial biomass, P:B, standard error of P:B, number of samples, and the degree of significance at which the null hypothesis (H_o: P:B = 0) could be rejected (t test). Mortality of the later copepodite stages, as determined by failure to take up stain, was low--never over 5% of the biomass.

Two assumptions implicit in the calculation of P:B as the rate of biomass increase are that mortality is low and that the population age structure does not change much during incubation; thus the P:B ratio should remain constant during the incubation. Two time series experiments were conducted to test these assumptions. In experiment T1, nauplii were not counted so their biomass and production are excluded from the P:B ratio. The effect of this exclusion is discussed later. The slope of the regression differed significantly from 0, with P:B = 0.32 day^{-1}, and with no significant deviation from linearity (Fig. 11). In experiment T2 the nauplii were included; P:B was 0.25 day^{-1}, also significantly different from 0, and with no significant deviation from a straight line (Fig. 12).

Experiments T2 and S3 were done with animals concentrated twofold; all others were done with natural concentrations of animals.

TABLE 6. Summary of results of P:B experiments.

Experiment	Date	Station	Temp. °C	Initial biomass (μg C/l)	P:B (day^{-1})	Std error of P:B	p (P:B = 0)	Number of samples
T1	Aug. 3, 1977	SC	26	20.6	0.32	0.051	<0.0001	15
S1	Sept. 21, 1977	SC	25	26.0	0.32	0.059	.0003	12
		OF	25	13.8	0.20	0.122	.13	11
S2	Oct. 12, 1977	SC	27	22.0	0.25	0.069	.01	12
		OF	27	25.9	0.26	0.117	.049	12
C1	Dec. 6, 1977	SC	22	10.1	0.30	0.040	.005	10
T2	May 2, 1978	SC	26	19.5	0.26	0.025	< .0001	18
C2	July 19, 1978	SC	26	10.8	0.36	0.054	< .0001	12
S3	July 25, 1978	SC	26	42.0	0.07	0.069	.35	10
		OF	26	42.5	0.30	0.042	<0.0001	12

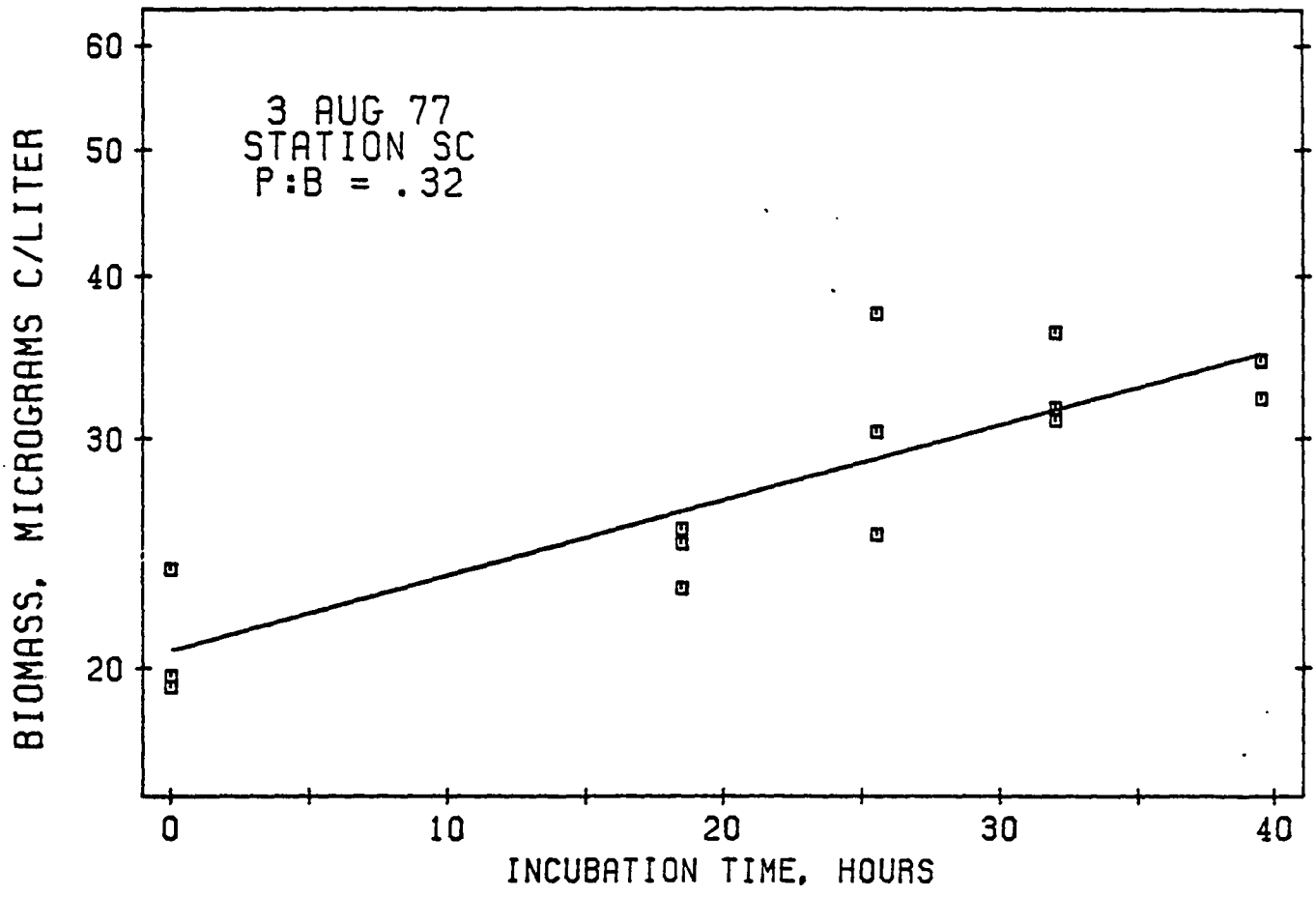


Figure 11. Growth of biomass in samples from time series experiment T1. The slope of the line, fitted by least squares, is the P:B ratio.

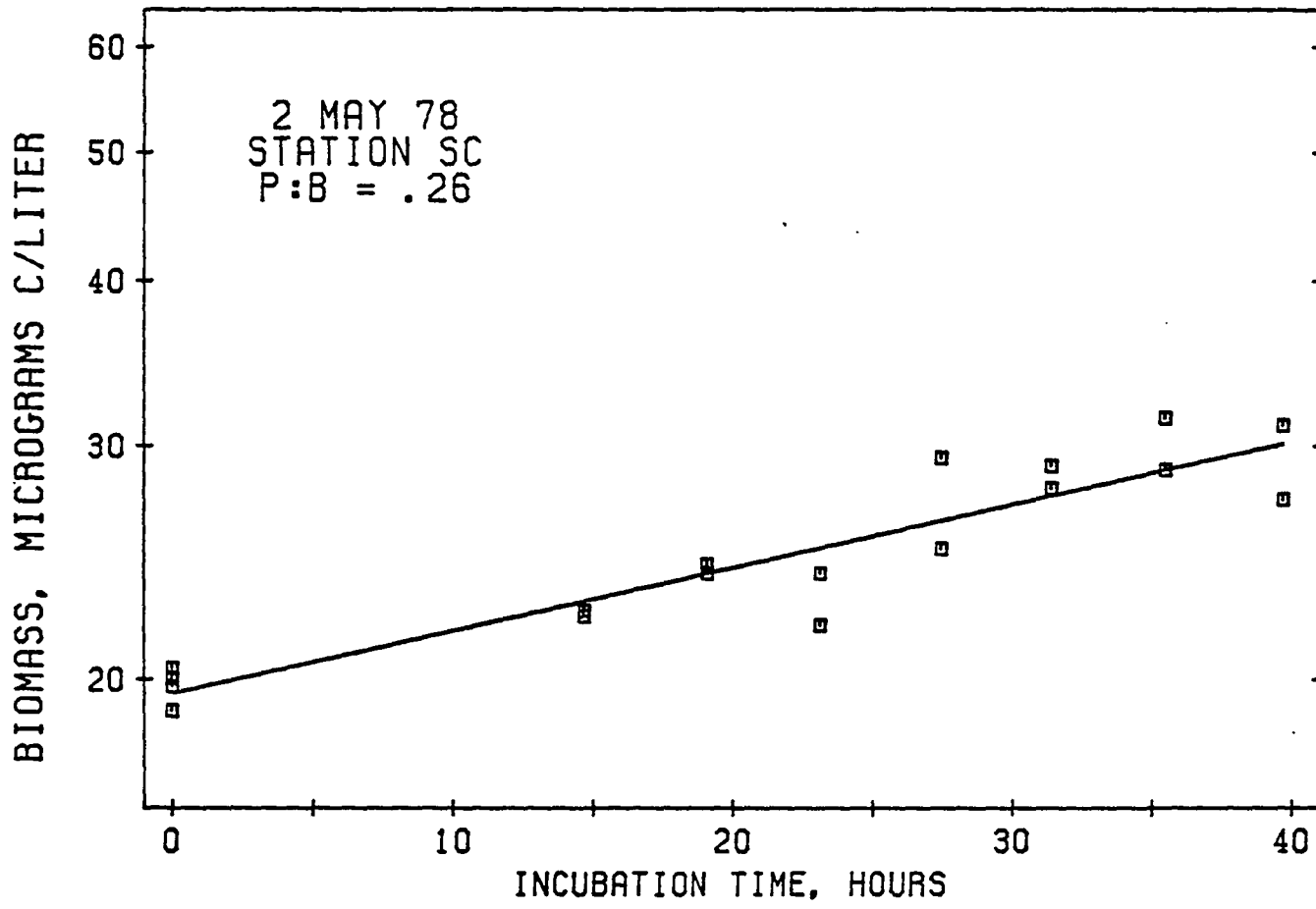


Figure 12. Growth of biomass in samples from time series experiment T2.

Two experiments were conducted to determine whether this concentration, or the use of 2-liter containers instead of 4-liter, had any effect on the P:B ratio. In experiment C1, two batches of water at two different concentrations (ambient and increased about 2-fold) were used. Aliquots of 3.8 liters each were partitioned among three zero-time samples and two each of: 4-liter bottles, paired 2-liter bottles, and single 2-liter bottles with the concentration increased another two times. A fourth pair of samples was combined into a 10-liter glass carboy; after incubation this sample was split into two equal volumes for analysis. Table 7 shows the initial and final biomass estimates and calculated P:B values for this experiment. Poor handling of the 10-liter samples resulted in excessive variance between aliquots; also, for the purpose of statistical testing the aliquots are not true replicates. None of the P:B values from the large bottles exceeded any of the values from the 4-liter bottles, though, so increasing container size beyond 4 liters is probably not warranted. Two-way analysis of variance on the remaining P:B values showed no difference between batches ($p > 0.1$), and a marginal difference between treatments ($p \approx 0.05$). Paired comparisons of treatment means by Duncan's multiple range test showed that P:B in the 4-liter bottles was significantly greater ($p < 0.05$) than that in the paired 2-liter bottles. All of the 4-liter bottles had higher P:B values than any of the 2-liter bottles.

Experiment C2 was conducted using two different batches of water. Incubation of aliquots initially containing 7.6 liters each was done in paired 4-liter bottles, 4-liter bottles with the concentration

TABLE 7. Results of P:B experiment C1. Initial biomass values are means of three; all others are single samples.

Batch	Incubation time (hours)	Initial biomass (µg C/l)	Container size (liters)			
			8	4	2 (paired)	2 (conc.)
			Final biomass (µg C/liter)			
A	29.8	6.18	7.03	9.60	5.50	5.57
	32.3		--	9.05	7.18	7.70
B	29.8	14.0	12.3	18.0	13.4	16.0
	32.3		--	20.7	17.0	19.0
			Resulting P:B ratios (day^{-1})			
A			0.11	0.41	-0.11	-0.10
			--	0.32	0.13	0.19
B			-0.10	0.20	-0.04	0.11
			--	0.29	0.14	0.23

increased two-fold, and in 2-liter bottles with a four-fold concentration increase. No significant difference existed among the treatments, although the 2-liter mean value was the lowest of the three (Table 8).

Three experiments were conducted using animals from stations OF and SC to test the hypothesis that P:B ratios are spatially variable. The results appear in Figures 13-15. In experiment S1 the P:B ratios were nearly identical at 0.25 and 0.26 day^{-1}. In experiment S2 the P:B ratio determined for station SC (0.32 day^{-1}) was higher than that for station OF (0.20 day^{-1}), but the large standard error of the slope at OF caused the difference to be insignificant ($p > 0.1$, analysis of covariance). In experiment S3 the P:B ratio at OF was 0.30 day^{-1}, significantly greater than that at SC, 0.07 day^{-1} ($p < 0.01$).

In the last experiment, one aliquot was retained from each station for counts of stages. Using these counts with carbon per stage from this study along with development times modified from Bartholomew (1973) as described in the next section, I estimated total production under the assumption that mortality would be 0 during incubation. The population stage structures were unusual (Table 9), with most of the numbers and biomass concentration in stages CIV and CV, and very few nauplii. The estimated P:B ratios were 0.36 and 0.38 day^{-1} for stations SC and OF, respectively.

Also in the last experiment, particle counts of the <35 μm water from two of the experimental bottles from each station, together with counts from control bottles without copepods, were used to estimate grazing by the total herbivore community in the bottles. Since this

TABLE 8. Results of P:B experiment C2. Initial biomass values are means of two; all others are single samples.

Batch	Incubation time (hours)	Initial biomass (µg C/l)	Container size (liters)		
			4 (paired)	4 (concentrated)	2 (concentrated)
			Final biomass (µg C/liter)		
A	24.0 27.8	12.0	14.4 18.5	14.9 13.9	15.6 13.3
B	30.4 33.5	9.65	17.8 18.0	19.1 18.6	13.9 16.7
			Resulting P:B ratios (day^{-1})		
A			0.19 0.38	0.22 0.13	0.27 0.09
B			0.46 0.45	0.54 0.47	0.29 0.39

Figure 13. Growth of biomass in experiment S1 using water and animals from stations OF and SC. The difference in slopes (P:B ratios) is not significant.

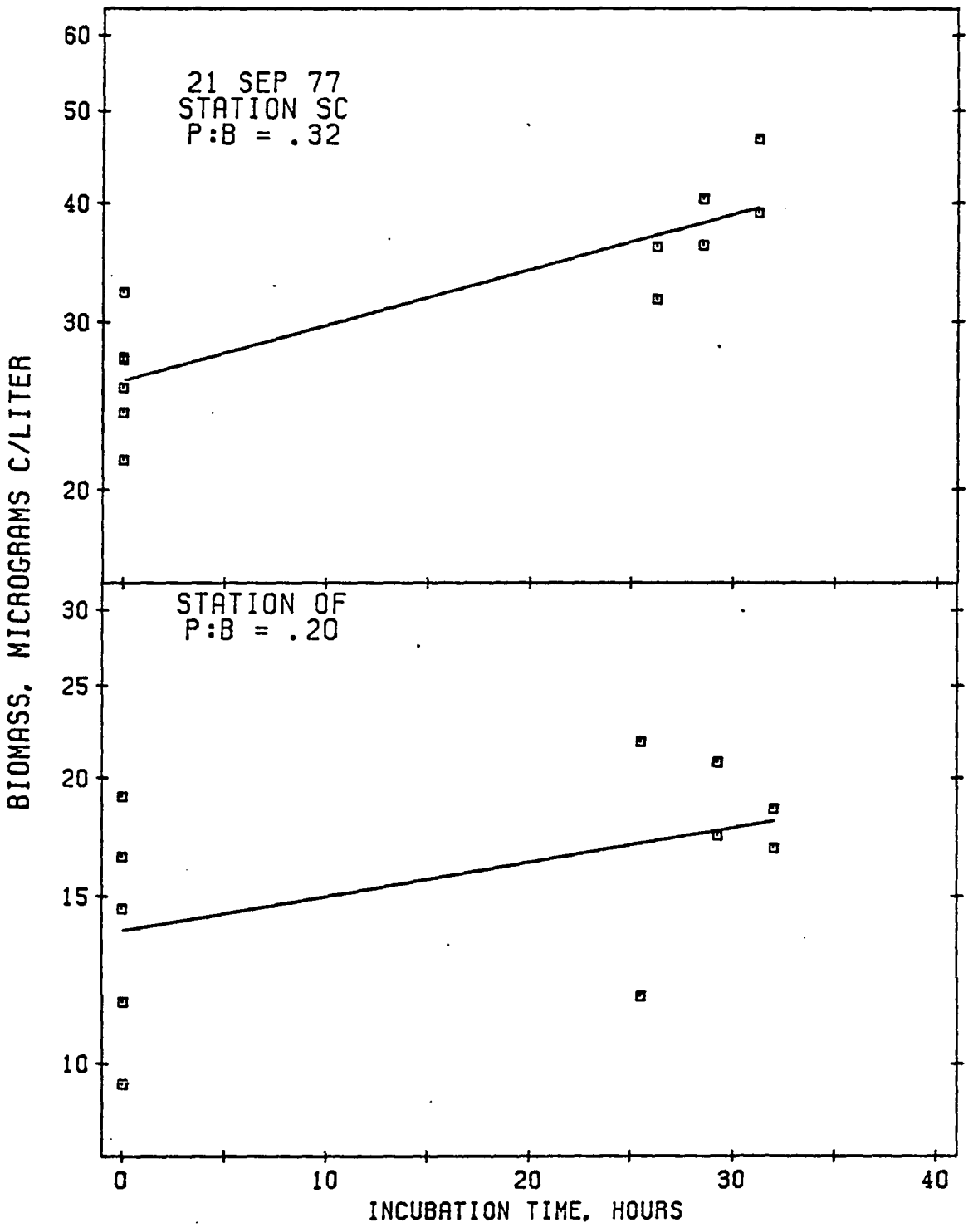

21 SEP 77
STATION SC
P:B = .32
STATION OF
P:B = .20
BIOMASS, MICROGRAMS C/LITER
INCUBATION TIME, HOURS
60
50
40
30
20
30
25
20
15
10
0
10
20
30
40

Figure 14. As in Figure 13, for experiment S2. The slopes are not significantly different.

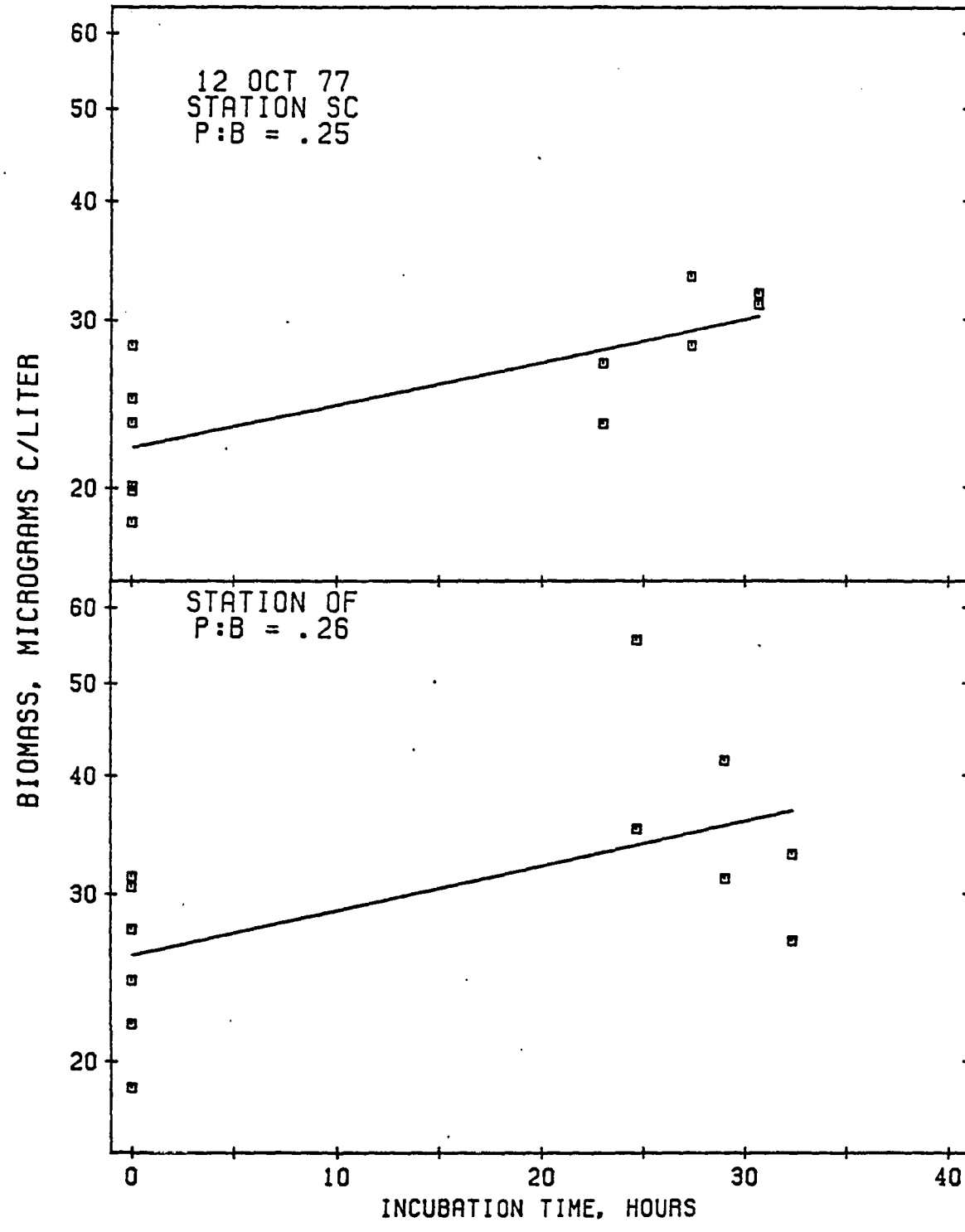

12 OCT 77
STATION SC
P:B = .25
STATION OF
P:B = .26
BIOMASS, MICROGRAMS C/LITER
INCUBATION TIME, HOURS
60
50
40
30
20
0
10
20
30
40

Figure 15. As in Figure 13, for experiment S3.
The difference in slopes is significant ($p < 0.01$).

