



THE ECOLOGY OF WASTE STABILIZATION PONDS

by

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being a thesis submitted
in fulfilment of the
requirements for the
Degree of Doctor of Philosophy
in the Department of Zoology,
University of Adelaide

January 1980

Awarded March 1981.

"Limnologists can and should play a prominent role in devising, testing, and evaluating methods for the treatment of organic wastes. As yet they have paid little attention to these problems, but the basic principles that have been discovered can best be applied by limnologists. If they do not enter into applied research and into the application of their principles and findings, others not so well fitted by training and experience will do so."

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SUMMARY

Ecological interactions were studied in two waste stabilization ponds at Gumeracha, South Australia, to relate the dynamics of the major organisms present to effluent quality and, therefore, the efficiency of pond function. The roles of those organisms in algal control, the stabilization of organic material, and nutrient removal were evaluated to assess their usefulness as tools for the management of WSPs. In this manner, biological principles for pond management were evaluated.

The seasonal dynamics of the phytoplankton were related to effluent quality. Phytoplankton blooms were triggered by increasing water temperature and resulted in a significant decrease in effluent quality. Effluent concentrations of BOD, SS, TOC, and organic nitrogen exceeded influent values during phytoplankton blooms. Removal of soluble $\text{PO}_4 - \text{P}$ and NO_3^- was highest during phytoplankton blooms. Estimated annual net production of the phytoplankton in pond 2 represented a nutrient store equivalent to over 100% of total nitrogen and total $\text{PO}_4 - \text{P}$ retained annually. The dynamics of filamentous algae (*Cladophora*) and the submerged macrophyte *Potamogeton ochreatus* were related to phytoplankton abundance and effluent quality. Floating algal mats and submerged macrophytes inhibited the development of phytoplankton blooms and improved effluent quality. Estimated annual net production of *Cladophora* in pond 1 represented a nutrient store equivalent to 47% of total $\text{PO}_4 - \text{P}$ and 12% of total nitrogen retained in the pond annually. Annual net production of *P. ochreatus* represented less than 3% of total $\text{PO}_4 - \text{P}$ and total nitrogen retained annually.

The population dynamics of the major zooplankton were related to phytoplankton abundance and effluent quality. Although temperature was the major factor determining the occurrence of zooplankton, competition and predation also appeared to be important in structuring the zooplankton community of the Gumeracha ponds. Phytoplankton blooms

correct?

were terminated by zooplankton grazing. The dominant herbivore, *Daphnia carinata*, was a cold water form. High water temperatures increased mortality and reduced the growth rate of *D. carinata* and prevented it from controlling phytoplankton during the summer. The dominant zooplankter during phytoplankton blooms was the carnivore *Mesocyclops leuckarti*. *D. carinata* was a "facultative browser" and ingested the sediments during periods of low phytoplankton abundance. *D. carinata* and *Simocephalus exspinosus* were both food limited at high population densities. Total annual net production of *D. carinata* in pond 1 during 1977 ($345 \text{ g dry weight/m}^2$), calculated using the population turnover-time model, was the highest yet recorded for any planktonic cladoceran. Annual net production of *D. carinata* determined using the population turnover-time model exceeded annual production determined using the biomass turnover model by 100%. Overestimation of daily production rate was highest during periods of high egg mortality. Total annual net production of *D. carinata* (biomass turnover model) represented a nutrient store equivalent to less than 5% of total $\text{PO}_4\text{-P}$ and total nitrogen retained in the ponds annually.

A fish introduction experiment was conducted in enclosures within the ponds. *Carassius auratus* had no significant effect upon phytoplankton and zooplankton populations or on effluent quality. Growth of *C. auratus* increased after introduction to the pond despite decreasing water temperature. Annual net production of *C. auratus* was high compared to fish production in natural waters but probably represented a nutrient store equivalent to less than 2% of total $\text{PO}_4\text{-P}$ and total nitrogen retained in the ponds annually.

Filamentous algae and zooplankton (to a lesser degree) are useful for controlling unicellular algae in waste stabilization ponds. Harvest of unicellular algae is the most effective pathway of nutrient

removal, but reasonable removal could be achieved using filamentous algae. The harvest of submerged macrophytes, zooplankton, and fish is not useful for nutrient removal.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

B.D. Mitchell

ACKNOWLEDGEMENTS

I would like to thank the Engineering and Water Supply Department of South Australia for allowing access to the Gumeracha ponds. Special thanks are due to the Wastewater Laboratory, Bolivar, for conducting the chemical analyses. In particular, I thank Moss Sanders for his patience and assistance. Additionally, I would like to thank Arthur Haughey (Auckland Regional Authority) and Gavin Wood and Ken Hartley (E&WS) for their comments.

I am grateful to my supervisor, Professor Bill Williams, for his support and encouragement throughout the course of the project. Dr. Keith Walker and Dr. Richard Marchant (Zoology Department, University of Adelaide) both gave freely of their time to make comments and suggestions during the project. I thank them both. To Dr. Mike Geddes (Zoology Department, University of Adelaide) who was ever willing to listen to a neophyte, I can scarcely express my gratitude. For your help, guidance, and friendship Mike, "Thankyou" hardly seems adequate.