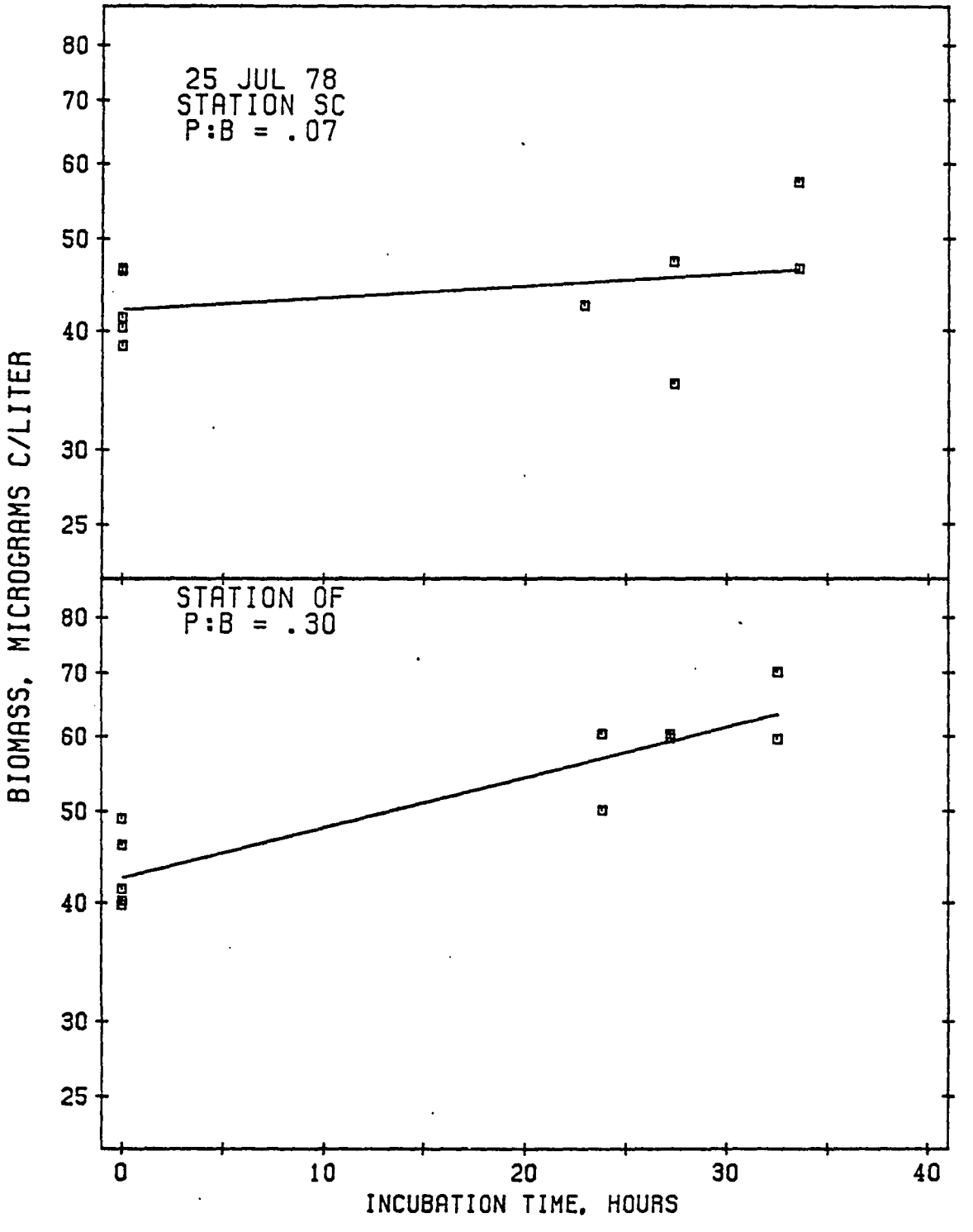

25 JUL 78
STATION SC
P:B = .07
STATION OF
P:B = .30
BIOMASS, MICROGRAMS C/LITER
80
70
60
50
40
30
25
0
10
20
30
40
INCUBATION TIME, HOURS

TABLE 9. Estimates of P:B from counts for experiment S3. For each stage a growth rate is calculated as $g_i' = \ln(W_1/W_0)$, where W_0 is the carbon content of stage i and W_1 is the carbon in the stage expected after 24 hours, assuming the growth rate from the midpoint of one stage to the midpoint of the next to be constant. All weights in μg C, biomass in μg C/liter, and production in μg C $liter^{-1}$ day^{-1}. The mean biomass B_i and production P_i are calculated as follows:

$$\bar{B}_i = \frac{N_i W_i}{g_i'} (e^{g_i'} - 1) \quad \text{and} \quad P_i = g_i' \bar{B}_i$$

where N_i and W_i are the number and mean carbon per animal in stage i.

Stage	W_0	W_i	g_i'	Station SC			Station OF		
				N_i	$\bar{B}_i$	P_i	N_i	$\bar{B}_i$	P_i
Egg	0.015	0.021	0.36	1.5	0.03	0.01	0	0	0
NI	0.015	0.033	0.78	7.0	0.16	0.12	0	0	0
NII	0.015	0.049	1.18	2.0	0.06	0.07	0	0	0
NIII	0.02	0.068	1.22	1.5	0.06	0.07	0	0	0
NIV	0.035	0.070	0.56	1.8	0.08	0.05	0.2	0.01	0.005
NV	0.06	0.080	0.28	2.0	0.14	0.04	0.5	0.03	0.01
NVI	0.07	0.089	0.24	0.8	0.06	0.02	0	0	0
CI	0.07	0.117	0.52	3.2	0.29	0.15	0	0	0
CII	0.10	0.226	0.82	4.4	0.10	0.13	1.0	0.02	0.03
CIII	0.19	0.429	0.86	4.9	1.48	1.27	3.8	1.14	0.98
CIV	0.38	0.81	0.76	11.5	6.55	4.97	21.8	12.41	9.43
CV	0.75	0.90 (1.14)	0.31	29.6	26.03	8.07	40.8	35.87	11.12
Adult:									
Female	0.90	--	0.14	5.2	4.68	0.66	7.8	7.02	0.98
Male	1.14	--	0	2.8	3.19	0	3.0	3.42	0
Total				78.2	42.91	15.63	78.8	59.92	22.56
					P:B = 0.36			P:B = 0.38	

consisted mainly of A. inermis copepodites, it can be assumed that most of the grazing was done by these animals. Net feeding rate was determined by subtracting the mean particulate volume in the 2-32 μm size range in two of the experimental bottles from the mean of duplicate counts on the controls. The feeding rates were 5.6 x 10^8 and 12.3 x 10^8 μm^3 $liter^{-1}$ day^{-1} for stations SC and OF, respectively. Particle concentrations in the controls were 1.7 and 2.9 ppm, respectively.

Discussion

Analysis of the method. Most of the production in these experiments occurred as somatic growth of the larger copepodite stages. Table 10 shows initial biomass, P:B, and initial production rate calculated with and without the nauplii and eggs included, for experiments S1-S3 and T1. The production figures listed for the nauplii are not truly production but rate of gain of biomass. Thus they include egg production, which might more appropriately be placed with the adults, and exclude production by nauplii that molted to copepodites during the incubation. Still, the figures suffice to show the disproportionate effect of egg production and naupliar growth on the production: although they acccunt for only 0.06-17% of the biomass, their "production" is 1-48% of the total.

A potential source of error in the P:B calculations is uncertainty in values for carbon per stage of the nauplii. These values (Table 4) are merely estimates, and no confidence limits were determined. Using the calculated values of P:B and BO with and without nauplii, I

TABLE 10. Biomass at time 0, production at time 0, and P:B including and excluding the biomass of nauplii.

Experiment	Station	No. of samples	With nauplii			Without nauplii			% Contribution of nauplii to:	
			BO	P(BO)	P:B	BO	P(BO)	P:B	BO	P(BO)
S1	SC	12	26.0	8.35	0.32	25.0	7.95	0.32	4	5
	OF	11	13.8	2.75	0.20	13.1	1.65	0.12	5	40
S2	SC	12	22.0	5.48	0.25	20.2	3.27	0.16	8	40
	OF	12	25.9	6.78	0.26	24.0	5.04	0.21	7	26
T2	SC	18	19.5	5.14	0.26	19.4	5.09	0.26	0.4	1.1
S3	SC	10	42.0	2.92	0.07	41.7	2.88	0.07	0.4	1.5
	OF	12	42.5	12.6	0.30	42.5	12.3	0.29	0.1	2.3

calculated the P:B that would result if the carbon/stage figures for nauplii were multiplied or divided by 2. The resulting values (Table 11) differ by 0-0.04 day^{-1} from the values based on the carbon per stage estimates in Table 4. These estimates are probably not off by as much as a factor of two because the carbon/volume values would be very different from those of the copepodites, and because the carbon content of NVI must be close to that of CI because of the short duration of the NVI stage (0.1 days; see below). In any event, none of the conclusions are changed by this variation of the naupliar biomass.

The two time series experiments showed that P:B values were constant during incubation of up to 40 hours. Mortality in the copepodite stages was small as determined by staining, but mortality of the nauplii was not determined. Mortality during incubation would cause P:B to decrease. At the same time, variation in egg production rates should cause P:B to vary during incubation because growth rates of early nauplii are zero but become large when stage NIII is reached. Egg production can be stimulated by handling (see Chapter IV), so an initial increase in production might be seen. Still, the linearity of the P:B regression lines for the two time series experiments shows that the combined effects of mortality and egg production did not change P:B during incubation.

It is instructive to compare P:B ratios determined by experiment with values estimated demographically. Although insufficient data for this exercise were collected during the period when the P:B experiments were done, I used stage frequency data taken in summer

TABLE 11. Analysis of effect of two-fold variations of naupliar carbon estimates on P:B

Experiment	Station	P:B values with naupliar weights at:			Resulting error in P:B
		Estimated values	½ Estimated values	2x Estimated values	
S1	SC	0.32	0.32	0.32	0
	OF	.20	.17	.23	15
S2	SC	.25	.21	.28	14
	OF	.26	.24	.28	8
T2	SC	.26	.26	.26	0
S3	SC	.07	.07	.07	0
	OF	0.30	0.29	0.30	2

1979 for comparison (see Chapter II). Time-weighed mean values of abundance of each stage were calculated for south Kaneohe Bay. The mean values were used to calculate a production value on the assumption that it would be equivalent to the production of a population with a stable age distribution equal to the observed mean distribution. The results of the calculations are summarized in Table 12. Appendix B gives details of the method used. Briefly, development times were estimated from the data in Bartholomew (1973); these were used to calculate mortality rates on the assumption that mortality is constant during each stage. The numbers of eggs and early nauplii were lower than expected, probably because of a difference in depth distribution caused by the sinking of eggs. These numbers were replaced by more realistic figures estimated from the mean summer egg production rate of 11 day^{-1} per female (see Chapter IV). Growth rates were also considered constant in a stage and were assumed to be 0 in stages NI, NII, NVI, CI, and the males.

Production was calculated as the sum of the production figures for each stage. These were calculated both as growth rate and as mortality rate times the biomass of each stage. Total production and production by nauplii, copepodites, and adults were calculated by each method and divided by the appropriate biomass to get P:B. The values obtained for all stages were 0.55 day^{-1} and 0.59 day^{-1} for production as growth and yield, espectively. The difference between the two arises from cumulative rounding errors, not from any property of the original data.

Table 12. Details of calculation of production of A. inermis from stage frequency data of summer 1979. Symbols are: N_i, number in stage i (no. liter^{-1}); W_i, weight of stage i (μg C liter^{-1}); B_i, total weight of all animals in stage i (μg C liter^{-1}); t_i, duration of stage i (days); m_i, mortality of stage i, and g_i, growth rate of stage i (day^{-1}); G, production estimated as total growth, and Y, as total yield or mortality (μg C liter^{-1} day^{-1}).

Stage	N_i	W_i	B_i	t_i	m_i	g_i	G	Y
Egg	1.37 (10.6)	0.015	0.158	0.3	0.66	0.0	0.0	0.10
NI	1.60 (8.67)	0.015	0.130	0.3	0.66	0.0	0.0	0.09
NII	6.40 (7.11)	0.015	0.107	0.3	0.66	0.0	0.0	0.07
NIII	8.06	0.020	0.161	0.4	0.33	1.39	0.22	0.05
NIV	5.49	0.035	0.192	0.4	0.33	1.39	0.27	0.06
NV	6.06	0.06	0.364	0.4	0.33	1.39	0.51	0.12
NVI	1.54	0.07	0.108	0.1	0.33	0.0	0.0	0.04
CI	10.26	0.07	0.718	0.8	0.27	0.0	0.0	0.19
CII	7.91	0.10	0.791	0.8	0.27	0.89	0.70	0.21
CIII	5.62	0.19	1.07	0.8	0.27	0.89	0.95	0.29
CIV	4.72	0.38	1.79	0.8	0.27	0.89	1.59	0.48
CV-F	2.25	0.62	1.40	0.8	0.27	0.18	0.25	0.38
F	3.53	0.90	3.18	---	0.71	0.31*	0.98	2.26
CV-M	2.25	0.88	1.98	0.8	0.27	0.89	1.76	0.53
M	0.88	1.14	1.00	---	2.86	0.0	0.0	2.86
Totals:								
Egg + N	47.5 (36.9)		1.22	2.2			1.00	0.53
Cop.	33.0		7.75	4.0			5.26	2.08
Adult	4.4		4.18	---			0.98	5.12
TOTAL	80.9		13.5				7.24	7.73
						P:B	0.55	0.59

* Production of females includes 0.07 day^{-1} as somatic growth and 0.14 day^{-1} as egg production.

The large disparity between these estimates and those obtained by incubation could arise from errors in estimating development times, from the variations of the actual age distributions from the mean, from depression of growth rates in the bottles, or from actual differences in P:B. Data are insufficient to determine the cause, although the better agreement of the measured and estimated values for July 1978 suggests that at least part of the difference between the summer 1979 estimates and the earlier measurements was due to a real difference in P:B. The experiments with the smaller bottles showed that the use of 2-liter containers caused a decrease in estimates of P:B, but that concentration of animals had no effect. Whether the use of the 4-liter bottles had a depressing effect on production is not known. The fact that Barlow's (1955) incubations gave rates of increase which were close to loss rates from the estuary suggests that incubation in bottles does not depress growth rates, although his water samples were larger than mine, 15 liters each.

Few P:B values of tropical zooplankton are available from the literature for comparison with my results. Mullin's (1969) review of the status of measurement of secondary production in the sea listed no examples from tropical waters. Several Soviet authors (e.g. Vinogradov et al. 1977) have determined P:B of mixed zooplankton in tropical waters, but their results are based on single values of growth efficiencies taken from the Soviet literature, when in fact these efficiencies can be highly variable, especially among species (Winberg 1971). LeBorgne (1977) has reported P:B ratios of mixed equatorial zooplankton of 0.24-0.26 day^{-1} using the method of Butler

et al. (1969). LeBorgne measured excretion rates of zooplankton caught in a 200 μm mesh net and nitrogen:phosphorus (N:P) ratios of zooplankton and particulate matter smaller than 200 μm, the presumed food of the zooplankton, to calculate P:B in terms of N and P. Excretion rates per unit of body weight of marine animals decrease as a power function of body weight with an exponent estimated to be -0.33 (Johannes 1964). P:B also decreases logarithmically with increasing body weight, but the slope may not be the same. Log-log graphs of P:B vs. dry weight of several copepod species (Zaika 1968) had slopes varying from -0.4 to -0.7. The usual caution should be applied in comparing these slopes to that for excretion rate, but the variation suggests that the relationship of P:B to excretion rates will vary with the size distribution of the animals. Thus P:B estimates taken from excretion rates of total zooplankton may be unreliable. Mullin (1969) has recommended that production measurements be limited to single species because specific rates are not additive.

Heinle's (1966) data on Acartia tonsa in the Patuxent River in the summer offers a source for comparison, since temperatures were close to those in this study (24-26.5°C). His mean value for P:B was 0.5 day^{-1}, but this was later revised to around 0.17-0.2 day^{-1} (Miller et al. 1977). A. inermis weighs about half as much as Acartia tonsa from Chesapeake Bay (Bartholomew 1973; Miller et al. 1977). If we use the relationship of P:B to dry weight for Acartia clausi in Zaika (1968), which has a slope of -0.7, then we would expect Acartia tonsa to have a P:B of around 0.17 based on the mean of all dates for A. inermis (0.28).

The method of estimating production presented here has been shown to yield values which are reasonable when compared to the few values which can be obtained from literature, although such a comparison should be made with caution. The method is superior in some respects to the demographic methods for the measurement of P:B in continuously recruiting populations because:

1. It can provide a P:B value which is specific to place and time.
2. No measurements or assumptions need be made about growth, mortality, or the duration of stages.
3. Inaccuracy of measurement of weights or carbon has less effect on the calculated production, although the effect on P:B could be greater.
4. Temperature effects on growth rates need not be accounted for.
5. No assumptions need be made about the population age distribution.

Problems with the method are:

1. Possible depressing effects of the enclosure on growth rates. This would of course also appear in experiments done to determine development times, which are needed in all demographic methods except those in which cohorts are followed through time.
2. Long processing time and the necessity to process the samples quickly. This problem could be alleviated by preservation of each sample and either determining the biomass of weighed animals or counting them and using carbon per stage to

calculate total biomass. The latter would eliminate some of the advantage of the method.

3. Variability between samples is high, thus requiring a large number of replicates.

4. It ignores losses to small predators such as Oithona nana (Lampitt 1978).

The variability between replicates is a result of the small number of the larger animals. If we use the abundances from the 1979 data we can estimate the expected coefficient of variation for one sample. The variance of the numbers of organisms in a sample is equal to the mean, assuming a Poisson distribution. The total variance of biomass in a given sample is:

$$S^2 = \sum (W_i^2 \cdot s_{\bar{N}_i}^2 + N_i^2 \cdot s_{\bar{W}_i}^2)$$

where W_i is the weight of stage i. N_i is the number of stage i per liter, and $s_{\bar{W}_i}$ and $s_{\bar{N}_i}$ are their standard errors. If we assume the standard errors of the naupliar weights to be on the same order as the weights, and using the standard errors determined for the copepodite weights, the second set of terms is negligible. Now if $C_i = 4N_i$ is the number of animals in the 4-liter samples, then $s_{C_i}^2 = C_i = 4N_i = 16s_{N_i}^2$. Then the coefficient of variation of a single sample can be calculated as:

$$CV = \frac{S^2}{B} = \frac{\sum W_i^2 \cdot N_i}{2\sum W_i \cdot N_i}$$

For the data from summer 1979, CV = 0.3. For an 8-liter sample this becomes 0.2. The actual coefficients of variation for a single

4-liter zero-time sample ranged from 0.12 to 0.26, while those from 8-liter samples were 0.03 to 0.09. Since these were less than the estimated values, randomization of the zero-time samples must have been complete, and the only way to further reduce the variance would have been to increase the number of samples. With the necessity of processing all samples within a few hours, this would have been impracticable for one person.

Spatial variability. Platt and Filion (1973) showed that phytoplankton productivity index (PI, mg C day^{-1} mg chl a^{-1}) and therefore presumably P:B, varied significantly among 6 stations in Bedford Basin on 6 of 10 sampling days. Therriault et al. (1978) showed significant variability in PI on 18 of 30 days among 6 stations in St. Margaret's Bay, Nova Scotia. Although these authors treat PI as synonymous with P:B, the carbon:chlorophyll ratio of phytoplankton can vary sufficiently to make such an interpretation questionable.

The variations in PI seen by these authors showed no concordance between dates and stations; that is, the spatial variability could not be attributed to a fixed effect of the stations. The results of Platt and Filion (1973) also showed that PI varied more between dates than between stations.

My results, on the other hand, are most striking for their uniformity. Except for one value, all of the P:B values in Table 6 fall between 0.2 and 0.36 day^{-1}. The coefficient of variation of the biomass values is 41%, while that for P:B is 31%; with the single low value removed the coefficient of variation P:B is only 17%, significantly lower than the value for biomass ($p < 0.005$, F ratio test).

The implication of these results is that P:B of zooplankton in a food-rich environment is rather invariant. This rate function is apparently insensitive to large changes in biomass and to the relatively small variability in age frequency distribution commonly seen in tropical copepods. For these organisms total production is more a function of biomass than of specific production. The results also imply that control of abundance of these copepods occurs either through predation or at infrequent intervals through limitation on their food supply.

The single low value at station SC is not likely to have resulted from experimental error. If the results of all three two-station experiments are pooled as suggested by Sokal and Rohlf (1969, p. 621) the overall result is still significant at $p = 0.05$. Although variation in P:B can be caused by variation in age structure (Zaika 1968), the spatial variation in the July 1978 experiment must have been due to other causes. Production rates estimated from projected growth of the observed stages were very close to each other, although higher than the values obtained by incubation. The production at station SC must have been otherwise limited, probably by food. The feeding rate at station SC as determined by particle counts was less than half that at OF. The concentration of particulate matter was also higher at OF, which is located in an area that is enriched by stream flow and usually has higher particulate and chlorophyll concentrations than station SC (Kimmerer et al. 1980). The enhanced feeding rate may have been a response to the higher concentration of food. Gross growth efficiencies calculated for stations SC and OF were 8 and 16%

respectively, based on an assumed carbon-volume ratio of 0.1. The value of gross growth efficiency for OF is within the range reported by Harris and Paffenhöfer (1976) for Pseudocalanus elongatus, but low compared to other reported values (e.g. Butler et al., 1969). The values given here are only estimates, since they neglect feeding by other species and feeding by A. inermis on particles larger than 32 μm. Still, since most of the feeding was being done by A. inermis, the conclusion remains that a difference in feeding caused the difference in P:B between the two stations on that date.

CHAPTER IV

EGG PRODUCTION RATE

Introduction

Egg production rate is a readily measurable rate function which bears the same relationship to population numbers as P:B does to biomass. Like P:B, egg production rate could be expected to depend upon the quality and concentration of food and on the size frequency distribution of the females in the population. Since it is easier to measure than P:B, it is a suitable rate function to examine for spatial variability.

To determine the egg production rate of a species such as *Acrocalanus inermis* which does not carry its eggs, an incubation method is required. There are several potential pitfalls in this method. One is that handling the animals may change their egg production rate. The second is the possibility of cannibalism by the animals on their own eggs. Another possible problem is that crowding may suppress egg production. Finally, egg production may not be constant during the experiment, so duration of incubation is critical.

I measured egg production rates of *A. inermis* on six occasions (experiments S1-S6) to test the hypothesis that these rates are spatially variable. Two additional experiments were also conducted to determine if crowding was important (experiment C1) and if egg production rate varied much during incubation (experiment Ti).

Methods

Females for the experiments were obtained in three ways. In the first (method A), surface water was dipped up in buckets and strained through a 333 μm Nitex mesh to remove large chaetognaths (see Table 2 for a list of mesh apertures used and the ranges of organisms retained by each). The water was then passed through screens of 100 μm and 35 μm using upward flow to keep the animals covered with water. The >100 μm fraction was added to the <35 μm fraction so that the eggs and early nauplii were excluded. In the second method (method B) animals were collected with a 183 μm mesh, 0.5 m diameter plankton net towed as slowly as possible. The catch was poured through a 333 μm mesh in a bucket of surface water for transport to the laboratory, where it was concentrated on a 200 μm mesh. Aliquots of the fraction retained, which contained almost entirely A. inermis adults and stage V copepodites, were taken with a plankton splitter and put into bottles of <35 μm surface water. In the third method (method C), animals were collected as in method B and held in buckets of surface seawater. About 20 females were removed for each sample by concentrating several liters of water containing the animals on a 200 μm mesh and then pipeting the females out under a dissecting microscope and placing them in the experimental containers.

All samples were incubated in containers of surface water from the stations at which they were collected. Two-liter bottles were used in all experiments except S1, when four-liter bottles were used, and C1, when several container sizes were used. The samples were

incubated either while suspended from floats in the lee of Coconut Island (experiment S1) or while floating in tanks of flowing seawater at Coconut Island.

After incubation of about 24 hours, samples were strained through a 35 μm mesh, and the fraction retained was placed in a beaker with about 2 mg/l of neutral red stain. After 20-30 minutes the animals were fixed in 2-5% formalin and refrigerated to maintain their color until they were counted. Egg production rates were calculated as the total eggs plus nauplii divided by the number of stained females, corrected to 24 hours. Females that died during the incubation were excluded from the calculations.

Methods A and B required a correction to the number of females present at the end of the experiment to account for the stage V copepodites which had molted to adult females during the incubation. This was done by taking the mean ratio of females to females plus stage V females in zero-time and final samples and multiplying it by the females plus stage V females in the final samples.

The 35 μm screens used in these experiments were tested periodically to insure that no eggs or nauplii passed through. Glassware was washed with hydrochloric acid and deionized water between experiments, and rinsed with sample water before use.

A single experiment was conducted on February 14, 1979, to determine the effect of concentration on egg production rates. Animals were collected at station SC by method B and separated into 12 aliquots of about 400 and 12 aliquotes of about 200 animals each. These were put into 250-ml, 1-liter, and 4-liter bottles for incubation,

resulting in 24 samples with concentrations nominally between 50 and 1600 per liter. Particle counts were done on water from all bottles and on water from three control bottles containing no animals. Feeding rates were calculated from the differences in particle concentration in the control and experimental bottles.

Another experiment was conducted on March 28, 1979, to determine whether incubation time had any effect on egg production rate. Animals were collected by method B from station SC. Four groups of five subsamples each were incubated for four consecutive six-hour periods. A fifth group of five subsamples was incubated for the entire 24 hours.

Results

The results of experiment C1, conducted on February 14, 1979, are shown in Figure 16. Egg production rate (Fig. 16a) increased significantly with the volume of water per animal ($r = 0.92$, $p < 0.001$). Similarly, feeding rate (Fig. 16b) increased and mortality rate (Fig. 16c) decreased with increasing volume per animal. The lowered feeding rates per animal in the smaller containers were not caused by lower food concentration, since the volume of the particulate matter in these containers was actually higher than that in the larger bottles. The maximum volume per animal in this experiment is 22 ml. In the experiments done to examine differences in egg production rates between stations the volume per animal was kept above 50 ml to prevent crowding effects; this corresponds to the upper end of the natural range of density of these animals.

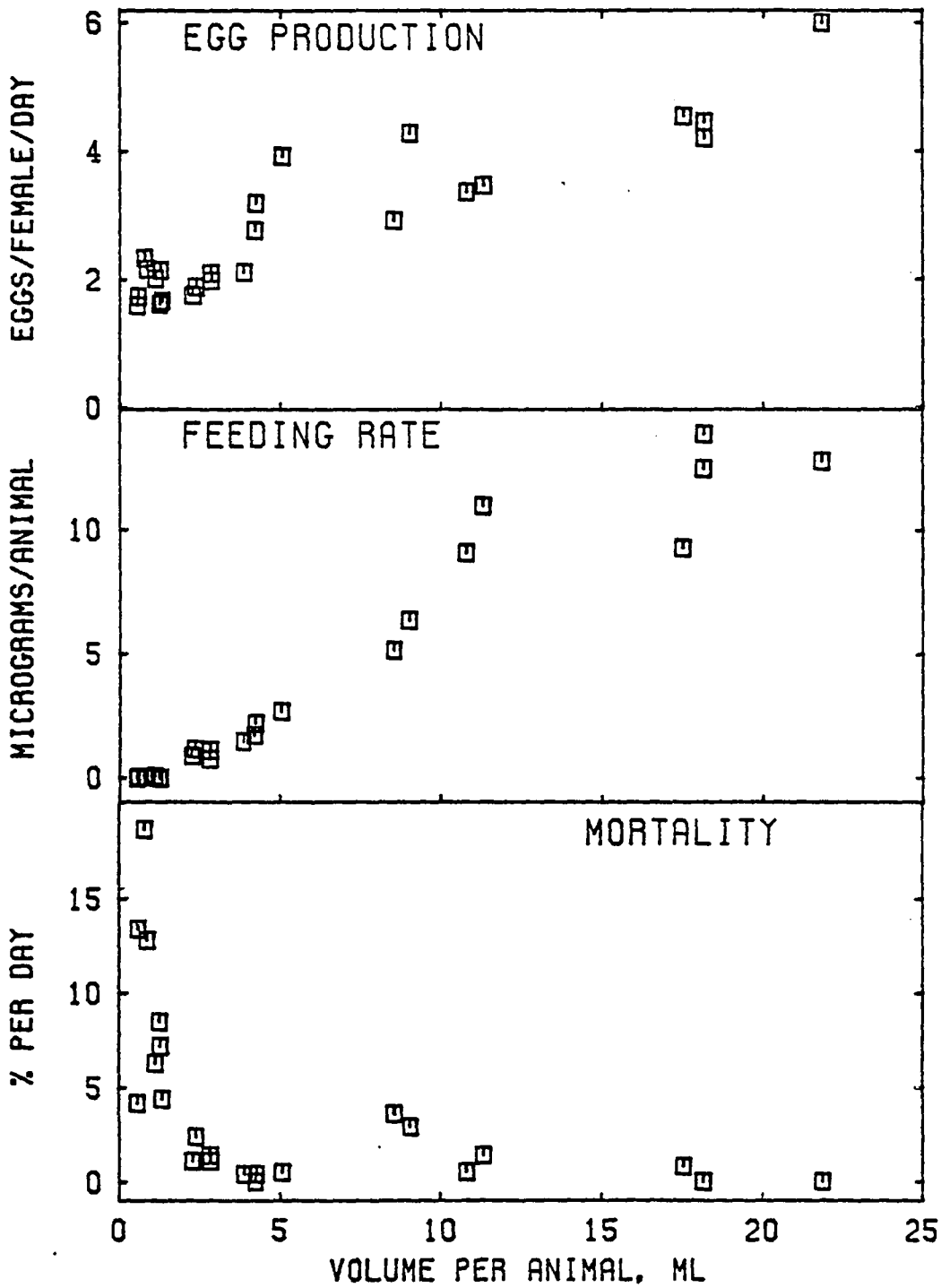


Figure 16. Effects of crowding, shown as volume of water per individual, on a) egg production rate, b) feeding rate, and c) mortality rate, from experiment C1.

The egg production rates determined in time series experiment T1 were very low overall (Table 13). The mean of the 24-hour samples was 1.12 per female per day, compared to only 0.53 per day for the mean of all six-hour samples. Because the variances differed greatly among the groups of samples, a Mann-Whitney U test was used to compare the results. The 24-hour samples had a significantly higher egg production rate than all of the six-hour samples taken together ($p < 0.005$, one-tailed test), or either of the first two sets of six-hour samples ($p < 0.01$), but not the last two sets.

Spatial variability in egg production rates was determined in six experiments. In experiment S1, animals were collected by method A from stations SC and OF (Fig. 2) and from a third station (GM) 2 km west of SC. For the remainder of the experiments animals were collected at stations I, II, and III by method C, except that in experiment S2 station III was omitted. The results of this series (Table 14) show significant spatial variability on four of the six sampling dates as determined by one-way ANOVA (t-test for July 6). The mean egg production rate for all dates in this experiment was 11 per female per day.

On the last three dates (Table 14) particle counts were done on the water used for incubation. There was a significant correlation ($r = 0.76$, $p < 0.001$) between egg production rate and the concentration of particles in the 2-32 μm size range (Figure 17).

TABLE 13. Summary of results of egg production time series experiment T1. Egg production rates in eggs per female per day.

	24-hour incubation	Six-hour incubations			
		A	B	C	D
	0.93	0.08	0.30	0.73	0.70
	1.12	0.08	0.49	0.98	1.36
	1.15	0.05	0.29	0.57	0.27
	1.35	0.09	0.34	1.55	0.72
	1.03	0.07	0.26	0.88	0.74
Mean	1.12	0.07	0.34	0.94	0.76

TABLE 14. Results of egg production experiments at two or three stations. Differences in egg production rates were tested by t test or one-way ANOVA.

Experiment	Date	Collection method	Station	Temp. (°C)	Egg production rate (eggs/female/day)		Significance of spatial difference	Particulate volume (ppm)
					Mean	Std. error		
S1	August 5, 1977	A	GM	26.0	10.5	1.0		---
			SC	"	8.4	0.9	0.002	---
			OF	"	15.8	1.0		---
S2	July 5, 1979	C	I	25.0	11.3	1.2	.01	---
			II	"	16.4	0.7		--
S3	August 1, 1979	C	I	26.5	9.5	0.3		---
			II	"	7.4	0.4	< .0001	---
			III	"	12.0	0.7		---
S4	August 31, 1979	C	I	29.0	5.1	1.1		0.178
			II	"	6.4	0.6	> .5	.335
			III	"	6.7	1.1		.371
S5	Sept. 19, 1979	C	I	27.5	14.6	1.4		.717
			II	"	16.9	0.8	.04	.705
			III	"	12.4	0.9		.648
S6	Oct. 15, 1979	C	I	27.0	10.8	1.6		.286
			II	"	10.4	0.9	>0.6	.313
			III	"	9.4	2.0		0.249

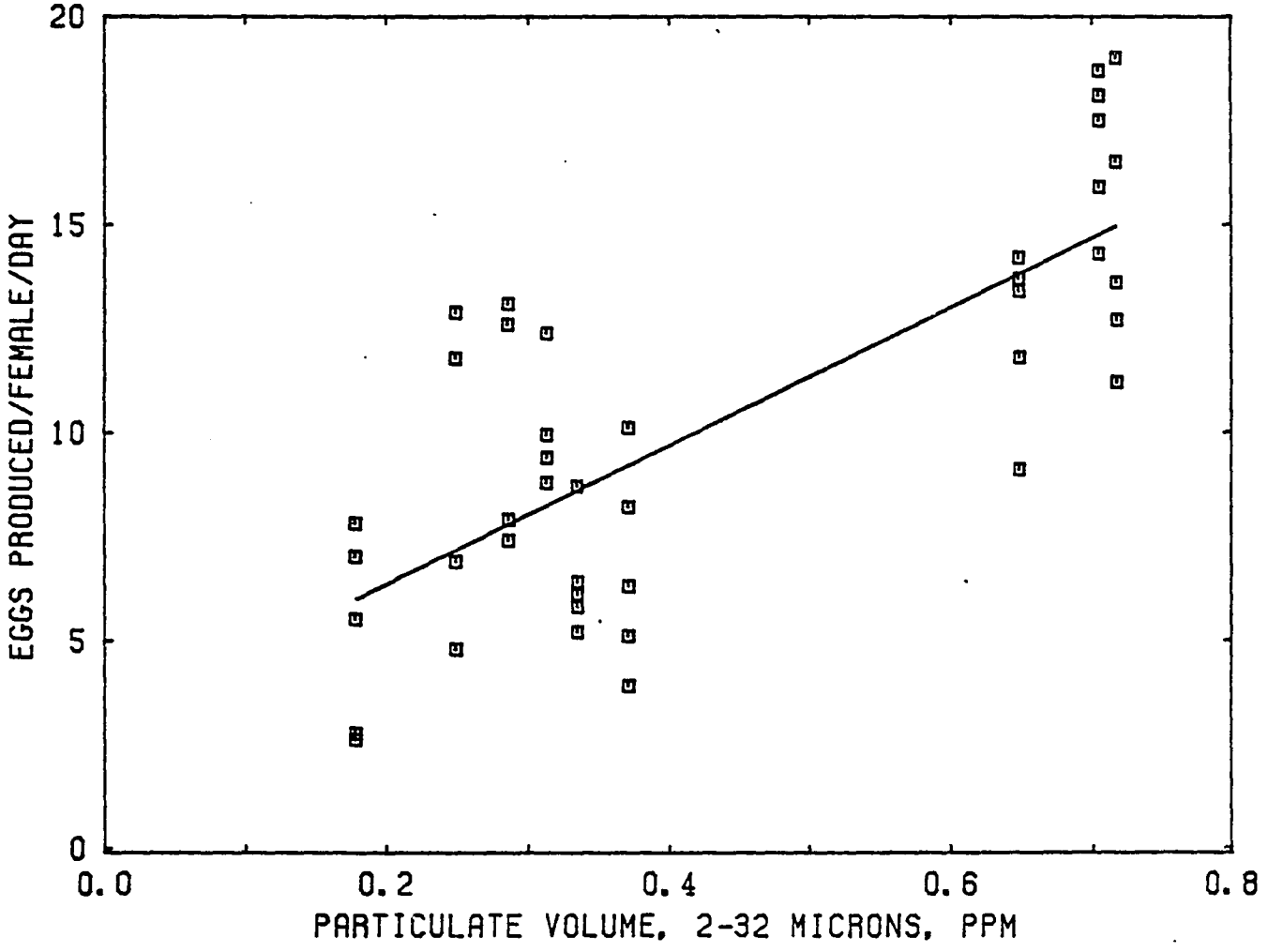


Figure 17. Relationship of egg production rate and ambient particulate volume, 2-32 μm diameter, for experiments 53-56.

Discussion

Unlike P:B, egg production rates were highly variable both in space and in time. The significant correlation of egg production rates with ambient particle concentration indicates that at least some of the spatial and temporal variability can be attributed to food concentration and therefore feeding rate. Actually the egg production rate should be a function of cumulative ingestion over some time period before egg laying. The egg development time of these animals is very short, though, and food concentrations should be autocorrelated over that time period. The observed correlation therefore indicates that food concentration is at least sometimes limiting the population growth rate of A. inermis. Egg production rates of temperate copepods such as Pseudocalanus spp. (Corkett and McLaren 1969) and Centropages typicus (Dagg 1978) have previously been shown to be limited by food at times.

Particle concentrations in Kaneohe Bay are greatly influenced by wind speed and are therefore more variable in time than in space (S. V. Smith, unpublished data). This in turn suggests that egg production rates should be more variable temporally than spatially. In fact, the mean coefficients of variation of the egg production data from Stations I, II, and III are 37% among dates and 15% among stations. Analysis of variance on data from experiments 2 to 6 showed that dates accounted for 58% of the variance, while stations and the interaction accounted for only 14%; the differences were significant ($p = 0.01$, F test). This result is similar to that obtained for stage frequency differences (Chapter II). Previous investigators of

variability in chlorophyll (Therriault and Platt 1978) and in phytoplankton P:B (Platt and Filion 1973; Therriault et al. 1978) in temperate waters have shown that the temporal component of variation exceeds the spatial component. The temporal component includes seasonal variation which is much smaller in tropical waters. Lewis (1978) partitioned the variance of the abundance of zooplankton species in a tropical lake into temporal and spatial (both fixed and ephemeral) components, and found that the spatial components exceeded the temporal component for about half of the species. Evidently the lack of strong seasonality or major meteorological events kept abundances of these species about constant throughout the year. The variability in rates reported here has a greater temporal component than spatial because of short-term meteorological events. The spatial component is entirely transient, as the means of stations I, II, and III from the last four experiments are nearly identical (Table 14); thus there was no fixed difference among the stations.

The significant variation of egg production rate with duration of incubation required that incubations be kept to the same length for comparisons between stations. The measured egg production rates may be higher than rates in the field, though, because of stimulation of egg production by handling. Hargrave and Geen (1970) suggested that handling prompts a burst of activity seen in initially high feeding rates, and Marshall and Orr (1972) stated that egg laying in Calanus, which may be delayed in the field until suitable food is found, can be precipitated by capture and handling. The time series experiment indicated that, if egg laying was stimulated by handling,

then there was a time delay in egg production of at least six hours. Since all other incubations were around 24 hours they are comparable, but might better be considered differences in potential rather than actual egg production rate.