I would like to thank the following people for invaluable assistance in the erection of fish enclosures: Pat DeDeckker, Alice Wells, Marg Brock, Phil Suter, Julie Harris, Mike Geddes, Dave Papps, and Mike Thompson. I thank Roger Croome (River Murray Commission) for assistance with algal identifications and the collection of fish from Millbrook Reservoir. I also thank Morris Richardson for permission to remove fish from his dam. Thanks are due to John Pillar (Fisheries Inspector, Loxton) for assistance in attempts to capture fish. I thank Les Gray (South Australian Fisheries), John Reynolds (New South Wales Fisheries), and John Glover (South Australian Museum) for information and advice concerning fish ecology and collection. Special thanks are due to Victor Theile for his eager assistance and continued good company in repeated, although somewhat fruitless, attempts to capture fish.

I would like to thank the following persons for assistance in the identifications of various invertebrates: Dr. Jon Martin (Genetics Department, Melbourne University), Dr. Nikolai Smirnov (Academy of Sciences, Moscow), Pat DeDeckker, Russell Shiel, and Dr. John Bishop (Zoology Department, University of Adelaide).

I would like to thank the following persons for supplying the information used to compile Table 1.1: B.P. O'Connell (Department of Water Supply and Sewerage, Brisbane), L. Henry (Water Quality Control Council of Queensland), A.D. Macqueen and A. Waugh (Water Resources Branch, Department of Northern Territory), D.N. Keep (Rivers and Water Supply Commission, Tasmania), T.J. Lewis (Public Works Department, Perth), S.R. Smith (Metropolitan Water Sewerage and Drainage Board, Melbourne), G.T. Coulson (Latrobe Valley Water and Sewerage Board), C.W. Berkely (Department of Health, Melbourne), J.B. McPherson and S. Hussainy (Melbourne and Metropolitan Board of Works Farm, Werribee).

This study was conducted while I received a Commonwealth Postgraduate Research Award; for this I am most grateful.

Finally, to Jen and Amber, who too often had to put up with my bad temper, sorry and thankyou.

Chapter 1. General Introduction

1.1 The Potential of Waste Stabilization Ponds

Global food and fuel shortages and problems of pollution have revised attitudes to the management of non-renewable resources. Urban, industrialized societies have been forced to re-evaluate many widely accepted practices. The treatment and ultimate disposal of domestic sewage is one practice currently under review. Sewage, formerly regarded as waste, is a potentially valuable source of raw materials. Current means of sewage disposal, however, contribute to eutrophication. Problems of wastage and environmental contamination can be partially offset by innovations and improvements in wastewater treatment (Gutteridge Haskins and Davey, 1976; Tourbier and Pearson, 1976).

Nutrient recycling from sewage could supplement global energy production. A city of 100,000 people produces sewage containing 100 tonnes of total phosphorus and 400 tonnes of total nitrogen annually. This amount of nutrient has a combined current value of \$57,000 as chemical fertilizer (Strom, 1979). The potential of this resource has belatedly been acknowledged in Australia (G, H & D, 1976) and its exploitation may take several forms:

- a) direct human consumption of sewage-grown microalgae (Gross *et al.*, 1978; Kofranyi, 1978);
- b) indirect consumption of microalgae via aquaculture schemes incorporating sewage effluents (Meske and Pfeffer, 1978; Sandbank and Hepher, 1978; Goldman and Rhyther, 1976; Reid, 1976; Hepher *et al.*, 1975; Rhyther *et al.*, 1975, 1972) or use as food for domestic livestock (Brune and Walz, 1978; Mokady *et al.*, 1978),
- c) direct culture of fish in sewage ponds (White and Williams, 1978; Schroeder and Hepher, 1976; Krishnamoorti *et al.*, 1975; Noble, 1975; Slack, 1974; Chatterjee *et al.*, 1967; Hey, 1953);

- d) land irrigation of effluents for agriculture or grazing (Strom, 1979; Searle and Kirby, 1973);
- e) use of sewage-grown macrophytes for stock food (Wolverton and McDonald, 1978; Culley and Epps, 1973; Seidel, 1971; Boyd, 1968);
- f) production of methane from sewage-grown macrophytes or micro-algae (Strom, 1979; Wolverton and McDonald, 1978);
- g) derivation of liquid combustible fuel from lipid-producing microalgae cultured in sewage effluents (G. Gartride, CSIRO Division of Chemical Technology, pers. comm., 1979).

Eutrophication may be alleviated by nutrient removal from sewage effluents. Chemical techniques for the removal of nitrogen include denitrification, ammonia stripping, ion exchange, and demineralization (electrolysis, reverse osmosis or distillation) (Rohlich and Uttormark, 1972). Phosphorus may be removed by precipitation of phosphates using lime, aluminium sulphate, sodium aluminate or ferric salts, ion exchange, reverse osmosis and distillation (Rohlich and Uttormark, 1972; Jenkins et al., 1971). These processes vary in cost but considerable expenditure is required for the production of effluents of consistent quality. In addition, coagulation techniques require the handling of large volumes of sludge. In any event, it has been shown that conversion of polyphosphates to orthophosphate during biological treatment is necessary for chemical phosphorus removal (Dobolyi, 1973).

Biological alternatives for nutrient removal include land irrigation (Rohlich and Uttormark, 1972), the culture and harvest of microalgae (Goldman, 1979a; Brar and Tollefson, 1975; Van der Borgh and Buyers, 1974; Shelef, et al., 1972; Hemens and Stander, 1969; Hemens and Mason, 1968; Fitzgerald and Rohlich, 1964; Witt and Borchardt, 1960) and the culture of emergent or submerged macrophytes (Dinges, 1978; Wolverton and McDonald, 1978; Corwell et al., 1977;

Jong, 1976; McNabb Jr., 1976; Seidel, 1976; Boyd, 1970). The incorporation of nutrients into animal tissue (e.g. zooplankton or fish) is an untested possibility.