The striking effect of crowding on egg production rate was accompanied by a reduction in feeding and an increase in mortality. Although A. inermis is small (3 μg dry weight) it still needs at least 20 ml of space to function normally. If this is true for other species, then the results of several investigators may be too low; for example, Dagg (1978) incubated individual Centropages typicus (40-50 μg dry weight) in only 15 ml of water. The effects of crowding appeared at different densities: mortality increased sharply below about 3 ml per animal, feeding rate decreased at around 10, and egg production rate appeared to be affected at all densities. Egg production rate may therefore be the best indicator of stress in these organisms.

In the previous chapter it was shown that the duration of each A. inermis naupliar stage was about half that for copepodite stages. Miller et al. (1977) showed that species of Acartia develop isochronically, that is, with a constant development time per stage. They speculated that this development strategy is an adaptation to high predation rates on the larger stages. By spending more of their time as nauplii, developing rapidly through the copepodite stages, and producing large numbers of eggs in a short time, this high predation rate is mitigated. The egg production rates reported by Heinle (1966) for Acartia tonsa were only 14-20 per female per day, not much higher

than for A. inermis. He assumed a steady population and calculated the birth rate necessary for replacement of adults. If instead we calculate the birth rate necessary to maintain his observed mean number of nauplii with his calculated death rates, using the relations in Chapter II, we get an egg production rate of 42-60 eggs per female per day, depending on the adult sex ratio. This is considerably higher than the egg production rate of A. inermis as one would expect from the great differences in naupliar mortality rates. The differences in reproduction and growth strategy between these two species can also be seen in the ratios of nauplii:copepodite:adults. For the summer 1979 data on A. inermis this was established to be 8.4:7.5:1, while for Acartia tonsa in Chesapeake Bay (Heinle 1966) it was 32.6:6.0:1.

Miller et al. (1977) speculated that the isochronal development strategy would be best suited to neritic environments with large numbers of planktivorous fish, while an anisochronal strategy might be more suited to nutritionally poorer habitats. Calanus and Pseudocalanus species, which inhabit more offshore areas than Acartia species, have shortened naupliar development times (Mullin and Brooks 1967; Paffenhöfer and Harris, 1976) and produce fewer eggs than Acartia (Marshall and Orr 1972; Paffenhöfer and Harris 1976; Dagg 1977). A. inermis, contrary to the speculations of Miller et al. (1977), lives in a nutritionally rich habitat with several abundant species of planktivorous fish (Smith et al. 1973). Acartia hamata is abundant in Kaneohe Bay, but only in the central and north sectors, where particulate concentrations are lower and the small planktivorous fish

are rarer. If this species is similar to its congeners in having a high reproductive rate and isochronal development, then the reason for these two alternative strategies may not be quite so straightforward. More information on size-specific predation rates on copepods is needed.

CHAPTER V

MICROCOSMS

Introduction

One possible mechanism for the origin of patchiness in phytoplankton and herbivores is from spatial variability in predator abundance. If predators are patchily distributed and if they exert some control on prey abundance, then their patchiness should be reflected in lower trophic levels. Since predators are usually less abundant than prey, the number of predators in small parcels of water should be more variable than the number of prey. If these parcels are then isolated from each other, it might be expected that the subsets of the ecosystem in the water parcels would become progressively less similar to each other because of the differences in predator abundance. Such an effect has been observed, for example in the Loch Ewe bag experiments (Gamble et al. 1977), where differences in herbivore abundance between bags were attributed to differences in predation pressure.

Distinct from the ability of isolated subsets of the planktonic ecosystem to replicate each other is their ability to replicate the ecosystem itself. If the subsets replicate the ecosystem well, then they must be globally stable. If they are stable, then spatial heterogeneity on scales larger than the dimensions of the isolated parcels cannot be a necessary condition for ecosystem stability. The converse

is not necessarily true, though: a collapse of the subsets into some new configuration does not imply global instability of the ecosystem. The reason for this is that the act of isolation and enclosure of the water parcels may itself have profound effects on the ecosystem subsets.

If differences between subsets of an ecosystem do arise, either from differences in predator abundance or otherwise, then mixing between them could be used to simulate turbulent diffusion between patches in the real ecosystem. If diffusion between patches stabilizes the ecosystem, then we might expect mixing between isolated subsets of the ecosystem to add stability. This stability can be measured in terms of the variance of common species or, if the abundance of some species decays toward extinction, the rate of decay.

Thus there are three questions which can be asked concerning the isolation of parcels of water from the Kaneohe Bay planktonic ecosystem. Rephrased as hypotheses, they are 1) that patchiness, as determined by differences in abundance of common taxa, will arise within the isolated parcels even without apparent physical differences between them; 2) that the subsets of the ecosystem are globally stable in isolation and will closely replicate the Kaneohe Bay ecosystem; and 3) that mixing between two such parcels will enhance the stability of the ecosystem subsets, as measured by the variance or rate of decline in abundances of common species.

I tested these hypotheses by isolating 1.3 m^3 parcels of Kaneohe Bay water in four tanks. Two of the tanks were partially mixed together daily and the other two were kept isolated. I performed two such experiments to provide serial replication.

Materials and Methods

Four cylindrical fiberglass tanks, numbered P1-P4, were placed in a row on the eastern tip of Coconut Island. Each was initially filled with water from Kaneohe Bay. The contents of two of the tanks were partially mixed together daily, and samples drawn periodically for counts and other analyses, as described below.

Experiment 1 was run from April 3 to April 24, 1978, and experiment 2 from September 20 to October 20, 1978. Another experiment (experiment L), conducted to determine the effect of varying the incident light level, is described in Appendix C. Table 15 lists the differences in the methods used, samples taken, and sampling frequencies between experiments 1 and 2.

Tanks were painted white on the outside and flat black on the inside. Each was fitted with a lid consisting of a wooden frame covered with transparent polyethylene to reduce evaporation and to prevent dilution by rainfall, and a layer of screening material to reduce light. In experiment 1 the screening material allowed 15% of the light to pass; this was used because the experiments of Perez et al. (1977) showed that the optimum light level needed to simulate conditions in Narragansett Bay was only 10% of the average for the water column. The screen used in experiment 2 passed 37% of the light, and its use was based on the results of experiment L (Appendix C). The location of the tanks afforded them full sunlight throughout the day. Mean incident solar radiation during the experiments was about 400 langleys/day. No cooling mechanism was used, as thermal inertia of the water was expected to dampen diurnal heating and cooling.

Table 15. Comparison of methods and samples taken in microcosm experiments 1 and 2.

	Experiment 1	Experiment 2
Dates	April 3-24, 1978	Sept. 20-Oct. 20, 1978
Light transmission of tank covers	15%	37%
How turbulence was maintained in tanks	Air-lift pump	Periodically rising and falling disk.
How water was mixed between tanks	Hand pump, return flow through siphon.	Dipped with bucket, return flow through siphon.
Which tanks mixed together	P2 and P3	P1 and P2
Sampling:		
Size of plankton samples	80 liters	40 liters
How water and plankton replaced	Pumped from Bay	Water replaced after screening, nutrients added.
Frequencies:		
Plankton taken	Daily	2 days
Plankton counted	3 days (1 day for P1 through day 11).	4 days
Particulate C, N	3 days starting with day 8.	--
Particle counts	Daily	--
Chlorophyll	--	4 days
Nutrients, total dissolved N	3 days	4 days

Temperatures in the tanks were later found to differ from each other and from Bay surface temperature by only a few tenths of a degree.

The tanks were initially prepared by washing with fresh water and filling with Bay water for one month's preconditioning. A preliminary experiment, not reported in detail here, was run using Bay water and about 10 cm of sediment. Between experiments the tanks were scrubbed with fresh water, allowed to dry, and rinsed with fresh water and Bay water before being filled.

Tanks were filled with a diaphragm hand pump which delivered about 3.5 liters per stroke through a 7 cm diameter plastic hose. The intake was placed 1 meter below the surface about 5 meters away from the Coconut Island fringing reef. During filling the tanks were connected by siphon hoses and the pump discharge was switched among tanks to keep initial populations as similar as possible.

Turbulence within the tanks in experiment 1 was provided by air lift pumps. The amount of turbulence was compared between tanks after termination of the experiment using plaster-of-paris blocks. Analysis of variance of weight loss among the blocks revealed no differences among the tanks. In experiment 2 turbulence was produced in each tank by a plexiglass disk attached to a plastic bottle which was alternately supplied with air from the laboratory air system and vented off. This provided a cyclic rise and fall of the disks.

Mixing between two tanks was done with the hand pump in experiment 1 and by dipping water with a bucket in experiment 2, with return flow through a siphon in both experiments. About 300 to 350 liters of water, or 25% of the volume of the tanks, was transferred. If mixing

in each tank were complete and rapid, then some of the water pumped from one tank to the other would return via the siphon to be pumped again. The net exchange with complete mixing would be 20%, so the actual exchange was between these two figures. The amount of exchange needed was determined by a rough approximation from the expressions for diffusivity of Okubo (1971). The diffusion rate between patches of water containing a contaminant is

$$D = \frac{\partial}{\partial x} K \frac{\partial H}{\partial x}$$

where K is the eddy diffusivity, H is the concentration of the contaminant being mixed, and x is a horizontal coordinate. D can be roughly approximated, assuming mixing between two patches of equal size, by

$$D \simeq K \frac{\Delta H}{(\Delta x)^2}$$

where ΔH is the difference in concentration, and Δx the distance, between two locations. The equivalent rate of exchange between containers would then be:

$$V \simeq \frac{D}{\Delta H} \simeq \frac{K}{(\Delta x)^2}$$

Okubo's (1971) expression (equation 4 in his paper) for oceanic turbulent diffusivity is

$$K = .01 \cdot d^{1.15}; \text{ then,}$$

$$V = .01 \cdot d^{-.85} \text{ sec}^{-1}, \text{ d in cm.}$$

For a distance scale of 1 km, V is 5%/day, while for 100 meters it is 35%/day. The exchange rate chosen, 20-25%/day, corresponds to

a distance scale of 150-190 meters. This length scale is at the lower end of the range of length scales at which patchiness appears to be important in enclosed waters (e.g. Powell et al. 1975) and in the open ocean (e.g. Fasham et al. 1974). If an effect of mixing on stability did not appear at this mixing rate, then it would not be expected at lower mixing rates, that is, longer length scales.

As a check on the applicability of the expression for diffusivity taken from Okubo (1971) diffusion experiments were done in the middle of the southern basin of Kaneohe Bay on July 10 and 17, 1979. Winds on both days were northwest trades, averaging 6 and 4 m/sec, respectively. Tidal ranges were 0.6 and 0.5 meters. Eight cruciform drogues suspended at 5 meters from small surface floats were tracked for six hours and their positions determined with a Del Norte Trisponder system every 20 to 30 minutes. Diffusivities were calculated using the matrix equations in Okubo and Ebbesmeyer (1976). On a length scale of about 100 meters, the mean diffusivities calculated were 453 and 286 cm^2/sec, compared with 387 cm^2/sec from Okubo's equation 4; thus the use of that equation for this crude calculation is justified.

The samples listed in Table 15 were taken as follows. First the water samples for particulate measurements and nutrients were taken with a plastic bottle. Plankton samples were then taken with a siphon, with the intake moved around in the tank so the sample was as random as possible. The water was passed through a 35 μm gauze and the fraction retained was preserved in formalin. In experiment 2 only, the screened water was immediately poured back into the tank. The mixing

devices and the sides of the tanks were thoroughly scrubbed with a brush, and the bottoms were scraped with a rubber squeegee. Water was then mixed between tanks P2 and P3 in experiment 1 and P1 and P2 in experiment 2. Finally, in experiment 1 the water removed in sampling was replaced by pumping from the Bay. In experiment 2, since the water had been put back into the tanks after screening, sufficient growth medium (Caperon and Meyer 1972) was added to replace the nitrogen removed in the samples (assumed to be 27 μg-at. of nitrate nitrogen, equal to the 1976 median particulate nitrogen content of the seston larger than 35 μm in 40 liters of south Kaneohe Bay water, data in preparation).

Water samples for particulate carbon and nitrogen analysis (experiment 1 only) were strained through a 100 μm gauze and filtered onto precombusted CF/C filters. These were dried at 60°C for two days and combusted in a Hewlett-Packard Model 185B CHN Analyzer. Particle counts on samples of whole water (experiment 1 only) were done on a Coulter Counter Model TA-II with a 70 μm orifice. Unstrained 1-liter samples (experiment 2 only) were filtered onto GF/C filters and frozen in acetone for later chlorophyll determination by <u>in vitro</u> fluorometry (Strickland and Parsons 1968). In both experiments filtrate was frozen in polyethylene bottles for later analysis for nitrate, ammonium, phosphate, and silicate, done on a Technicon AutoAnalyzer II system (Technicon Industrial Systems 1973). Total dissolved nitrogen was also determined on the AutoAnalyzer following ultraviolet oxidation of the water samples (Strickland and Parsons 1968).

Concurrent plankton samples were not taken from the pier, but samples were taken twice a month from station SC (Figure 2) for the sewage abatement project. Sampling methods are described in Chapter II.

Results

Medians and ranges of count data for several zooplankton taxa from station SC for April through October 1978, and the values from April 5 and September 27, are presented in Table 16 for comparison with the microcosm data.

Results of experiment 1 are shown in Figures 18 to 26. The most striking features of all these data are the sharp decline in abundance of the copepods A. inermis and Oithona simplex and the chaetognath Sagitta enflata and the close replication of the count data from all four tanks.

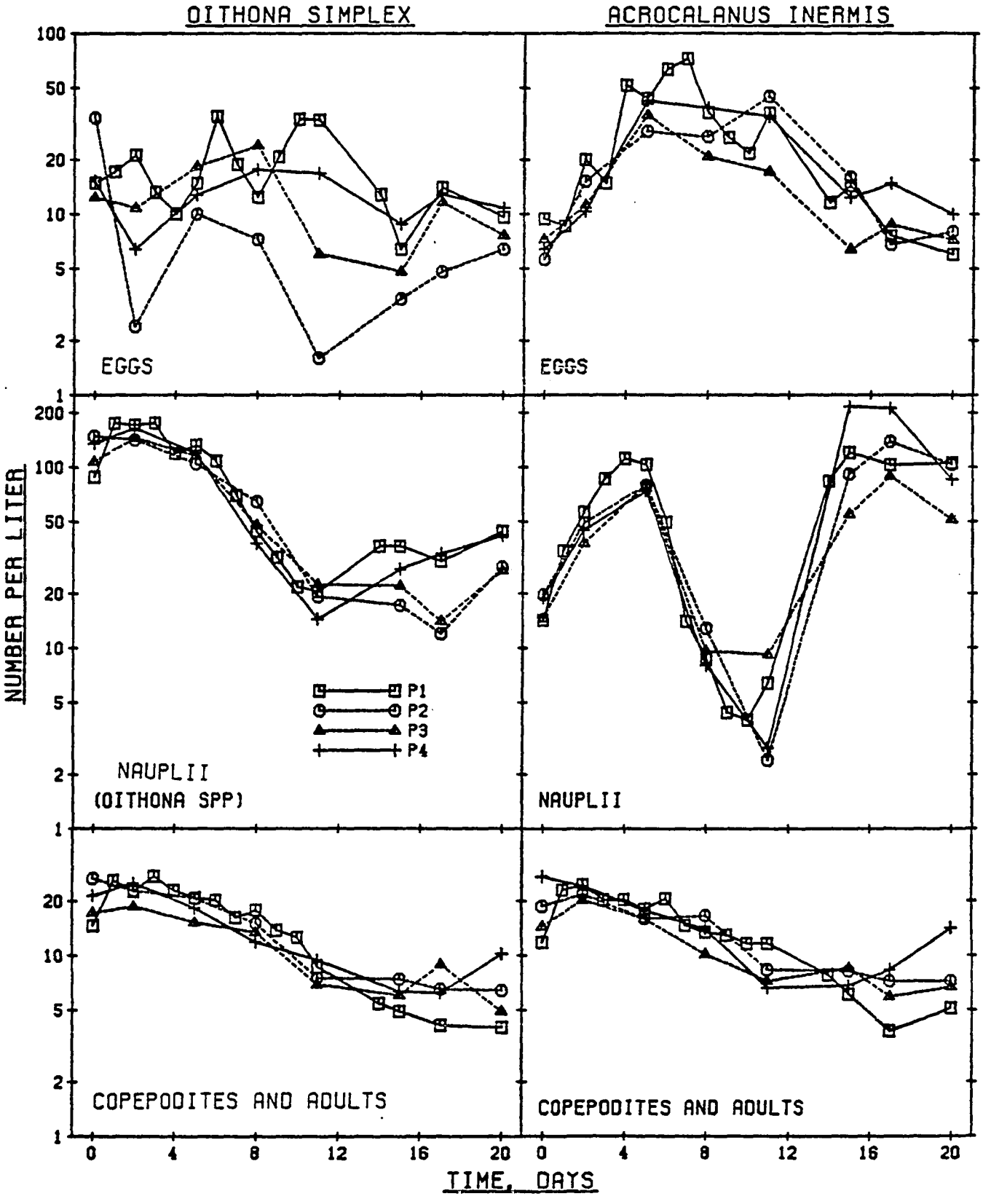
Figure 18 shows the abundance of eggs, nauplii, and post-nauplii of O. simplex and A. inermis. O. simplex copepodites and adults declined gradually from about 20/liter, approximately equal to the ambient concentration, to 5/liter and then leveled off. At the same time, total Oithona nauplii decreased from about 150 to about 20/liter, then increased slightly in the unmixed tanks. These nauplii include both O. simplex and O. nana; copepodites and adults of O. nana (Fig. 19) did not change much during the experiment. O. simplex eggs were much more variable, with final abundance not significantly less than initial.

A. inermis post-nauplii also declined gradually after the first few days of the experiment. Nauplii went through two cycles of rapid

TABLE 16. Medians and ranges (number/liter) of abundance of several common zooplankton taxa at station SC, April to October 1978. Also abundance on sampling dates closest to start of microcosm experiments 1 and 2.

Taxon	Median	Range	Abundances on:	
			April 5	Sept. 27
A. inermis nauplii	24.4	13.3- 77.7	13.3	19.3
A. inermis post-nauplii	28.1	11.7- 43.2	12.7	36.3
Oithona spp. nauplii	244.0	109.0-298.0	206.0	256.0
O. simplex post-nauplii	81.8	32.6- 96.5	35.0	81.8
O. nana post-nauplii	4.8	1.7- 27.1	3.8	8.0
S. enflata	2.1	1.4- 4.2	3.0	2.7
Rotifers	1.0	0.0- 7.3	0.6	0.9

Figure 18. Microcosm experiment 1. Abundance of A. inermis eggs, nauplii, and post-nauplii, O. simplex eggs and post-nauplii, and Oithona spp. nauplii. The key applies to all parts of the figure. P2 and P3 were the mixed tanks.


OITHONA SIMPLEX
ACROCALANUS INERMIS
NUMBER PER LITER
EGGS
EGGS
NAUPLII
(OITHONA SPP)
NAUPLII
P1
P2
P3
P4
COPEPODITES AND ADULTS
COPEPODITES AND ADULTS
TIME, DAYS

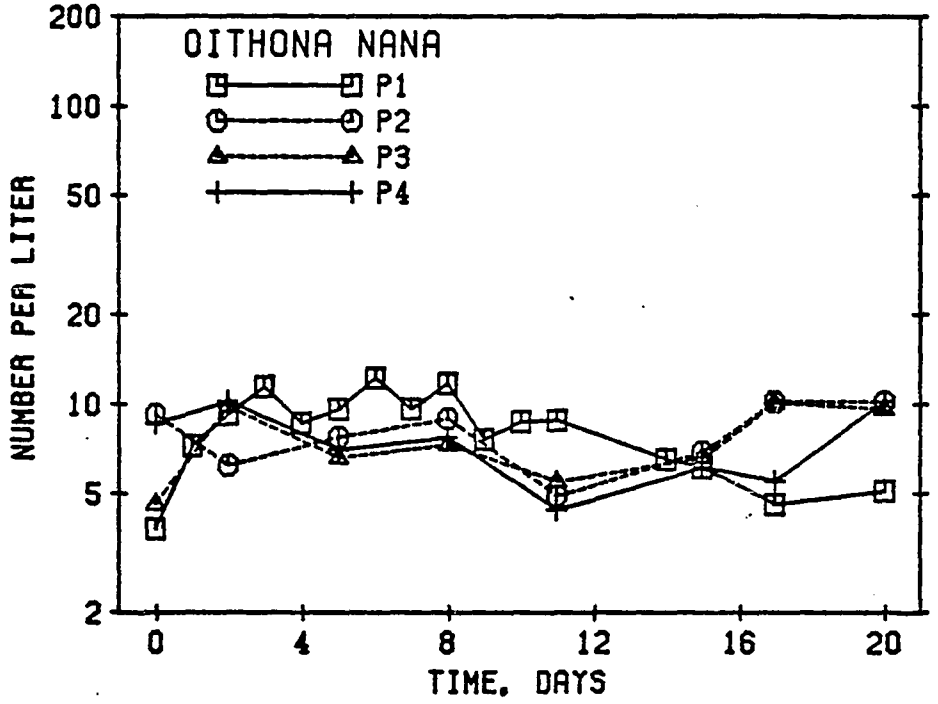


Figure 19. Microcosm experiment 1. Abundance of Oithona nana post-nauplii.

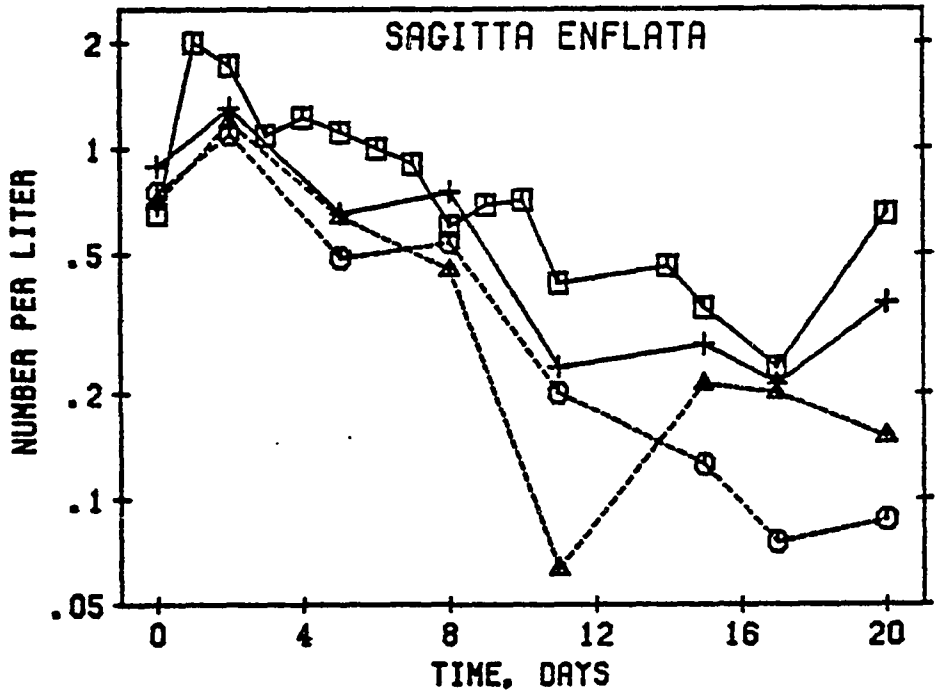


Figure 20. Microcosm experiment 1. Abundance of Sagitta enflata. Key as in Figure 19.

growth followed by decline, although the second period of decline was interrupted by termination of the experiment. As with O. simplex, between-tank variability of egg abundance was high, but eggs had a broad peak in abundance followed by a decline.

Animals were not usually identified to stage, but it was noted in the counts that A. inermis copepodites became progressively less abundant as the experiment continued, until after day 8 almost all of the post-nauplii were adults. Also, nauplii were mainly stage III or earlier. Stage frequencies of about 500 animals from each tank were determined for days 0 and 17 (Table 13). Stage frequencies for day 0 were typical for Kaneohe Bay although high in copepodite stages, suggesting that egg production rate in Kaneohe Bay had been low. In the later sample almost all of the animals were either adults or egg - NIII, with very few late nauplii or copepodites. A similar situation existed with O. simplex, which had very few copepodites by the end of the experiment. Oithona nauplii, though, were mainly the larger stages.

Sagitta enflata (Fig. 20, p. 118) also declined throughout the experiment, more so in the mixed tanks P2 and P3. Most of the chaetognaths in the tanks were small, immature animals, although near the end of the experiment a few reached maturity. These results suggest either damage to the larger animals or avoidance of the pump intake.

While the other copepods decreased in abundance, the harpacticoid Euterpina acutifrons increased (Fig. 21) from a mean of 3 to a mean of 14 (all stages). This species apparently reproduced successfully, since all stages were seen throughout the experiment. Recruitment can be seen in Figure 21 from the tapering off in naupliar abundance

TABLE 17. Initial and final stage frequencies of A. inermis in microcosm experiment 1.

Stage	% Abundance: Initial				% Abundance: Final			
	P1	P2	P3	P4	P1	P2	P3	P4
Egg	15.6	16.3	17.6	12.8	7.7	8.9	8.6	4.5
NI	16.7	17.1	14.8	11.0	10.4	15.8	19.5	5.1
NII	2.6	1.2	4.5	5.4	25.1	36.2	45.9	15.6
NIII	8.3	8.8	8.8	6.8	49.5	34.2	20.8	69.5
NIV	5.5	5.3	6.2	6.0	0.6	0	0	2.0
NV	3.9	3.5	4.7	6.2	0	0.2	0	0.4
NVI	3.1	2.3	2.7	3.3	0	0	0	0.2
CI	5.7	3.9	3.3	3.7	0	0	0	1.0
CII	5.9	5.1	4.9	5.4	0	0	0	0.2
CIII	9.0	9.3	6.6	9.9	0	0	0	0
CIV	12.0	10.3	9.4	13.3	0	0.2	0.4	0
CV	8.1	11.5	11.3	9.7	0.4	0.2	0.6	0.4
Adult female	2.6	4.7	3.7	4.6	5.5	3.2	3.7	1.2
Adult male	1.0	0.8	1.4	1.9	0.8	1.0	0.6	0
Total counted	508	514	512	517	509	505	514	508

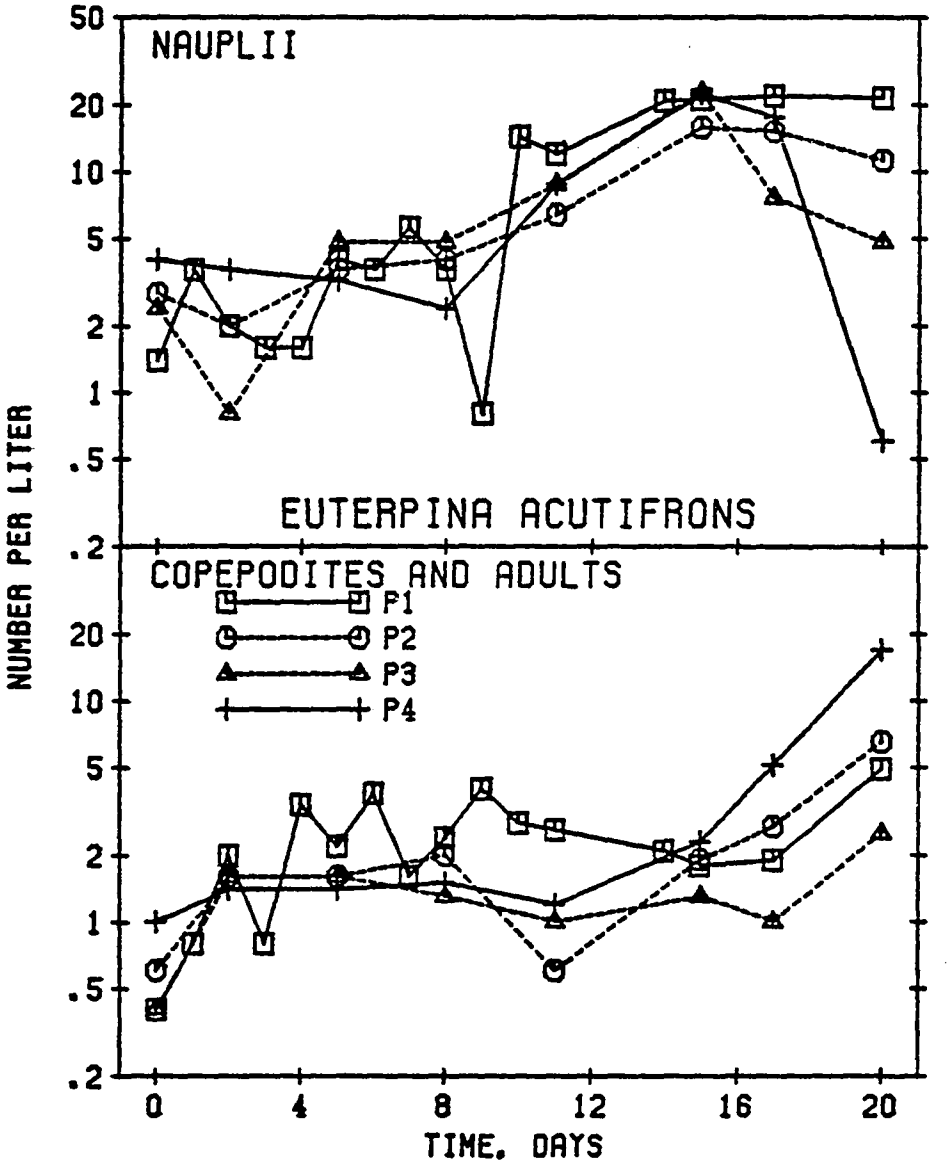


Figure 21. Microcosm experiment 1. Abundance of <u>Euterpina acutifrons</u> nauplii and post-nauplii.

and increase in post-naupliar abundance starting with day 14. Many females in the last few samples were carrying eggs, especially in tank P4.

Rotifers are not abundant in the Kaneohe Bay plankton (Table 16), but grew rapidly in the microcosms (Fig. 22), especially in tanks P1 and P4, then began to decline after day 16.

Larval stages of benthic polychaetes (not shown) did not increase significantly in abundance during the experiment, but their lengths increased by up to 1 cm. These larger larvae apparently lived in the sediments which had accumulated in the tanks, but were caught in the plankton siphon. Mean abundances were 3-4/liter. Most of the large polychaetes were Armandia sp., which may have been spawning when the tanks were filled.

Particulate volume (Fig. 23) showed a significant decrease ($p < 0.001$ by analysis of covariance) over the course of the experiment. Total numbers of particles (Fig. 24) decreased toward the end in the mixed tanks while increasing in the unmixed tanks. This suggests that smaller particles were becoming progressively more abundant in P1 and P4. This can be seen more clearly in the particle size distribution from days 0 and 19 (Fig. 25). The early size distributions showed a broad hump in volume in the middle of the size range that later shifted toward a narrower peak, centered on 6 μm diameter, which was much sharper in P1 and P4 than in the mixed tanks.

Particulate carbon and nitrogen, determined on five dates, also decreased significantly ($p < 0.01$) and were higher in P1 and P4 than in the other tanks near the end of the experiment (Table 18). Total

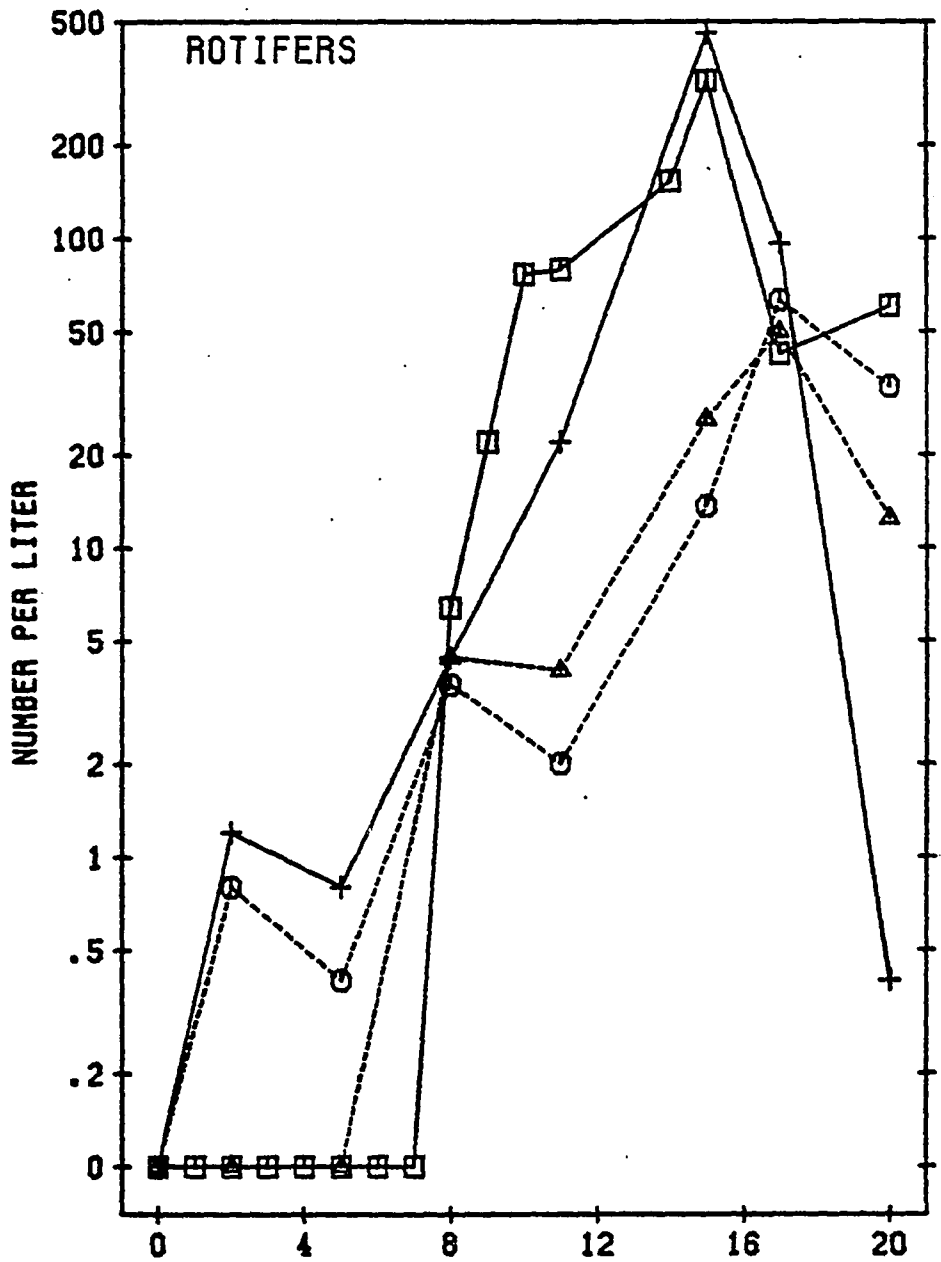
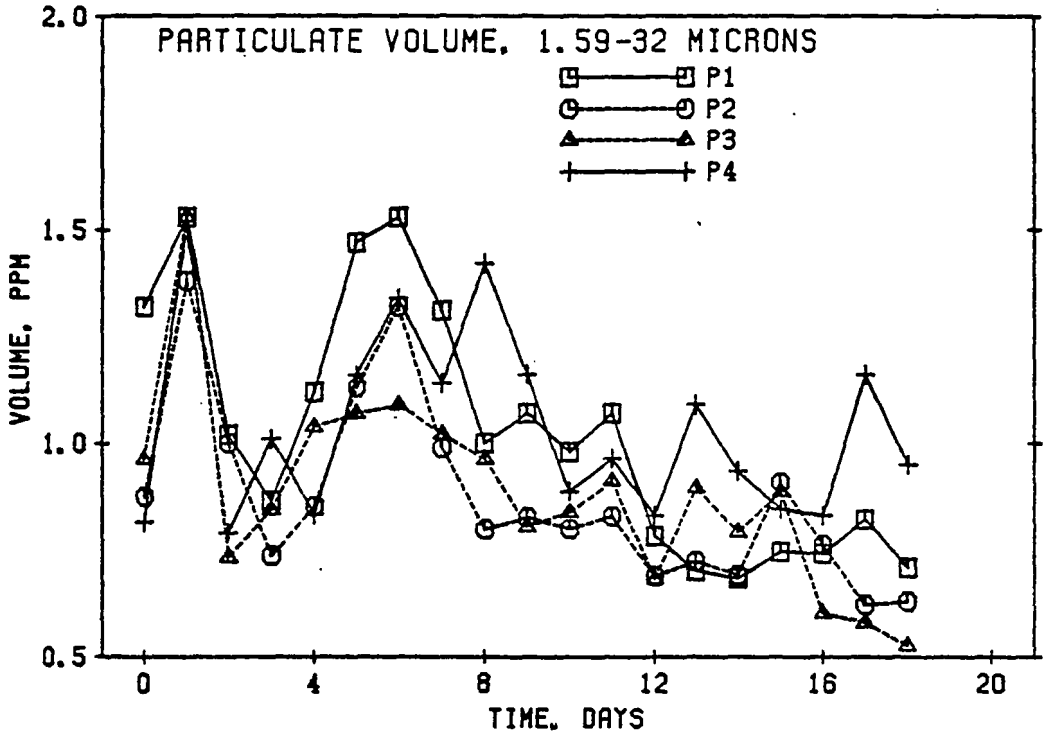
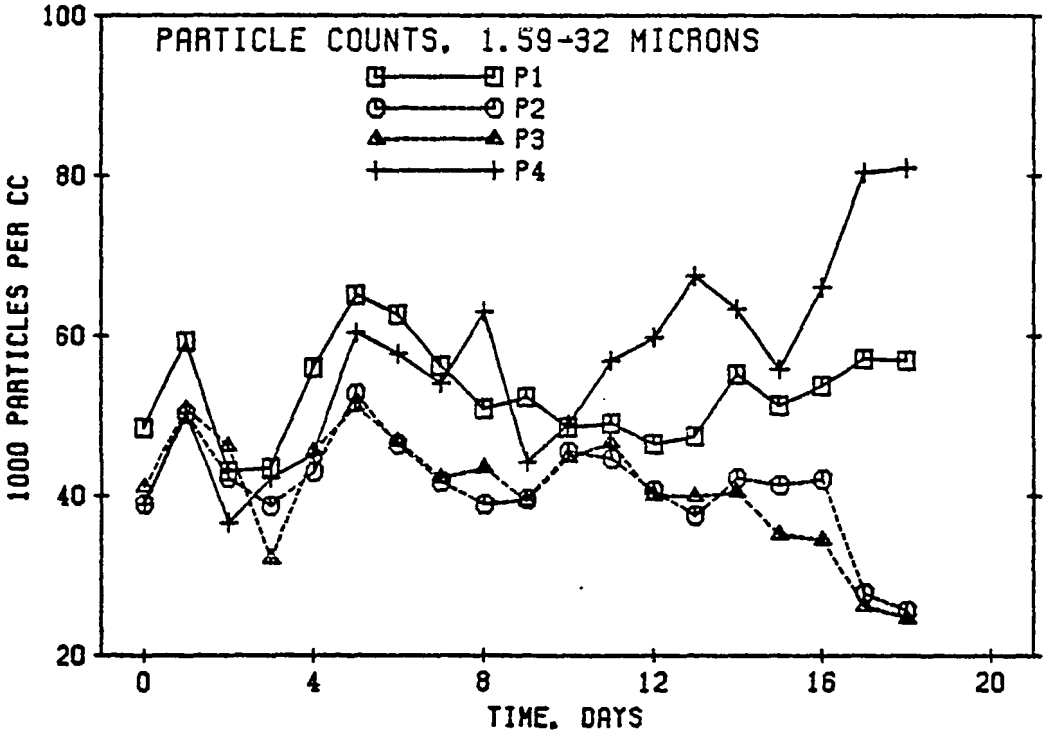


Figure 22. Microcosm experiment 1. Abundance of rotifers. Key as in Figure 21.

Figure 23. Microcosm experiment 1. Particulate volume.

Figure 24. Microcosm experiment 1. Particle counts.