Obviously, biological techniques for nutrient removal and recycling are the same; removal is essential for re-use. Aerobic (maturation) waste stabilization ponds (WSPs) provide ideal sites for the types of schemes listed above. These ponds are already an integral part of many treatment plants, provide for easy access, have uniform shapes and depths, are controllable in terms of water flow and depth, and have bottoms free from obstructions thus allowing convenient harvest of plant and animal biomass by conventional techniques.

This thesis examines the effectiveness of aerobic WSPs as a wastewater treatment technique, and investigates means of improving pond efficiency. In particular, biological alternatives for pond management, including nutrient removal, are studied.

1.2 Project Aims

Information about the biological characteristics of WSPs is fragmentary and clearly inadequate for effective management to meet current effluent quality criteria. This project contributes basic biological information on maturation ponds to aid in management and manipulation for nutrient recycling. The project design is outlined below:

- 1). The current state of knowledge of WSP ecology is reviewed and major problems highlighted. The rationale for concentrating upon the role of zooplankton, fish and macrophytes in addressing these problems is outlined.
- 2). The efficiency of maturation ponds in stabilizing organic material and removing nutrients is examined at Gumeracha, South Australia.
- 3). The seasonal cycle of phytoplankton is described and population

fluctuations correlated with effluent quality. Annual net production of phytoplankton is estimated.

- 4). The influence of submerged macrophytes and filamentous algae upon planktonic algal abundance and effluent quality is determined. Annual net production of submerged macrophytes is determined. Annual net production of filamentous algae is estimated.
- 5). The seasonal cycle of zooplankton is described. The influence of zooplankton upon algal abundance and effluent quality is determined.
- 6). The population dynamics and annual net production of the dominant species of zooplankton are studied intensively due to their importance for the stabilization of organic matter and the control of algae.
- 7). The effects of a higher order consumer (fish) upon algae and zooplankton, and the concomitant influence upon effluent quality are examined. Annual net production of fish is determined.
- 8). The relative nutrient "stores" represented by annual net production of phytoplankton, filamentous algae, macrophytes, zooplankton, and fish are calculated. These "stores" are compared with annual pond nutrient retention and nutrient partitioning between trophic levels is examined. Harvest of the annual net production of each group is examined as an alternative pathway of nutrient removal from the ponds.

The current literature on the ecology of WSPs is reviewed below. This review provided the basis for the investigations subsequently undertaken during the project.

1.3 Waste Stabilization Ponds - Advantages

The term 'Waste Stabilization Pond' (WSP) describes any shallow, man-made basin utilizing natural biological processes for the reduction of organic matter and the destruction of pathogenic organisms in waste-

water (Marais, 1971; Gloyna, 1971; McKinney et al., 1971). Several different types of WSP are currently in use (Gloyna, 1971). A WSP Aerobic ponds may be of three types: high rate aerobic, aerated, or maturation ponds. may be anaerobic, facultative or aerobic. High rate aerobic ponds are shallow ($<0.5\text{m}$), mechanically mixed, have short retention times and high algal production. Aerated ponds have virtually all oxygen supplied mechanically. Algae are thus replaced as a source of oxygen and algal growth is low. These two types of aerobic pond have high energy inputs compared to other pond types and thus high operational costs. Maturation or polishing ponds (Ramani, 1976) receive effluents treated to a secondary level and provide high-quality effluents. By combining different pond types in series, WSP systems may be designed to meet a variety of treatment objectives.

The advantages of WSPs for waste-water treatment result from their simplicity (Shelef, 1976). Ponds require a relatively low initial capital investment and simple flow schemes require low energy inputs (desirable in view of current energy shortages). Simple operation and maintenance mean reduced operating costs. WSPs cost substantially less per capita to construct and operate than other types of primary and secondary treatment (Shelef, 1976; Gloyna, 1971). These features, plus the ability to markedly reduce waste-water biochemical oxygen demand (BOD), suspended solids (SS) concentrations, and bacteria and virus numbers, to smooth peak hydraulic loads and deal adequately with seasonal industrial and agricultural wastes, have made WSPs attractive to less developed countries, small communities, and certain stages of urban development (Boatright and Lawrence, 1977; Gloyna, 1962). WSPs can also provide "ultimate" waste disposal via evaporation and seepage. WSPs have higher land requirements than other methods of treatment, and are not without operational problems. These will be discussed below.

1.4 Pond Usage in Australia

Waste stabilization ponds are used extensively by small communities throughout country areas of Australia. In addition, ponds are used at Werribee, Victoria, to treat daily peak and wet weather flows from approximately 75% of Melbourne's population. At Bolivar, South Australia, domestic waste-water from a population of 600,000 in Adelaide and trade waste equivalent to a population of 700,000 is treated in ponds. A large pond system at Dutson Downs in the Latrobe Valley, Victoria, treats largely industrial waste, and smaller plants serve some metropolitan areas in Sydney. Current Australian ponding and effluent disposal practices are summarized in Table 1.1.