PARTICULATE VOLUME, 1.59-32 MICRONS
P1
P2
P3
P4
VOLUME, PPM
2.0
1.5
1.0
0.5
0
4
8
12
16
20
TIME, DAYS


PARTICLE COUNTS, 1.59-32 MICRONS
P1
P2
P3
P4
1000 PARTICLES PER CC
100
80
60
40
20
0
4
8
12
16
20
TIME, DAYS

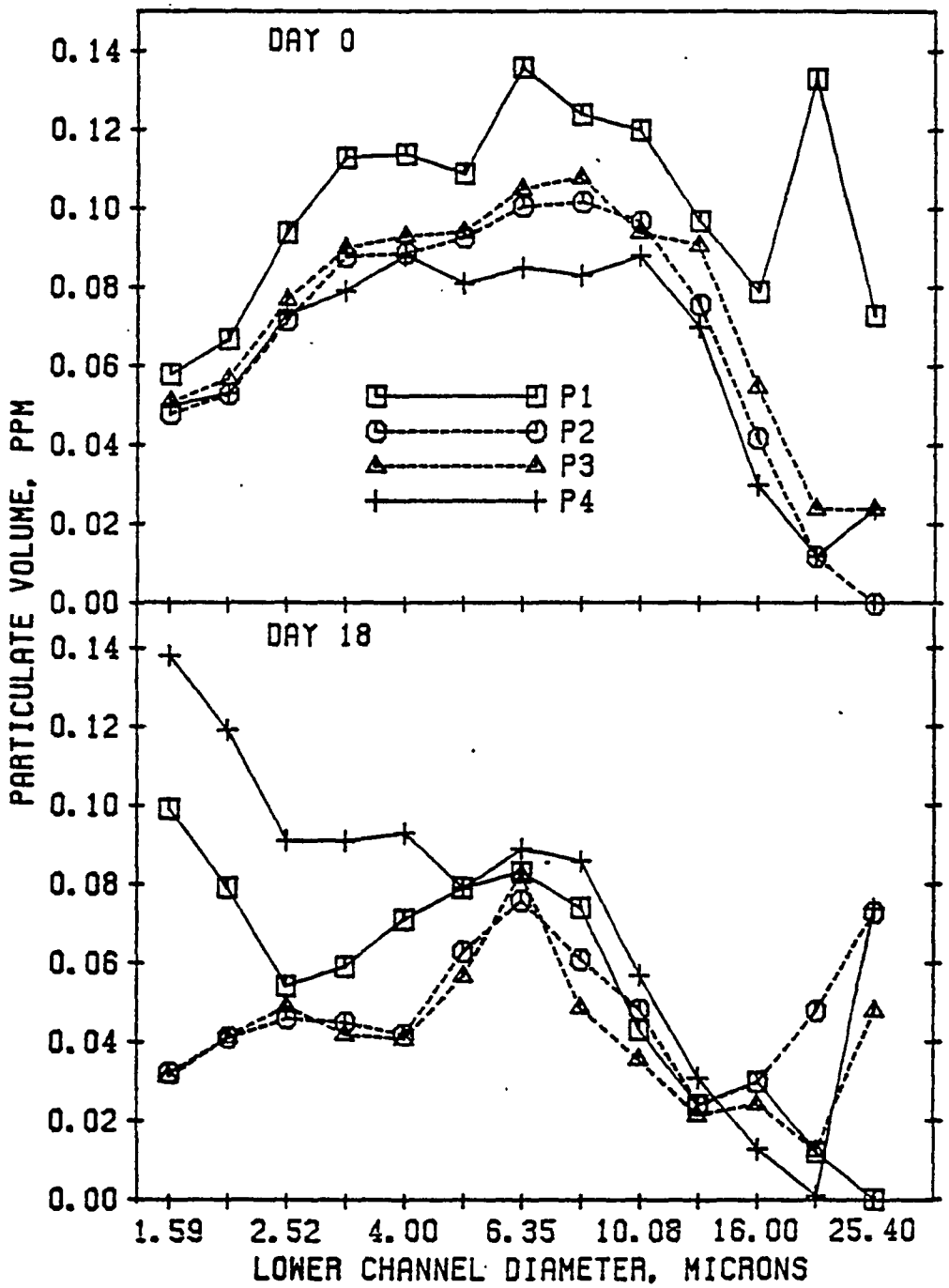


Figure 25. Microcosm experiment 1. Size frequency distribution of particulate volume for day 0 (April 4) and day 18 (April 22) vs. diameter at the lower limit of each channel.

dissolved nitrogen increased slightly but significantly ($p < 0.001$) over the course of the experiment, while ammonium increased only in the mixed tanks (Fig. 26). Nitrate showed a similar trend, going from a mean of 0.09 µg-at/l to 0.34 µg-at/l in P2 and P3 and 0.18 µg-at/l in P1 and P4. Silicate and phosphate showed no trend, with silicate remaining above 5 µg-at/l and phosphate above 0.5 µg-at/l in all tanks.

TABLE 18. Particulate carbon and nitrogen in microsome experiment 1. Values in µg/l.

Day	Carbon				Nitrogen			
	P1	P2	P3	P4	P1	P2	P3	P4
8	82.4	62.8	82.5	82.6	13.3	11.1	19.5	13.3
11	63.5	60.7	70.5	70.9	12.0	11.4	12.2	12.1
14	68.9	63.5	65.0	75.0	12.2	11.7	11.1	13.9
17	61.3	59.7	60.4	73.2	11.6	10.9	10.7	12.1
20	69.8	50.2	52.5	61.9	12.6	10.3	9.9	12.3

Phytoplankton were not counted in these experiments, but it was noted that centric diatoms were present in the preserved samples only during the first few days. A bloom of Chaetoceros socialis occurred on day 1 but soon disappeared. Settled water samples taken on days 6 and 7 contained no diatoms but several large dinoflagellates.

Of several differences in the design of experiments 1 and 2, the most important one was the method of replacing water removed for sampling. Figures 27, 29, and 30 show the rapid decline in common zooplankton taxa which occurred without the addition of fresh Bay water (note the changes in axis scaling). Copepod eggs were not

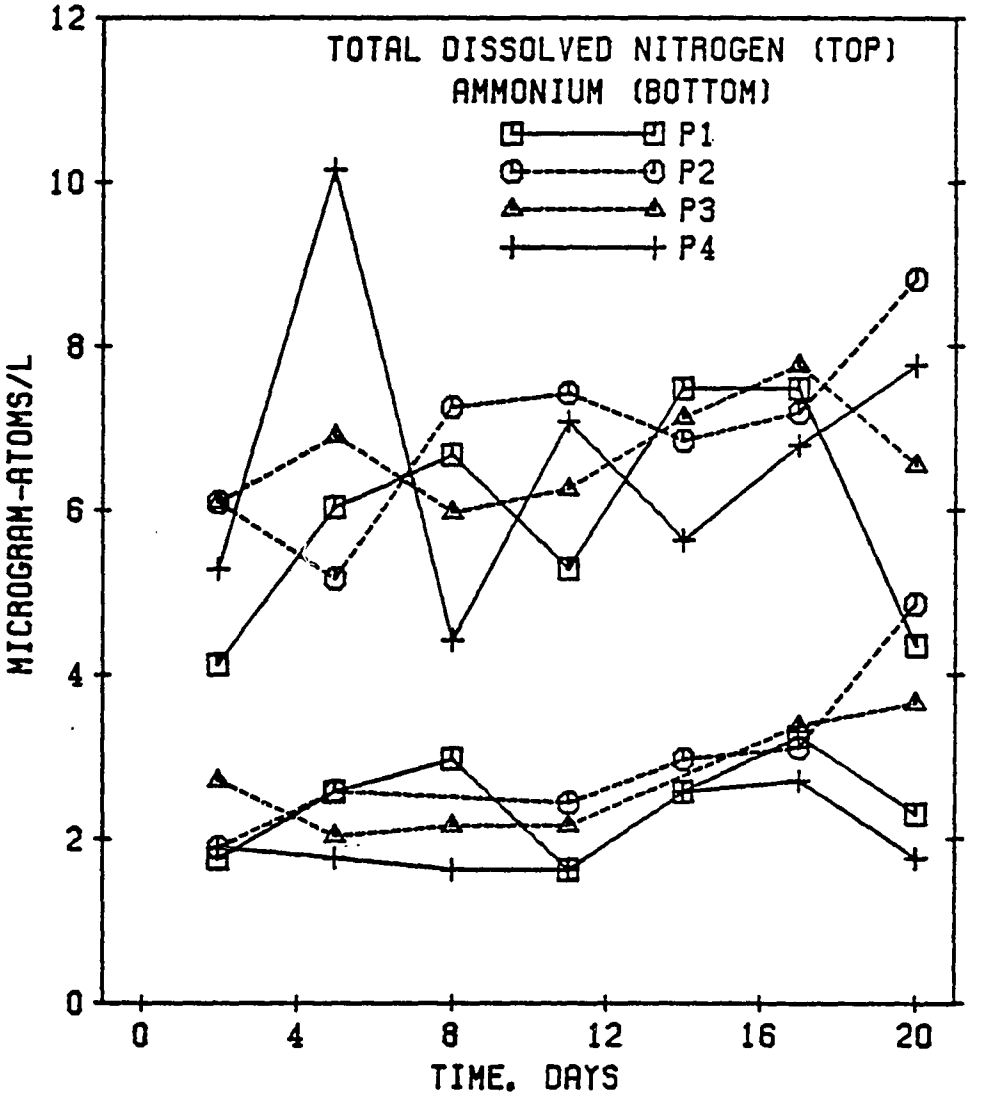


Figure 26. Microcosm experiment 1. Concentrations of total dissolved nitrogen and ammonium.

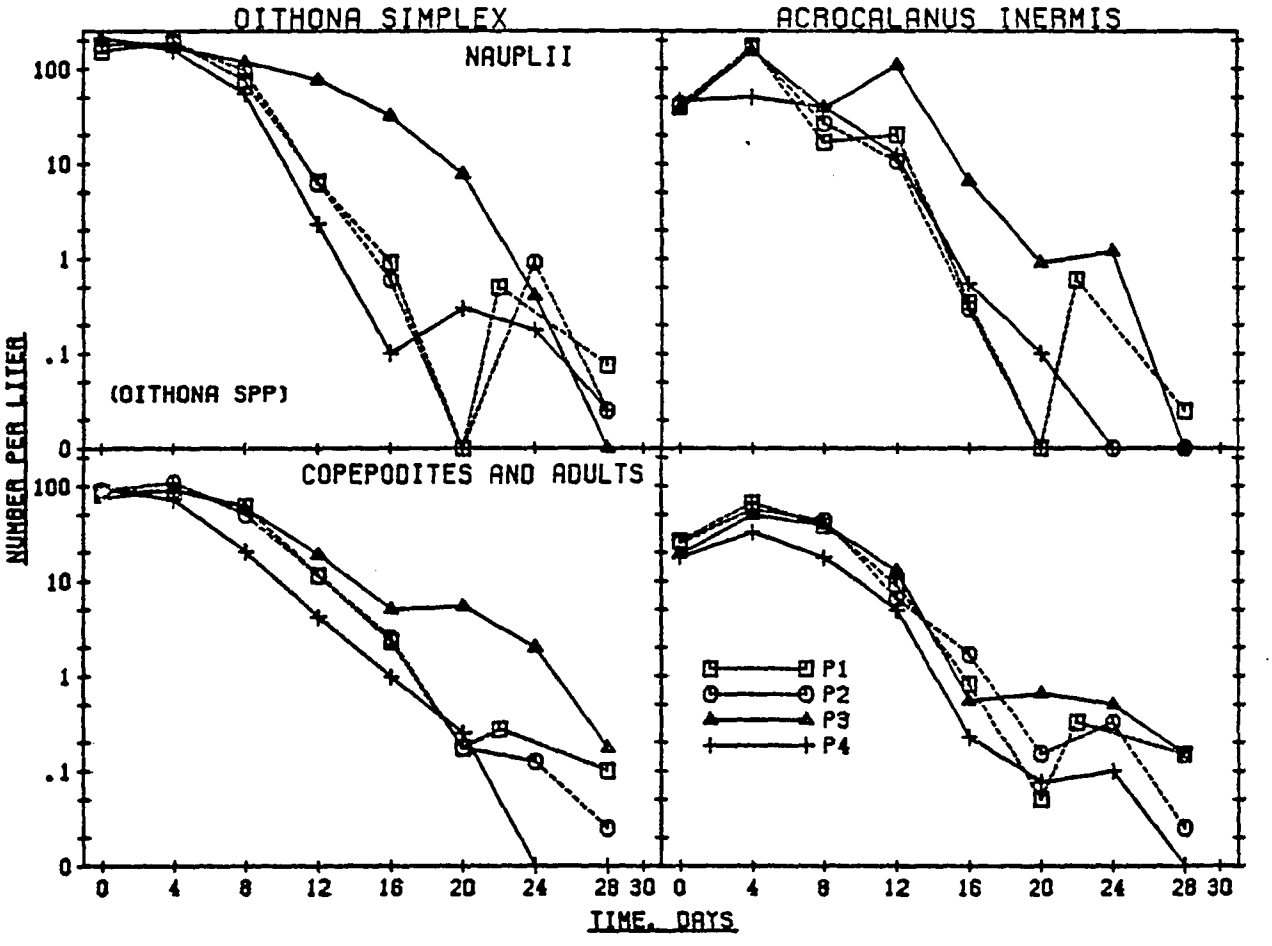


Figure 27. Microcosm experiment 2. Abundance of A. inermis nauplii and post-nauplii, O. simplex post-nauplii, and Oithona spp. nauplii. The key applies to all parts of the figure. Tanks P1 and P2 were the mixed tanks.

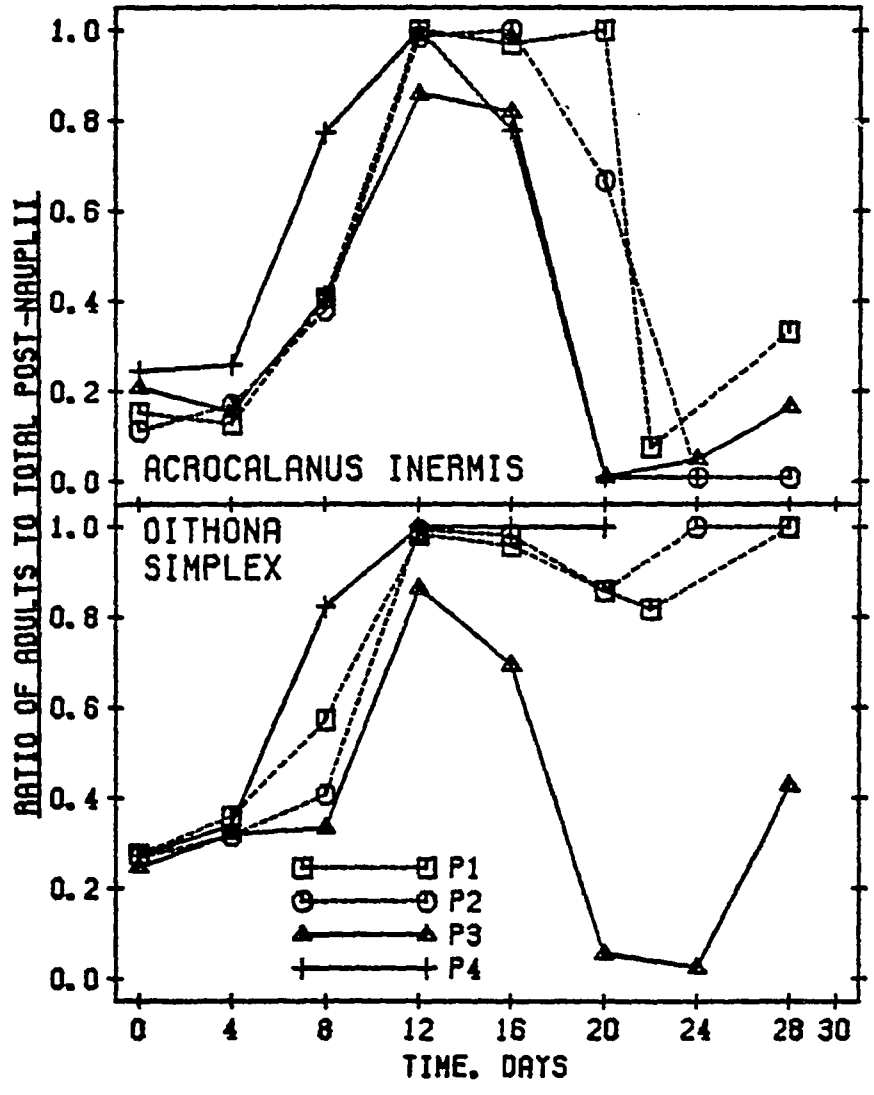


Figure 28. Microcosm experiment 2. Ratios of adults to copepodites plus adults of A. inermis and O. simplex.

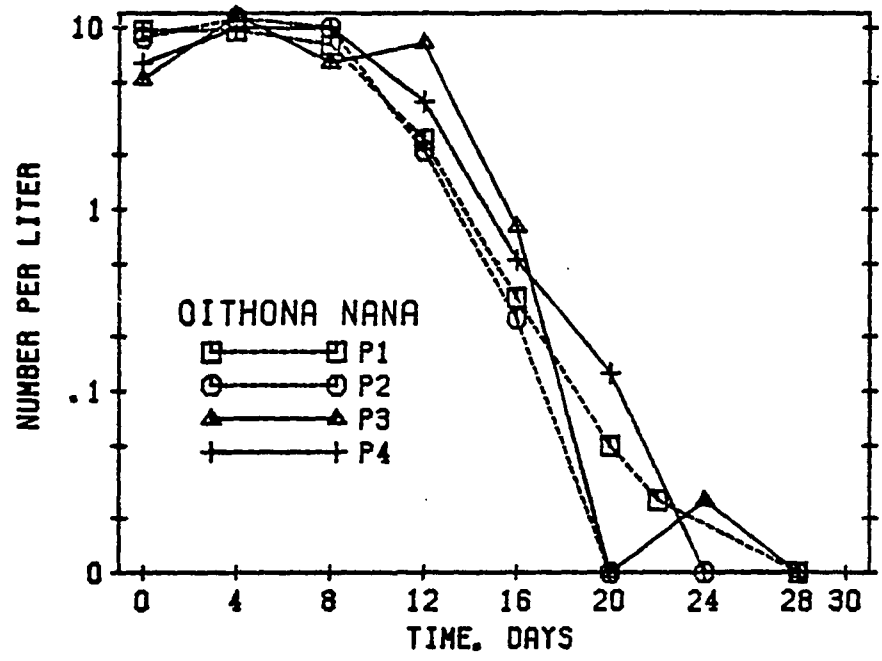


Figure 29. Microcosm experiment 2. Abundance of O. nana post-nauplii.

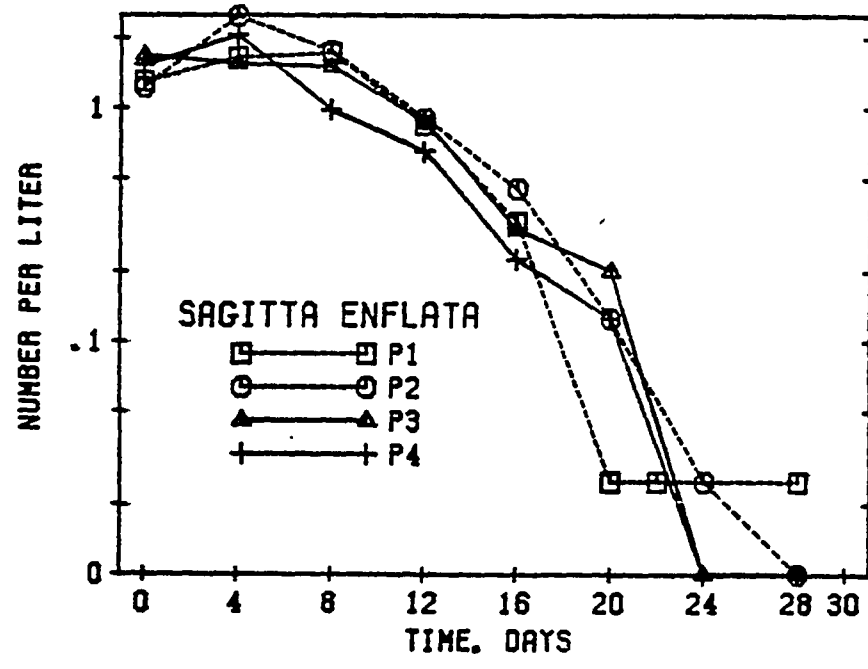


Figure 30. Microcosm experiment 2. Abundance of Sagitta enflata.

counted in this experiment because the samples contained too much detritus, but Olithona and A. inermis nauplii and O. simplex and A. inermis copepodites and adults declined very rapidly (Fig. 27). As before, the post-naupliar stages shifted toward mostly adults by day 12 (Fig. 28), but the drop in the proportion of A. inermis adults in that figure shows that some recruitment took place. Recruitment occurred in both species in tank P3, as can be seen in Figures 27 and 28, but at the end of the experiment both species were nearly gone.

In this experiment, unlike experiment 1, O. nana (Fig. 29) declined slightly more rapidly than O. simplex. S. enflata also declined very quickly (Fig. 30).

Rotifers were not counted in samples before day 20, and were not abundant. They then underwent extremely rapid growth, reaching 3000/liter in P4 on day 20: maxima in tanks P1-P3 were 1000, 690, and 220, respectively. The dinoflagellate Peridinium sp. also underwent a bloom late in the experiment, with abundance as high as 8.1/ml in P1-P3, but the abundance in P4 never exceeded 6/liter. Polychaetes, as before, grew to large size by the end of the experiment, although they were not as numerous as in experiment 1. No other taxa were common at the end of the experiment.

Chlorophyll and phaeopigments (Fig. 31) showed little variability except for peaks in the mixed tanks on day 4, in tanks P1-P3 on day 24, and in P4 at the end of the experiment. The peak on day 24 occurred after several days of very light winds, but average daily light levels were not unusual and the tanks did not warm measurably.

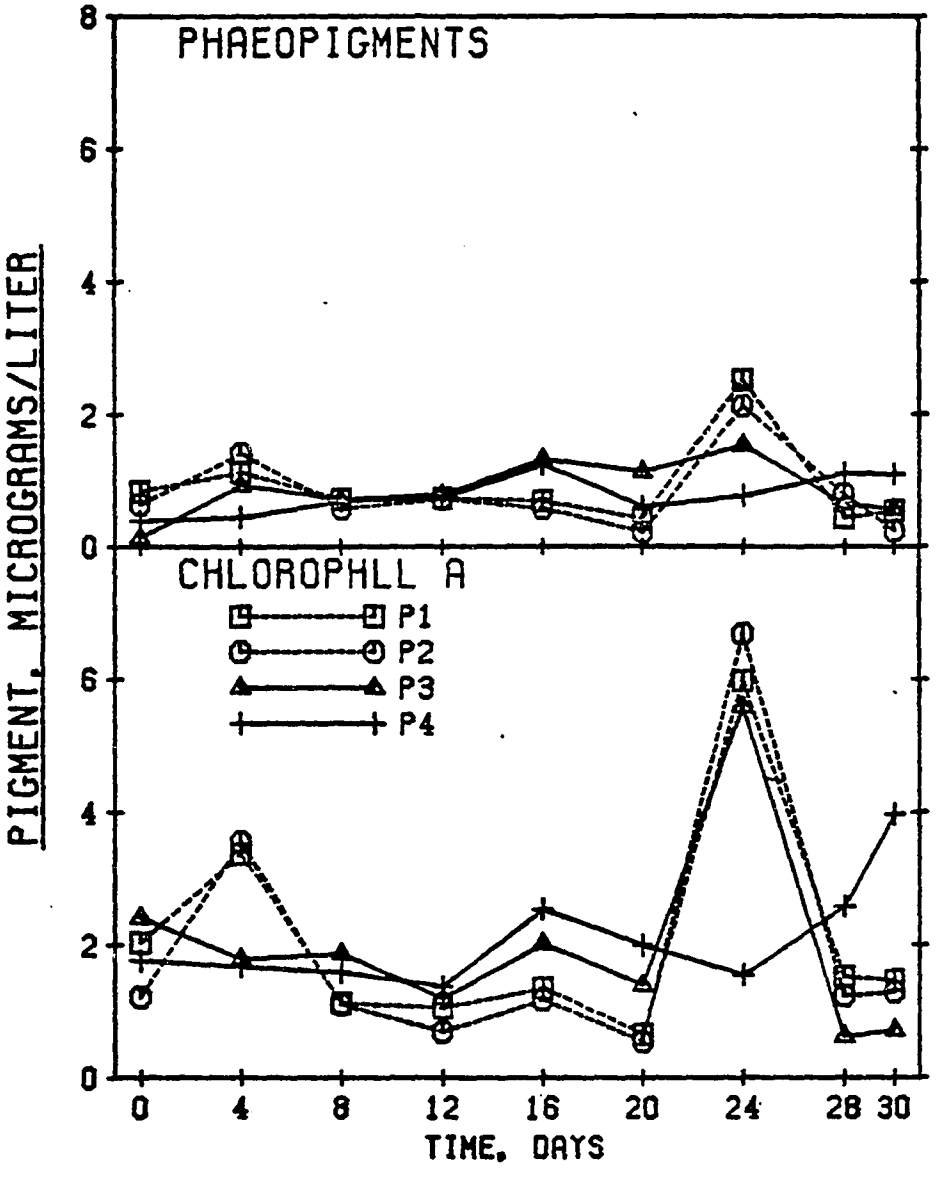


Figure 31. Microcosm experiment 2. Chlorophyll and phaeopigment concentrations.

As in experiment 1, ammonium (Fig. 32) increased in the mixed tanks but not in the unmixed tanks. This time, though, total dissolved nitrogen increased nearly two-fold in P3 and P4, and less in P1 and P2. Nitrate again tracked ammonium, so a large increase in dissolved organic nitrogen must have occurred in P3 and P4. Silicate showed no coherent pattern, but phosphate decreased from a mean of 0.15 to zero or barely detectable by day 28 in all tanks.

Discussion

It is clear that a powerful forcing function was acting on the populations in all of the tanks in all experiments and that they replicated the Bay ecosystem poorly. The rapid population declines in all tanks indicate that these small subsets of the Kaneohe Bay ecosystem became structurally unstable upon enclosure. This does not imply that the subsets themselves, or the Kaneohe Bay ecosystem, are globally unstable, though. The structural instability probably resulted from aspects of the enclosure such as a reduction in turbulence, changes in light level, or other effects of the enclosure which can be loosely termed "wall effects." The possible reasons for the declines in abundance of common taxa will be discussed further.

The strikingly close replication of events in the tanks indicates that the forcing functions were acting on all tanks in the same way. Some features appeared in all tanks well into the experiments. For example, sharp changes in abundance of several of the common species occurred at the same time in all tanks in each experiment. Other features which occurred nearly simultaneously in all tanks were the

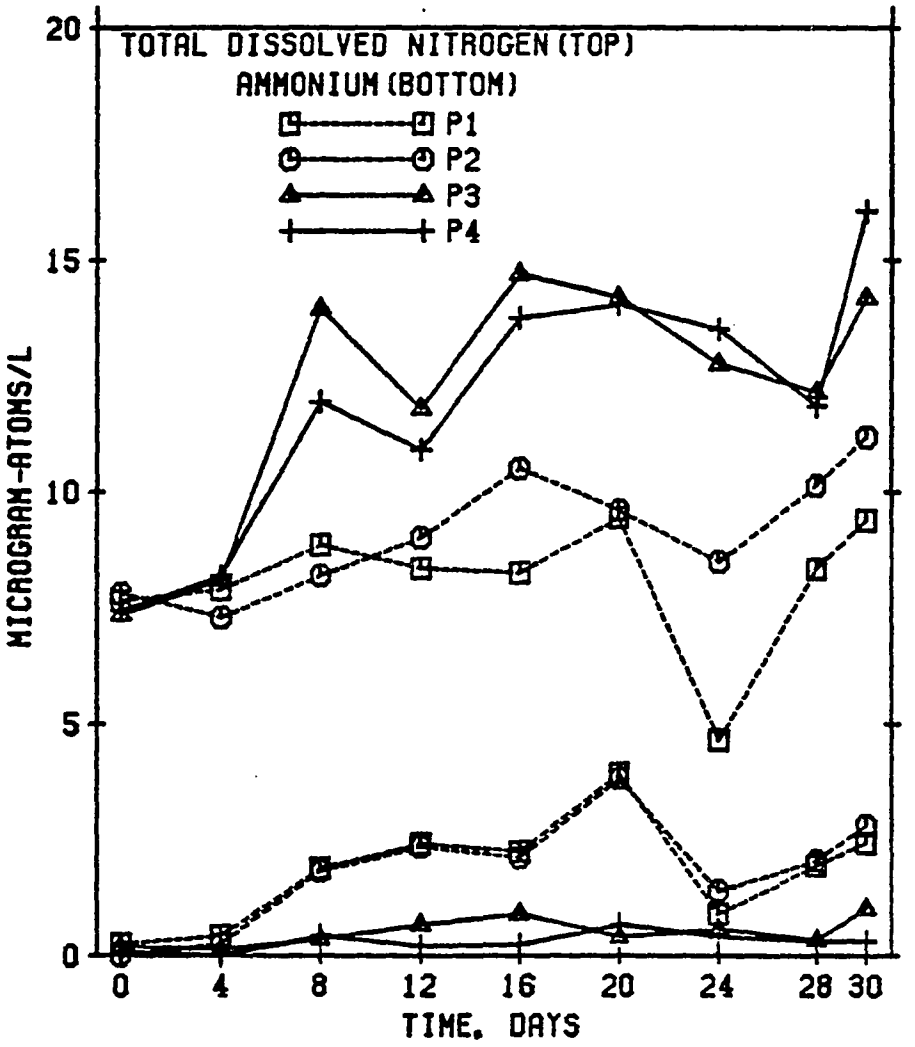


Figure 32. Microcosm experiment 2. Total dissolved nitrogen and ammonium.

increases in ammonium in all tanks starting on day 11 in experiment 1, and the peak in chlorophyll in three tanks on day 24 in experiment 2. Although these co-occurrences could be a result of repeated re-inoculation of all tanks with Bay water in experiment 1, no such inoculations took place in experiment 2. Thus the changes that happened in all tanks several weeks into the experiments were either preordained by the species composition of the inoculum, or a result of changes in light level or temperature.

Takahashi et al. (1975) stated that variables measured in the CEPEX bags changed more over time than between samples on the same date, and used this to argue that spatial heterogeneity does not result from biological events. In my experiments the variance between dates also exceeded that between tanks, especially for the count data. In order to support the conclusion that patchiness cannot arise from events within the water mass, though, we must compare between-tank variability to spatial variability, not temporal variability. As I have pointed out, temporal variability in the field greatly exceeds spatial variability because of seasonal and meteorological effects. In the tanks, successions take place which depend upon the species composition of the inoculum and of any organisms added. In fact, variation between tanks in the count data was on the order of a factor of 2, which is comparable to that for plankton hauls separated by hundreds to thousands of meters in Kaneohe Bay.

Calculation of the dissimilarity index (Chapter II) for the size frequency data from day 0 (one day after initial fill) in experiment 1 gives a value of 58, which is comparable to the values obtained for

stations separated by 1 km. Thus it is quite possible that patchiness observed in the field can arise biologically, and even more so when we consider the effects of schooling and swarming, which are excluded from the microcosms.

It is clear from the graphical results that mixing between the tanks had no effect on stability. None of the common zooplankton species had a reduced variance or rate of decline that could be attributed to the mixing. The few differences between the mixed and unmixed tanks are more likely a result of mechanical stirring than of any effect acting through the dynamics of the enclosed populations, since such an effect would be greatest on the larger, less common organisms. The abundance of Sagitta enflata actually decreased in the mixed tanks relative to the unmixed tanks in experiment 1, but rates of decline were equal in all tanks in experiment 2, so the cause of the increased mortality in experiment 1 was probably mechanical damage by the pump. The other differences between mixed and unmixed tanks were more difficult to explain. They undoubtedly resulted from mechanical stirring in the mixing process, although all tanks were thoroughly stirred during daily cleaning. The high concentration of small particles which appeared in tanks P1 and P4 in experiment 1 may have been bacteria, small flagellates, or detritus, but it is not clear why they were lower in the mixed tanks. Also, the increase in ammonium in the mixed tanks in both experiments suggests either increased excretion or decreased uptake. If the small particles in P1 and P4 in experiment 1 were autotrophic, it is possible that their absence in the mixed tanks allowed a rise in ammonium. In any case, the high ammonium values

overall in experiment 1 point to limitation by light or by another nutrient.

The cause of the rapid decline in abundance of most common species in all experiments bears further investigation. Other enclosed ecosystems have reasonably replicated events in the source water over periods up to several months (e.g. Takahashi et al. 1975; Gamble et al. 1977; Perez et al. 1977) except for the 750-liter tanks of Heinle et al. (1979). In those experiments, like mine, rotifers increased markedly and copepods decreased. The copepods failed to reproduce after 10 days in those tanks, and adults were smaller than normal, both apparently because of starvation. Menzel and Steele (1978) stated that a minimum volume of 10-100 m^3 is required in order for a microcosm to replicate its source with two trophic levels, and it is tempting to speculate that the larger microcosms can maintain their populations because of internal spatial heterogeneity. It has been noted that considerable patchiness can exist within those containers (Conover and Paranjape 1977; Takahashi et al. 1975). Perez et al. (1977), however, showed reasonable replication of most variables for one month in 150-liter containers. "Total grazers" (Perez et al. 1977), presumably mostly Acartia clausi or A. tonsa, did not crash in those experiments. Oviatt et al. (1977) maintained the same microcosms for over six months without a crash in the zooplankton populations. Thus size alone does not determine the realism of simulation attained in a microcosm. One difference between my experiments and those of Perez et al. (1977) and Oviatt et al. (1977) is their use of a small box containing sediment to simulate the effect of the benthos on the water column; however,

Perez et al. (1977) showed that reducing the amount of sediment to zero actually increased the mean number of planktonic grazers, and a preliminary experiment run with sediment in my microcosms had the same outcome as the experiments reported here. The failure of my microcosms to replicate Kaneohe Bay could also be attributed to the fact that this subtropical ecosystem may be fundamentally different from the temperate systems used in all other microcosm studies. The smaller organisms and correspondingly higher turnover rates, for example, could have accelerated the decline in species abundance. Still, this fails to explain the crashes seen in the experiments done in Chesapeake Bay (Heinle et al. 1979), where the fauna are more similar to Narragansett than to Kaneohe. Thus the reason for the difference remains unresolved.

The abundance of the common copepods declined either because of a decrease in recruitment or an increase in mortality or both. A rise in mortality could have resulted from an increase in predation or from disease or parasitism. In experiment 2, A. inermis adults were infested by what appeared to be epizoic diatoms, but these probably did not increase their mortality rate. Ikeda (1977) reported apparently healthy copepods covered with diatoms, and I have seen freshly caught E. acutifrons covered with small cells but otherwise apparently healthy.

No other evidence of disease or infestation was visible on any animals in these experiments. It is possible that in experiment 1 the eggs of A. inermis became diseased, though. Egg development time is normally only eight hours, yet the abundance of eggs did not track

that of nauplii. Thus most of the eggs must not have been hatching. While this could have resulted from malnutrition in the females, the results of Chapter IV suggest that egg production rates should decrease under food deprivation. Thus disease appears to be the logical explanation for the unviability of these eggs.

The release of predation pressure caused by exclusion of fish and removal of larger chaetognaths caused an initial increase in copepod abundance in experiments 1 and 2. For the subsequent decline to have been caused by predation would require an increase in abundance of some predator, but no new predator appeared in the tanks to explain this decline. Thus predation does not appear to have increased copepod mortality in these experiments.

The remaining possible cause of the decline in copepod abundance is a failure to recruit. Very few of the A. inermis nauplii molted past NIII. Since this is probably the first stage that feeds, the nauplii were most likely starving. Nauplii of Calanus pacificus can starve and still molt once (Fernandez 1979) but as adult copepods differ in their ability to withstand starvation (Dagg 1977), nauplii probably do too, and small tropical copepods such as A. inermis and O. simplex are not likely to be resistant to starvation. Thus starvation is a reasonable explanation of the failure of A. inermis to molt past NIII.

The stage at which O. simplex ceased to grow was not determined, but it must have happened during naupliar development to account for the disappearance of copepodites in experiments 1 and 2. It is reasonable to assume that starvation prevented recruitment in this species also.

Several other findings suggest that the copepods were not feeding heavily on the particulate matter in the tanks. There was never an increase in particulate counts or chlorophyll to match the decrease in copepod abundance; thus the feeding rates must have been low throughout the experiments. The ratio of phaeopigment to total chlorophyll in experiment 2 also did not change appreciably with the decline in copepod abundance. Finally, it is unlikely that the copepods were reworking detritus, as was observed in the Loch Ewe experiments (Davies et al. 1975), because the C:N ratio of particulate matter in experiment I did not change as copepod abundance decreased.

Particulate matter, as measured by particulate counts in experiment 1 and chlorophyll in experiment 2, was not in short supply in either experiment, so it must have been somehow unsuitable as food. Detritus can be a poor food source (Paffenhöfer and Knowles 1978), but, as pointed out above, the low C:N ratios rule out the possibility that the copepods were reworking detritus. Phytoplankton vary in their suitability as food, though, both for post-nauplii (Parsons et al. 1967) and for nauplii (Fernandez 1979). Centric diatoms, normally very abundant in Kaneohe Bay, disappeared from the tanks early in the experiments, and this could have contributed to starvation in the nauplii. The loss of diatoms may have been due to reduced turbulent energy of the water in the tanks compared to that in the Bay. Although the tanks were scrubbed thoroughly each day, it is possible that rapid growth of algal film occurred on the sides of the tanks. Algae attached to the tank walls would have a considerable advantage over planktonic algae and could efficiently strip nutrients from the water.

The high nutrient levels in these experiments show that the limiting nutrient, if any, must have been a trace nutrient.

Under the assumption that the decline in abundance was caused by a failure to recruit, the mortality and maximum recruitment rates of the copepods in these experiments can be estimated from the data on abundance of nauplii and post-nauplii. The rate of change of post-nauplii in experiment 1 is:

$$\frac{dC}{dt} = CoW + R - (W + M)C$$

where C is the abundance of animals (number/liter), Co is their abundance in the replacement water, R is the recruitment rate (number liter^{-1} day^{-1}), W is the washout or sampling rate (day^{-1}), and M is the mortality rate. For experiment 3 the first term, CoW, is omitted because there was no replacement of animals. Since nauplii are lost through molting to copepodites an additional loss term is subtracted from the recruitment rate R for nauplii.

Because the time-varying form of the mortality and recruitment functions was unknown and because of difficulties in fitting data to functions of this kind (Silvert 1979) a stepwise approach was used. The above equation was rearranged to give (for experiment 1):

$$R - M\bar{C} = \bar{C}\,\frac{\Delta \ln(C)}{\Delta t} + W(\bar{C} - Co)$$

where $\Delta \ln(C)$ is evaluated over each time interval Δt, and $\bar{C}$ is the geometric mean abundance in the interval. Mortality was estimated by assuming it to be constant and by assuming recruitment to be near zero during the intervals with the maximum rates of decrease. The expression above had a maximum value in the first time step (and

later in experiment 1 for A. inermis nauplii) where abundances of both species increased in both experiments. For post-nauplii the maximum recruitment was evaluated for this time step by assuming mortality to be constant; for nauplii the recruitment determined in the same way was corrected by adding on the recruitment of the post-nauplii. The resulting mortality rates and maximum recruitment rates are presented in Table 19. The recruitment rates are maxima because the expression ($R = M\bar{C}$) could be increased either by increasing recruitment or by decreasing mortality. Both were probably the case for A. inermis, because the reported recruitment rates correspond to egg production rates of about 20 per female per day, greater than the maximum seen in the egg production experiments (Chapter IV). The egg production rate for O. simplex in experiment 2 (the abundance of females in experiment 1 was not determined) was only 6 per female per day.

TABLE 19. Estimated values for mortality and recruitment rates for O. simplex and A. inermis in microcosm experiments. See text for a description of how these were estimated. Mortalities are in day^{-1}, and recruitment rates in numbers $liter^{-1}$ day^{-1}.

Experiment	Taxon	Mortality	Recruitment
1	O. simplex post-nauplii	0.15	4.5
	Oithona nauplii	0.34	70
	A. inermis post-nauplii	0.13	5.5
	A. inermis nauplii	0.69	40
2	O. simplex post-nauplii	0.34	35
	Oithona nauplii	0.51	130
	A. inermis post-nauplii	0.42	27
	A. inermis nauplii	0.81	106

Mortality rates for post-nauplii and for Oithona nauplii were low in experiment 1 compared to data determined for A. inermis in the field (Chapter III), but closer for A. inermis nauplii in experiment 1 and for all in experiment 2. The higher mortalities in experiment 2 for all but A. inermis nauplii probably occurred because the animals were older on the average than in experiment 1, as they were not being replaced.

In summary, the microcosms failed to replicate the Kaneohe Bay planktonic ecosystem and therefore did not provide an adequate test of the hypothesis that mixing among patches can stabilize the ecosystem. The results did, however, suggest that mixing among patches is not likely to be important. The microcosms probably failed to replicate the Bay because of a shift in species composition of the phytoplankton, caused perhaps by a decrease in turbulence, and the resulting starvation and recruitment failure of the copepods. Thus the experiments also did not test the hypothesis that small subsets of the ecosystem are globally stable because of the large change in physical conditions imposed on them.

CHAPTER VI

CONCLUSIONS

Although spatial variability in rate functions occurs in Kaneohe Bay, it is not likely to be an important property of the ecosystem. Temporal variability in stage frequency distributions and egg production rates greatly exceeded spatial variability, even over short time intervals, and P:B showed little variability either in space or in time.