Ponds vary in size (approximate maximum 100 ha), are characteristically 1.0-1.5 m deep (but may be up to 3m deep), and are subject to a wide range of loading conditions. Large cities usually employ aerated ponds for tertiary treatment, while ponds for secondary treatment are usually facultative. Anaerobic ponds are used widely for pretreatment prior to aerobic ponding (Parker et al., 1959, 1950; Hussainy, 1978). Country towns use fully aerobic maturation ponds for tertiary treatment, facultative or aerobic ponds for secondary treatment, and anaerobic ponds for primary treatment. Anaerobic ponds are also used extensively for the treatment of farm wastes, especially from piggeries (Environmental Control Council and Water Quality Control Council of Queensland, 1975; Bryson, 1972), and cannery waste (Parker, 1966).

Direct ocean discharge is the most common method of effluent disposal in Australia; in many cases this occurs at the secondary level of treatment. This practice, the result of population distribution throughout Australia, meant that eutrophication of inland waters lagged somewhat behind other urban nations (Williams, 1969). Many Australian lakes and reservoirs are now exhibiting signs of eutrophication (Hart, 1974) and discharge of incompletely treated sewage effluents is a contributing factor.

Table 1.1 Waste stabilization pond use throughout Australia. Compiled from information supplied by sewage treatment authorities and Gutteridge, Haskins & Davey, (1976).

State	Number of towns using ponds and population served	Surface area of ponds (ha)	Annual flow (Ml)	Type of treatment	Disposal of pond effluent
South Australia	Adelaide + 15 (400-33000)	340 85	31755 7206	Secondary and tertiary. Most tertiary, some secondary, a few primary.	Irrigation and ocean discharge. Several irrigation, some river discharge.
New South Wales	Sydney + 106 (700-113000)	19 312	4501 56035	Tertiary. Most tertiary, secondary in 2, primary in 1.	Ocean discharge. Land disposal or river discharge.
Victoria	Melbourne Dutson Downs + 68 (1050-5700)	1450 283 200	70000 12100 35920	Primary and secondary. Primary and secondary. Many tertiary, several primary.	Ocean discharge. Ocean discharge. Most irrigation, several stream and ocean discharge.
Northern Territory	5 (220-25000)	52	3190	Primary and secondary.	Ocean, river or creek discharge.
Tasmania	25 (500-8830)	44	5980	Most primary, some secondary.	River or ocean discharge.
Queensland	Brisbane + 54 (120-25000)	3 40	3285 9655	Most secondary, several tertiary, some primary. Secondary(after septic tanks).	Ocean discharge. Several land, several river and creek, some seepage.
Western Australia	48 (100-20865)	64	6282	Most secondary, some tertiary, a few primary.	Most soakage, some irrigation, several river, few ocean discharge.

1.5 Problems in Waste Stabilization Ponds

The advantages of WSPs have been offset by a lack of theoretical data upon which to base pond management. The approach to pond design and operation has been largely empirical, often resulting in overloading and mismanagement of ponds. This has resulted in criticism of the usefulness of ponds for wastewater treatment (Barsom and Ryckman, 1970). Although WSPs have been in use in several countries for many years, only within the last two decades have specific design criteria in terms of volumetric requirements, organic loading rates and detention times been developed (Goyna, 1971). Pond performance is largely dependent upon climatic conditions (temperature and solar radiation) but until recently ponds had been constructed on the sole basis of the above criteria with little rational basis for varying design in areas of differing climate (Bliss, 1976). The failure of pond effluents to meet current quality requirements is the result of mismanagement due to poor understanding of pond function, rather than limitations of ponds as a treatment technique.

The performance (efficiency) of WSPs has been traditionally measured as the percentage removal of 5 day BOD (the relative oxygen requirement of the effluent or a measure of the degradable load added to receiving waters), SS, viruses, and enteric coliform bacteria. Current effluent quality criteria extend beyond these requirements. Nutrient and/or heavy metal removal is now recognised as an integral part of the treatment process. Conventional sewage treatment has centred upon mineralization of organic compounds rather than removal of nitrogen and phosphorus.

The major operating problem of WSPs has been the presence of algae in effluents, their contribution to BOD and SS and, hence, the effect of effluent quality on receiving water bodies. Fundamental processes in WSPs convert unstable organics into algal cells. Much

higher standing crops of algae may be produced than are necessary to satisfy the oxygen requirement of the added sewage (Bartsch and Allum, 1957). During summer, filtered effluent BOD and SS may be negligible while total BOD and SS can exceed influent value (McKinney *et al.*, 1971). This results from the presence of algae in effluents. High standing crops of algae can contribute significantly to the total oxygen demand of the pond (Bartsch and Allum, 1957) and senescent or dead algal cells in effluents would increase the BOD of receiving waters (Ward & King, 1976). In the past, WSPs have exported their BOD and nutrient load, albeit in a changed form, to rivers, lakes, and the ocean; it was assumed that algae in effluents would survive in receiving waters, thereby causing no harm (Fitzgerald and Rohlich, 1958). Algal-laden effluents, however, represent a potential accumulated oxygen deficit and nutrient surplus.

Chlorination of WSP effluents for the destruction of pathogenic organisms is a widespread practice. Effective chlorination is a complex, exact process (Hom, 1970) and regrowth of coliforms occurs if doses are inadequate (Shuval *et al.*, 1973; Svore, 1968). Apart from the effects of residual chlorine on organisms in receiving waters (Bellanca and Bailey, 1977; Tsai, 1973 and 1968), potentially carcinogenic chlorinated hydrocarbons have been identified from chlorinated domestic sewage effluents (Harris, 1976). The most common cause of dead algal cells in WSP effluents has been improper, excessive chlorination (Oswald, 1976; Oswald and Ramani, 1976; Hom, 1970). Brief exposure to residual chlorine can produce a significant loss of chlorophyll *a* and permanently decrease rates of carbon uptake by phytoplankton (Brooks and Liptack, 1979). The difference between chlorine concentrations resulting in nearly full (<0.1 mg/l) and no recovery (≥ 1 mg/l) of photosynthetic processes is quite small.