Apparently in south Kaneohe Bay most of the time the production of small copepods such as A. inermis is not food limited. The low variability in P:B compared to biomass suggests that the populations were growing at a constant rate most of the time; the single low P:B value was related to low feeding rate and food concentration. Egg production rate, apparently more sensitive to food concentration, varied more than P:B both spatially and temporally. The high temporal variability in stage frequency distributions of A. inermis was probably caused mainly by this variability in egg production rates. For example, the extremely low egg production rate seen in the March 1979 experiment could easily have led to the kind of top-heavy stage frequency distribution seen in the July 1978 P:B experiment. The variability in egg production rate in turn resulted indirectly from meteorological changes affecting the food supply in the entire south Bay. The data on egg production rates are insufficient to show what

caused these changes or how often the egg production rates were reduced because of low food concentrations. Nevertheless, most of the egg production rates fell between 9 and 15 eggs/female/day, with considerably lower values on two dates. Thus egg production rate may also not be food limited much of the time. This means that these populations of copepods are either controlled by predation or that, if they are controlled by food limitation, this limitation acts only infrequently. Probably some combination of these is the case.

The relative lack of importance of spatial variability in rate functions is inferred mainly from their relatively greater temporal variability. In particular, there was almost no fixed spatial component of the variation in any property measured. This was true in spite of a steep gradient in particulate concentration between stations OF and SC during trade wind conditions (Kimmerer et al. 1980). Although this gradient was much more pronounced before sewage diversion at the end of 1977, it was still detectable in 1979, and particulate concentrations remained higher at OF than at SC throughout this study. Still, the stage frequency distributions showed no significant fixed spatial variation even between OF and SC. The single instance of a significant spatial component of variation of P:B occurred because the P:B was unusually low at SC, not high at OF, compared to the long-term mean.

The time-varying spatial component of variance was greater than the fixed spatial component for stage frequencies and egg production rates, but less than the temporal component. This agrees with the results of Platt and his co-workers (Platt and Filion 1973;

Therriault et al. 1978), who found the phytoplankton productivity index to vary more temporally than spatially, and not to have a significant fixed spatial variance component.

If temporal variation in system forcing functions were affecting all components of the system equally then it could not mitigate destabilizing effects such as competition and predation. There is some evidence that these forcing functions (wind speed, nutrient input rate, etc.) affected different populations differently. The stage frequency distributions of A. inermis and O. simplex were quite different, indicating that their egg production rates responded differently to environmental forcing functions. In the microcosm experiments the nauplii of Oithona spp. survived through several stages while those of A. inermis failed to molt past the first feeding stage. Both of these are evidence that the two species feed on different sizes or kinds of food. Therefore variability in environmental forcing functions, by altering the food supply, could favor one species over the other. Since the forcing functions vary far more temporally than spatially, the relative advantage to these two species should shift more in time than in space. This indicates that the time-varying component is of greater importance to the ecosystem.

Most studies of patchiness focus on horizontal variability. This one is no exception, because in relatively shallow, vertically well-mixed Kaneohe Bay at least the non-motile plankton should be evenly distributed in the water column. This assumption is not justified for motile organisms, which can adjust their depth, and the data

presented here suggest that A. inermis undergoes an ontogenetic vertical migration. Still, with vertical or oblique net samples and with such a shallow water column the effect of vertical variability may be small. In the open ocean, however, vertical gradients in abundance can be several orders of magnitude larger than horizontal gradients. A given organism migrating vertically through these gradients experiences enormous variability in abundance of food and predators. If spatial heterogeneity is important to the stability of ecosystems, it seems that vertical heterogeneity should play a much greater role than horizontal heterogeneity. Clearly the former is far more important in determining the feeding rates of individual organisms.

The microcosm experiments were intended as analogs to parcels of Bay water, with turbulent diffusion between parcels simulated by daily mixing between two of the tanks. Instead of behaving similarly to Bay populations, however, the populations in the tanks underwent drastic shifts in abundance upon enclosure. This indicates that the subsets of the ecosystem which were placed in the tanks were structurally unstable with respect to that enclosure. This instability resulted in some way from an alteration of the driving functions of the system. Several possible mechanisms come to mind. One immediate result of enclosure was a large reduction in turbulence in the water, which probably caused the elimination of planktonic diatoms from the system. Another immediate result was the reduction of predation pressure by exclusion of large predators; this caused an initial rise in herbivore abundance and the herbivores may then have grazed down

their food supply. This does not explain why the release of grazing pressure by the decline in herbivores did not permit a comeback by the food organisms. Nutrients were apparently plentiful, although concentrations of only the major nutrients were determined, so it is possible that some trace nutrient became limiting. If so, the benthic community may have been successfully competing for this nutrient. Another possibility is disease or infection, which apparently occurred in the eggs of A. inermis. The most likely explanation for the collapse of the copepod populations, though, is the loss of a suitable food supply.

The close tracking of populations in all of the tanks indicates that the forcing functions brought on by enclosure acted on all tanks equally. This was a surprising result, since it was expected that differences in abundance of relatively rare predators between the tanks might cause them to diverge. Especially in experiment 2, all changes that occurred were in a sense preordained by the makeup of the community in the Bay water put in the tanks, but the abundances of relatively rare organisms were unimportant to the outcome of the experiment. This again points to limitation from the bottom of the food web, either through reduction in turbulence or through nutrient depletion, as the cause of the collapse.

Whatever the cause, it could be argued that the rapid alteration of the system by the enclosure made the mixing experiments superfluous. There was obviously little effect of mixing on system stability, but the system being examined could no longer be considered representative of Kaneohe Bay. An exact replication of Bay conditions was of course

neither needed nor expected, since the experiment could be performed on any ecosystem, including an artificial one. The fact that mixing did not stabilize these experimental ecosystems suggests that it might not do so in real ecosystems, but the collapse of the enclosed systems does not imply that subsets of the Bay system are themselves unstable.

Another surprising result of the microcosm experiments was that the levels of chlorophyll and particulate matter did not seem to be affected very much by the abundance of herbivores. Either the coupling between trophic levels (i.e. the effect of a trophic level on the next higher or lower level) is not close, as has been suggested by Perez et al. (1977), or the herbivores are considerably more selective in their feeding than has been thought. The latter is also suggested by the starvation of the copepods in the face of a seemingly plentiful food supply. Either case points up a need for further information on the trophic structure of ecosystems. Such information is essential for an understanding of such relative subtleties as the effects of spatial and temporal heterogeneity on ecosystems. Nevertheless, my results suggest that horizontal spatial variability is not important to stability of the Kaneohe Bay planktonic ecosystem.

APPENDICES

APPENDIX A

RELATIVE STAGE FREQUENCIES OF MICROCOPEPODS FROM SPATIAL SAMPLING IN 1976 AND 1977

TABLE 20. Relative frequencies of stages for A. inermis in experiment 1. Stations are arranged from north to south in this and subsequent tables.

Station	CI	CII	CIII	CIV	CV	Adult
11	46.3	25.4	15.0	7.2	4.0	1.8
10	35.2	14.7	21.3	9.0	10.6	9.0
9	37.2	19.2	16.3	14.2	9.2	3.7
8	37.3	18.3	17.3	14.1	7.9	4.8
7	28.6	25.3	23.5	10.5	6.1	5.7
6	33.2	18.2	17.5	15.0	11.0	5.0
5	23.1	15.9	14.9	20.2	16.9	8.6
4	32.4	21.2	14.7	13.4	10.3	7.7
3	40.3	18.8	11.2	8.0	13.4	8.0
2	31.0	12.6	17.9	13.0	10.6	14.6
1	29.6	19.4	12.9	11.1	17.5	9.2

TABLE 21. Relative frequencies of stages for O. simplex in experiment 1.

Station	CI	CII	CIII	CIV	CV	Adult
11	10.4	16.3	15.3	14.1	11.6	31.9
10	10.8	15.4	19.5	12.1	15.4	26.2
9	13.1	16.2	14.4	15.2	11.6	29.1
8	12.5	14.3	13.9	10.6	18.4	30.0
7	11.1	14.6	15.6	12.7	13.7	32.1
6	12.5	11.6	22.7	14.3	11.3	27.4
5	15.3	10.9	15.6	8.7	14.2	35.0
4	20.4	15.9	13.5	10.4	11.9	27.7
3	27.8	16.2	10.1	8.3	9.3	28.0
2	26.0	17.6	11.6	11.3	8.6	24.6
1	19.7	15.2	13.5	9.0	13.5	28.8

Table 22. Relative frequencies of stages for A. inermis in experiment 2

Station	NI	NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV	Adult
1	6.6	9.5	23.2	14.6	14.1	6.2	4.6	1.7	1.3	4.2	4.4	9.0
2	2.6	7.3	18.7	17.8	11.9	3.6	5.6	3.3	3.6	6.8	6.8	11.4
3	4.2	5.0	30.7	21.6	11.5	4.2	4.8	1.3	1.4	3.5	4.2	6.8
4	2.3	5.1	26.9	24.5	14.7	2.3	3.5	2.1	1.5	1.9	4.6	9.9
5	1.7	4.6	26.8	20.4	16.4	0.3	2.7	1.4	2.7	4.0	3.1	14.6
6	0.8	2.0	32.0	20.7	13.3	1.6	2.4	0.8	2.4	4.3	6.2	12.6
7	2.1	2.7	27.1	22.2	17.7	1.6	2.1	0.1	2.3	3.4	6.6	11.4
8	3.5	2.6	28.1	22.9	14.9	4.1	3.0	1.7	1.1	1.9	3.0	12.5
9	11.8	13.7	20.0	15.8	6.9	1.6	1.6	2.5	2.1	5.0	5.2	13.0

Table 23. Relative frequencies of stages for O. simplex in experiment 2.

Station	CI	CII	CIII	CIV	CV	Adult
1	10.1	10.1	10.4	16.8	13.3	38.8
2	8.9	8.9	14.4	14.9	14.4	38.2
3	16.2	22.7	13.2	13.0	9.3	20.1
4	9.8	23.6	17.7	14.2	10.3	24.1
5	10.2	26.3	17.4	11.3	11.3	23.3
6	13.0	22.1	20.2	16.5	11.4	16.3
7	10.2	20.6	21.6	13.6	12.0	22.0
8	12.4	34.5	21.8	12.1	8.4	10.4
9	19.3	34.0	24.3	8.9	4.8	8.2

TABLE 24. Relative frequencies of stages for A. inermis in experiment 3.

Station	NI	NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV	Adult
1	2.0	0.3	7.8	11.3	10.6	1.7	15.4	8.9	14.0	11.3	6.8	9.5
2	4.5	0.3	10.5	9.3	12.4	3.0	18.4	10.9	9.0	6.3	5.6	9.3
3	0.6	0.6	6.8	12.1	14.9	2.1	15.2	11.5	11.2	10.5	4.3	9.6
4	2.0	0.3	11.3	14.0	15.3	5.6	17.7	11.7	6.6	5.6	5.6	3.6
5	1.1	0.3	7.0	12.4	14.0	3.5	20.6	10.8	13.2	7.0	2.7	7.0
6	1.8	0.6	14.0	10.2	13.0	4.3	19.3	13.0	8.4	4.9	4.3	5.6
7	2.8	0.9	8.2	14.5	16.4	6.3	19.2	14.1	6.9	5.9	2.8	1.5
8	1.9	0.3	14.1	16.0	14.1	8.4	19.9	11.4	6.1	3.0	2.6	1.5
9	2.8	2.0	11.5	14.1	15.5	6.0	19.6	11.8	7.5	3.4	1.7	3.4
10	2.8	2.1	12.5	12.9	11.1	3.2	20.7	13.9	8.2	5.0	3.2	3.9
11	2.4	2.8	9.6	10.3	12.8	3.9	22.7	13.5	10.3	4.6	3.5	3.2
12	3.1	2.4	8.9	7.2	10.7	5.5	23.5	15.9	11.7	4.8	3.8	2.0
13	0.3	4.6	7.7	10.2	11.4	5.2	24.2	11.8	9.3	6.8	3.4	4.6
14	1.5	4.6	9.2	11.5	9.6	5.4	24.3	8.4	7.3	4.6	5.0	8.1
15	1.6	7.2	11.5	8.5	13.2	8.9	23.1	7.2	6.6	1.5	3.9	6.2
16	1.6	7.7	10.4	9.0	10.7	5.7	18.8	11.7	6.7	6.0	3.3	7.7

TABLE 25. Relative frequencies of stages for O. simplex in experiment 3.

Station	CI	CII	CIII	CIV	CV	Adult
1	5.6	5.6	2.8	16.8	14.6	54.4
2	5.9	7.7	5.4	10.9	14.5	55.4
3	5.5	4.5	6.4	11.4	13.3	58.6
4	12.6	5.8	6.3	10.7	14.1	50.1
5	16.6	5.5	4.4	9.4	13.8	49.9
6	17.5	9.0	7.3	10.1	11.2	44.5
7	19.4	6.9	3.8	12.9	11.2	45.4
8	21.2	8.5	8.5	13.1	13.1	35.3
9	18.8	9.1	8.6	7.2	16.4	39.5
10	20.9	9.6	6.1	10.4	12.6	40.1
11	18.4	7.6	7.0	7.6	9.2	49.9
12	23.7	13.8	7.1	5.9	13.8	35.5
13	24.0	6.2	9.0	11.0	11.4	38.0
14	34.8	12.9	8.8	10.0	8.1	25.1
15	36.9	16.6	9.5	7.1	7.5	22.1
16	35.0	14.9	5.6	7.7	9.7	26.7

APPENDIX B

DETAILS OF THE METHOD USED TO CALCULATE PRODUCTION FROM SUMMER 1979 STAGE FREQUENCY DATA

Symbols used

N_i	Abundance of stage i (#/l)
W_i	Mean weight of individuals in stage i (μg C)
m_i	Mortality rate in stage i (day^{-1})
g_i	Growth rate of stage i (day^{-1})
R_i	Rate of input of animals to stage i (# day^{-1} l^{-1})
W_{oi}	Weight of stage i at beginning of the stage (μg C)
B_i	Biomass of animals in stage i (μg C/l)
P_i	Production rate of animals in stage i (μg C l^{-1} day^{-1})
t_i	Duration of stage i (days)

Assumptions inherent in the method are:

1. The mean age distribution for summer 1979 can be used as a substitute for a stable age distribution in calculating production.
2. Growth and mortality are constant for a given stage.
3. Sex ratios of CIV and CV are 1:1.
4. Egg production rate is day^{-1} per female (see Chapter IV).

This method is similar to that of Mullin and Brooks (1970) except that growth and mortality are considered constant during a stage, not between adjacent stages.

Development times were modified from those presented by Bartholomew (1973). He gave a development time of 0.5 day per stage for the naupliar and 0.8 day for the copepodite stages. My egg production data (Chapter IV) show that the egg and first two naupliar stages are passed in less than 24 hours at summer temperature (26-28°C). Also, his data show maximum growth to NVI occurring in 2 days from NI, suggesting shorter times for each stage. If all stages were sampled equally, then the number per unit time (N_i/t_i) should not increase between stages i and i + 1, and will generally decrease (Fager, 1973). In order for these ratios to decrease from nauplii to copepodites, a time per stage of 0.4 day had to be used. The duration of NVI is evidently much shorter; this was estimated from the mortality rates.

Since the durations of stages NIII-NV were considered equal, mortality was estimated by regressions of $\ln(N_i)$ on the time after molt from NII to NIII. The mortality rate for stages CI-CV was estimated in the same way. Mortality for NVI was assumed to be the same as in NV, and duration of the stage was calculated from the equation:

$$\frac{N_{i+1}}{N_i} = \frac{m_i e^{-m_i t_i}(1 - e^{-m_{i+1} t_{i+1}})}{m_i(1 - e^{-m_i t_i})}$$

The numbers of eggs and NI-NII were calculated from:

$$R_i = \frac{N_i m_i}{(1 - e^{-m_i t_i})}$$

where R_i for eggs is the egg production rate, assumed to be 11 day^{-1} per female. Adult mortality was calculated separately for each sex from the rate of molting of CV to adults:

$$R_a = N_V m_V / 2(e^{m_V t_V} - 1) \doteq m_a N_a$$

where the factor 2 is to account for the 1:1 sex ratio of the NV.

Counts of eggs and early nauplii were much lower than expected on the basis of an egg production rate of 11 day^{-1} per female. These stages may be inadequately sampled because of depth distributions. Using the rate of egg production and the rate at which NII molts to NIII, which is:

$$R_{III} = N_{III} m_{III} / (1 - e^{-m_{III} t_{III}})$$

then we can calculate the egg-NII mortality rate and the numbers expected in each stage. Note that the assumption of constant mortality has no effect on calculated production because no growth occurs in these stages.

Since growth rates were assumed to be constant in each stage, they are constrained to 0 in stages NI, NII, NVI, and CI, the latter two because weights are the same. This may be a bad assumption, especially for CI. Then the growth rates in the other nauplii were constrained to 1.39 to match the weights at the molts from NII to NIII and NV-NVI. Similarly, growth rates of CII-CIV were calculated to be 0.87 day^{-1} in each stage. The CV males were assumed to grow at that rate until molt to adult, at which point they reached adult weight; hence, the adult males were assumed not to grow. CV female

growth rates were calculated from the CIV weight at the end of stage CIV and the mean CV weight. Final CV weight was used as input to calculate initial adult female weight and growth rate.

production was calculated by two methods:

1. $\text{Yield}_i = m_i B_i = m_i N_i W_i$

2. $\text{Growth}_i = g_i B_i = g_i N_i W_i$

These two equations are derived from the relationships of integrated growth and mortality to mean weight and numbers in a stage. P:B is calculated as total P divided by total B.

APPENDIX C

METHODS AND RESULTS OF EXPERIMENT L, RUN TO DETERMINE THE EFFECT ON THE MICROCOSMS OF VARYING THE LIGHT LEVEL

Methods

The methods were similar to those used in microcosm experiments 1 and 2 with the following exceptions: tanks were cleaned and sampled only weekly; water removed in sampling was not replaced; and tanks were not mixed together. Also, the lids on the tanks had various amounts of shading, as shown in Table 26.

Results

As in the other experiments, the abundances of common planktonic organisms remained steady for at least a week, and then declined rapidly. Because the time trends were similar to those in experiments 1 and 2, only the final day's results are presented (Table 27). In this experiment chlorophyll and particulate matter decreased and temperature increased with increasing light. The water in the most heavily shaded tank was very turbid by the end of the experiment, with a chlorophyll value much higher than is usually found in Kaneohe Bay. Differences between tanks in abundances of common planktonic species showed a clear treatment effect only for a few taxa. *Euterpina acutifrons* and polychaetes were most abundant in the 32% shade tank, suggesting a greater shift in this tank toward a benthic community, but least abundant in the 63% shade tank. *Acrocalanus inermis* was most abundant in the 85% shade tank but, as in the other

TABLE 26. Shading for microcosm tanks (P1-P4) in experiment L

	P1	P2	P3	P4
Shading material	Gray plastic window screen	Light black shading screen	None	Heavy black shading screen
% Shading:				
Nominal	--	53	--	70
Measured	63	75	32	85

TABLE 27. Summary of final values of several variables in microcosm experiment L.

Variable	Percent shading			
	32	63	75	85
Temperature, °C	26.6	25.7	25.7	25.3
Chlorophyll, µg/liter	1.09	1.40	1.36	3.40
Particulate volume, ppm	1.14	0.70	0.54	1.37
Particles/cc x 1000	33.5	34.0	45.4	196.0
Plankton number/liter				
A. inermis nauplii	0.03	2.24	0.90	5.12
A. inermis post-nauplii	0	0.34	0.38	0.58
A. inermis eggs	0.06	0.27	0.10	0.77
Oithona spp. nauplii	0	0	0	0.20
O. simplex post-nauplii	0	0.06	0	0
O. nana post-nauplii	0	0	0.01	0.26
E. acutifrons nauplii	8.20	0.38	2.70	4.86
E. acutifrons post-nauplii	7.14	0.37	0.86	1.06
S. enflata	0.002	0.26	0.15	0.09
Polychaetes	0.13	0.01	0.04	0.04
Medusae	0	0.38	0.87	1.77

experiments the nauplii were mostly NIII or earlier, and there were few copepodites. Small medusae became increasingly abundant as the light level decreased, but the importance of these predators is unknown, and they were uncommon in the other experiment.

Although there were clearly differences between the tanks that could be attributed to the differences in light levels, the outcome of this experiment was essentially the same as that of the others. It is therefore clear that light limitation did not cause the rapid collapse of the plankton populations in the tanks, and that the amount of shading used did not have much effect on the outcome. For experiment 2 the 63% shading material was used, since the populations in that tank appeared to have collapsed slightly less than in the other tanks.

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