The effects of WSP effluents upon receiving waters are complex and dependant upon effluent quality, dilution factor, and the ability of

algae to survive. Effects may be small in some cases (Oswald and Ramani, 1976; Patrick, 1976), but oxygen depletion and elevated BOD can result (Atherton and King, 1971; Bain et al., 1970; King et al., 1970). Bacterial degradation of algae in receiving waters will release nutrients and contribute to eutrophication. Most wastewater treatment plants currently in operation were primarily designed for BOD reduction and nutrient removal is generally less than 50% (Rohlich and Uttormark, 1972). Although it has been suggested that wastewaters represent a small proportion of the total nutrient input to certain surface waters (Boyd et al., 1976; Bachmann and Jones, 1976), point sources can be significant contributors to eutrophication (Wurhmann, 1964). Diversion of effluents or the introduction of tertiary treatment (nutrient removal) can significantly reduce the total annual nitrogen and phosphorus input to lakes and alleviate problems associated with eutrophication (Bailey et al., 1979; Forsberg et al., 1977; Larsen et al., 1975; Sonzogni and Lee, 1974; Rohlich and Uttormark, 1972; Edmondson, 1970; Williams, 1969).

While WSP effluents currently satisfy BOD, SS, and coliform bacteria criteria, nutrient removal requires attention. Primarily, this involves the removal of algae from effluents; algal biomass represents a large "store" of nitrogen and phosphorus. The detrimental effects of algal-laden effluents and the possible value of algae as a byproduct have urged the development of chemical and mechanical alternatives for algal removal (John et al., 1976; Parker, 1976; Middlebrooks et al., 1974; Oswald and Golueke, 1968; Golueke and Oswald, 1965). Most of these techniques require considerable capital investment and skilled supervision, detracting from the advantages of WSPs as a means of wastewater treatment for small communities. Chemical techniques may preclude further use of the harvested algae (Rao, et al., 1975). Furthermore, techniques such as centrifugation or flocculation may

concentrate pathogenic bacteria and viruses (Cooper, 1962). In-pond techniques of algal control, such as biological harvesting via zooplankton and/or fish grazing, have been discounted before their potential has been adequately researched (Middlebrooks et al., 1974).

1.6 The Biology of Pond Function

Waste stabilization ponds evolved from the concept of natural purification, that is, the observation that organic contaminants could be stabilized by naturally occurring organisms when waste-water was discharged to rivers and streams. At some point downstream the river would regain its natural state, the organics having been assimilated by the aquatic community (e.g. Bayly and Williams, 1973). This process is the function of a complex community consisting of many species and is largely achieved by trophic interactions between the community's constituents. The biology of WSP communities has been neglected. Trophic interactions have been ignored in the design and operation of ponds as physical factors have been regarded as the major determinant of pond function.

1.6.1 Algae-Bacteria Interactions. The most intensely studied aspect of WSP biology concerns the interaction of algae and bacteria and their role in the stabilization of organic matter. Algae utilize the stable, inorganic products of bacterial metabolism (McKinney, 1976; Ganapati, 1975; Gloyna, 1971; Oswald, 1964). The aerobic, heterotrophic bacteria metabolize organics producing CO_2 , H_2O , NH_3 , phosphates and bacterial cells. NH_3 reacts with CO_2 and H_2O producing $(\text{NH}_4)\text{HCO}_3$ (increasing buffer capacity for pH control) and nitrogen is available for further metabolism. Nitrification reactions, having a high oxygen demand (Wetzel, 1975), do not occur in anaerobic or facultative WSPs (McKinney, 1976). Oxidation of $\text{NH}_3\text{-N}$ to nitrate - and nitrite - nitrogen occurs during aerobic treatment (Rohlich and Uttormark, 1972).

The algae (autotrophs) in WSPs reduce the stable, oxidized end products of bacterial metabolism to produce new algal cells and

dissolved oxygen during photosynthesis. The oxygen released is essential for the aerobic bacteria. That is, the process of organic stabilization is essentially reversed as organic matter is synthesized from previously stabilized inorganic compounds. Algae and bacteria also undergo endogenous respiration, and approximately 20 per cent of the bacterial and algal protoplasm is not metabolized and remains as inert, non-biodegradable organics, or suspended solids. Materials are continually recycled producing non-biodegradable organics. That is, nutrients are continuously converted to a stable form, this conversion being a prime means of nutrient removal in WSPs (McKinney, 1976).

The biochemistry of this process is well understood (Ganapati, 1975). Several fundamental problems await investigation. These include the identification of the bacteria involved in the stabilization of organic matter, the agencies of removal of pathogenic bacteria, and the precise relationship between algae and bacteria (Mitchell, in press).^{*} The relationship has been assumed symbiotic. This may be the case for *Senedesmus*, *Nostoc*, and *Aulosira*, but for some species of *Chlorella* and *Oscillatoria* the relationship is antagonistic (Ganapati and Amin, 1972). Algae produce antibacterial substances (Ward and King, 1976; Fogg, 1962) and may compete with bacteria for phosphates (Ward and King, 1976). BOD reduction in high-rate oxidation ponds may be primarily effected by algae adapted for heterotrophic nutrition (Abeliovich and Weismann, 1978).

The interactions of algae and bacteria are variable. However, the algae-bacteria model of WSP function has so dominated design procedures that a simplistic concept of pond communities has resulted. A typical model of the biology of an aerobic WSP is presented in Figure 1.1. This model implies that algal numbers are regulated solely by the

* This paper is included in Appendix 3.

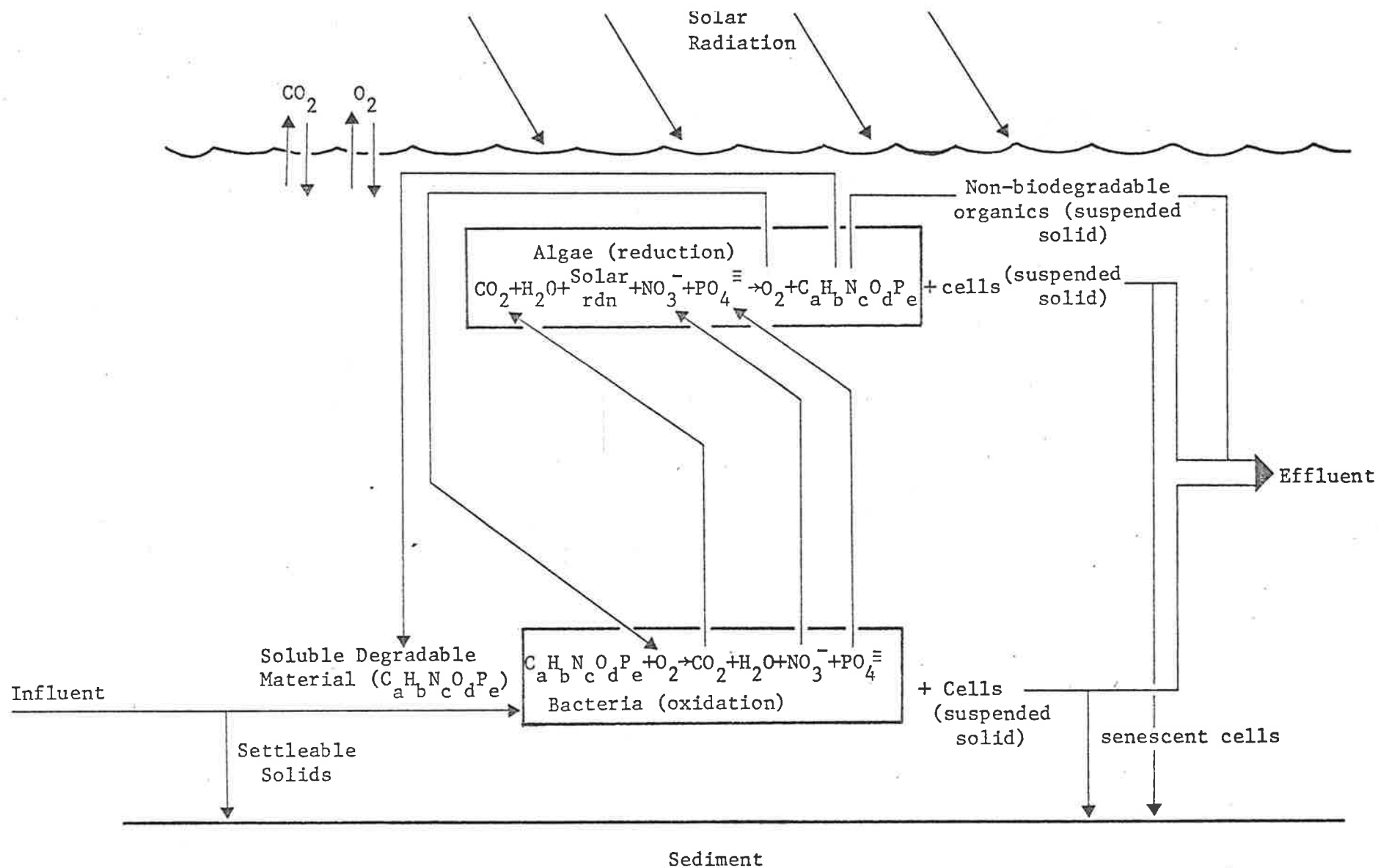


FIGURE 1.1 Principal Biological Reactions in a WSP (traditional sanitary engineering model, based on Bliss (1976) and Gloyna (1971))

rate of bacterial oxidation of organic material. This minimizes the importance of other biotic factors, particularly higher trophic levels, in regulating algal populations. The general practice has been to assume that nitrogen and phosphorus are abundant and readily usable (e.g. Gloyna, 1971) and that algal activity is controlled by light, alkalinity, mixing and detention time (King, 1976; Gloyna, 1971, 1968). The algae in WSPs can become carbon or nitrogen limited under certain conditions (King, 1976, 1972). Population cycles of algae in WSPs have been described in few studies (Shillinglaw and Pieterse, 1977; White, 1975; Rodgi and Patil, 1971; DeNoyelles, Jr., 1967). These suggest that the factors controlling algal fluctuations in WSPs are those operating for natural water bodies: light, temperature, nutrient limitation, and grazing.

The fate of nutrients in WSPs has been neglected. Nitrogen forms in facultative pond sediments have been identified by Brockett (1977) and Lewin (1973) has shown that complex polyphosphates (from detergents) are rapidly hydrolysed to soluble orthophosphate during biological sewage treatment. No information is available concerning nutrient cycling, storage in sediments, or partitioning between trophic levels in WSPs.

In view of WSP operating problems the influences of other organisms, particularly from higher trophic levels, upon algal populations are important and require attention. The importance of other members of the WSP biota in pond function will be briefly reviewed.

In contrast to the algae, the study of other organisms in WSPs has been neglected. This reflects the influence of the above model and the idea that organisms other than unicellular algae and bacteria serve no useful role in the stabilization process and are therefore unimportant or even detrimental. In addition to the influence upon algae, a more direct involvement in waste stabilization is implicated for many groups - plant and animal (Mitchell, in press).

1.6.2 Protozoa. The autotrophic Phytomastigophora and the saprozoic Zoomastigophora may play an important role in the stabilization of organic matter (Pillai and Subrahmanian, 1944). The phagotrophic ciliates graze upon bacteria and may prevent self-limitation in that group. A high rate of assimilation of organic material by the bacterial community would thus be maintained (Curds, 1975). Protozoa may also help in the clarification of effluents by reducing bacterial numbers via predation and/or flocculation.

1.6.3 Rotifera. The filter-feeding rotifers of the order Monogononta are common in WSPs (Hussainy, 1978; Goulden, 1976; White, 1975; De Noyelles, 1967). Although this group plays a secondary role in the removal of organic matter (Doohan, 1975) it may significantly influence algal populations via grazing, e.g. *Brachionus* (De Noyelles, Jr., 1967).

1.6.4 Crustacea. Planktonic microcrustacea (suborder Cladocera and subclass Copepoda) are common in WSPs and effect BOD, SS, nutrient and bacterial removal (Andronikova, 1978; Schroeder and Hephner, 1976; Dinges, 1976; Kryutchkova, 1968; Loedolff, 1965). The influence of zooplankton grazing upon algal populations warrants special attention in WSPs but has been studied rarely (White, 1975). Until recently, zooplankton were considered detrimental to pond function (see review by Dinges, 1973). Zooplankton may be useful for WSP management.

1.6.5 Insecta. The most significant group of insects in WSPs is the Chironomidae, midge larvae, though composition of the insect community appears to be a function of organic loading and detention time. Little attention has been accorded the functional role of these communities in WSPs. Kimerle & Anderson (1971) have demonstrated that midge larvae are important in organic matter decomposition processes and that emergence and respiration may account for 7 per cent of the energy fixed in primary production. Midge larvae may also

contribute to the efficiency of waste stabilization by extending the aerobic zone of decomposition further into the substratum. However, insects are usually associated with operational and public health problems (Peters, 1975; Glover, 1969; Kimerle and Enns, 1968).

1.6.6 Fish. Fish have been cultured in ponds receiving sewage wastes for many years (Hickling, 1968) but only recently have the effects of fish on WSP function been investigated. These studies suggest that planktivorous and herbivorous fish effect appreciable BOD, SS, nutrient and coliform bacteria removal (Carpenter *et al.*, 1976; Reid, 1976). Fish may act as a nutrient store and be valuable for nutrient recycling schemes (Kitchell *et al.*, 1975; Hrbacek *et al.*, 1961). Many features of the complex effects of fish predation on aquatic communities (Anderson *et al.*, 1978; De Bernardi and Guissani, 1975; Hillbricht-Ilkowska and Weglenska, 1973; Grygierek *et al.*, 1966; Straskraba, 1965; Brooks and Dodson, 1965; Hrbacek *et al.*, 1961) have yet to be investigated in relation to WSP function. While planktivorous fish may increase algal populations in WSPs (White, 1975) the effects of omnivorous species remain to be tested.

1.6.7 Macrophytes. Aquatic vascular plants have generally been regarded as detrimental to pond function due to their association with insect problems (Kimerle and Enns, 1968). However, submerged and emergent macrophytes are able to effect considerable BOD, SS, nutrient and coliform bacteria removal when cultured in sewage effluents or WSPs (Corwell *et al.*, 1977; Wooten and Dodd, 1976; Wolverton *et al.*, 1976; Spangler *et al.*, 1976; Seidel, 1976; McNabb, Jr., 1976; Jong, 1976; Dinges, 1978, 1976; Culley and Epps, 1973; Boyd, 1970). Macrophytes and algae interact in a complex manner (Philips *et al.*, 1978; Schindler and Comita, 1972; Goulder, 1969) and macrophytes may inhibit the development of algae (Crawford, 1979, 1977; Kimball and Kimball, 1977; Nicholls, 1973; Fitzgerald, 1969; Hasler and Jones, 1949).

Macrophyte harvest may remove significant amounts of nitrogen and phosphorus from lakes (Carpenter and Adams, 1977; Wile, 1975; Boyd, 1971). Macrophytes may provide valuable methods for WSP management.

Biological events in WSPs are more complex than Figure 1.1 suggests. A more realistic model of trophic interactions in a WSP is presented in Figure 1.2. In this model, partially suggested by Loedolff (1965), algae-bacteria interactions are part of a much larger, more intricate food web. Such a model provides the conceptual basis for combined aquaculture-waste treatment schemes incorporating organisms from several trophic levels (e.g. Carpenter *et al.*, 1976; Goldman and Ryther, 1976). Other components of the WSP community influence algal populations, in particular, zooplankton, fish, and macrophytes. The possible role of these groups in nutrient removal also makes their study in WSPs important. For these reasons, this study investigates the seasonal cycles of algae, zooplankton and macrophytes in WSPs, the effects of interactions between these groups on effluent quality, the impact of fish upon WSP communities and function, and the relative value of algae, zooplankton, fish and macrophytes for nutrient removal from WSPs.

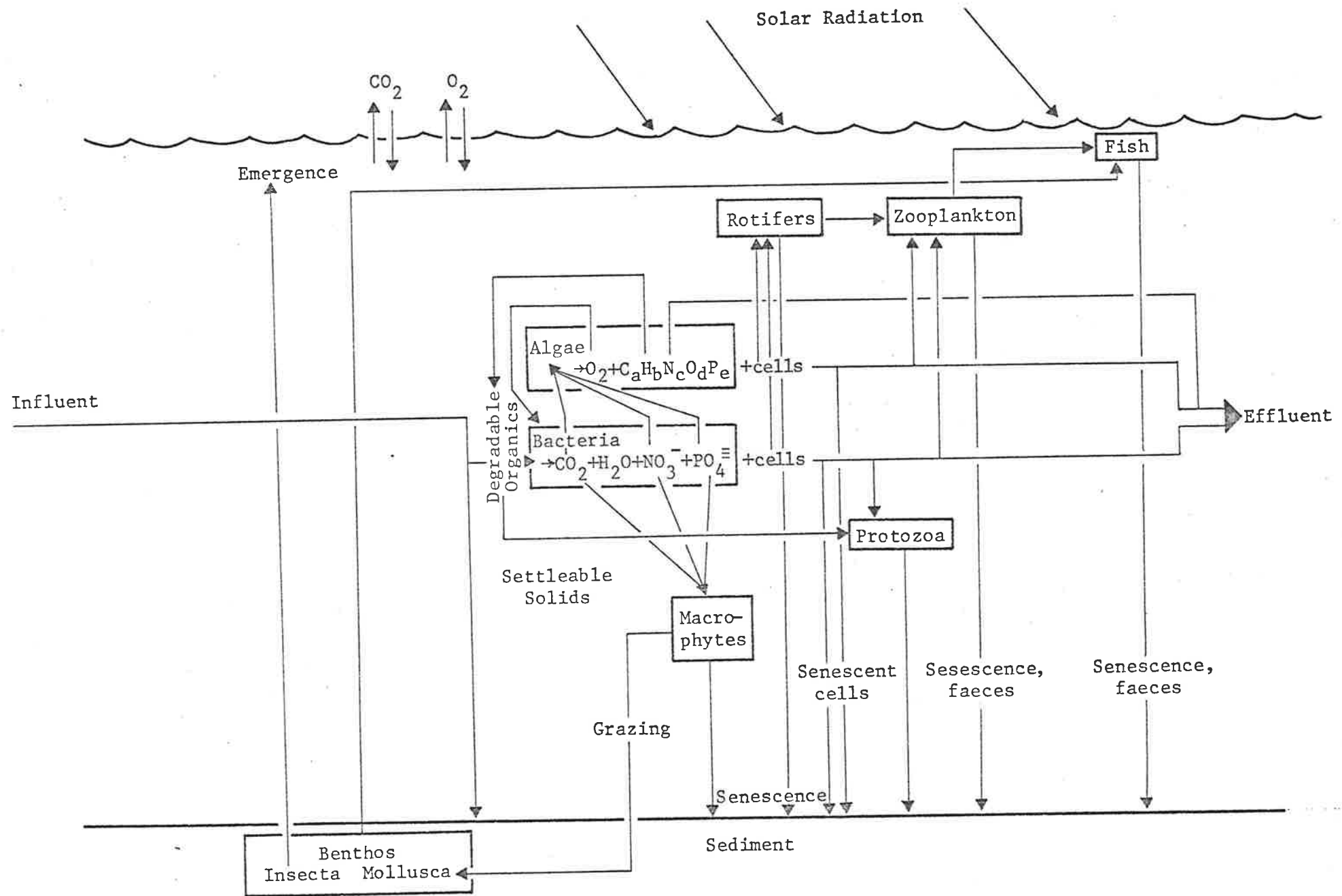


FIGURE 1.2 Principal Biological Reactions in a WSP (total pond community or trophic model).

Chapter 2. Study Site and Physico-Chemical Characteristics

2.1 Study Site

Two ponds were studied at the small, rural town of Gumeracha ($138^{\circ} 52' 54''$ E, $34^{\circ} 49' 9''$ S; 330 m above sea level), 35 km north-east of Adelaide, South Australia (Figure 2.1,A). Pond effluent enters the Torrens River which is impounded by a small weir 3 km downstream from the treatment plant (Figure 2.1,B). Water is diverted from this weir into Millbrook Reservoir (surface area 178 ha, mean depth 9.3 m). Approximately 9 km downstream from the weir the Torrens River enters Kangaroo Creek Reservoir (surface area 121 ha, mean depth 20.2 m). During annual low flow periods in the river (January to March), pond effluent may contribute up to 1.7% of mean daily river flow (calculated from Engineering and Water Supply Department, 1978, p.20).

The Gumeracha plant, shown in Figure 2.2, was commissioned in 1965. Raw sewage passes through an Imhoff tank (large suspended solids are removed to sludge scrapes), a biological trickling filter, a humus tank and into pond 1. Pond 1 effluent flows into pond 2 (in series) and pond 2 effluent is chlorinated before release into the river. The ponds were designed to provide tertiary treatment. Both ponds are 1.1 m deep; pond 1 has a surface area of 1440m^2 and pond 2 a surface area of 1245m^2 . The plant site is landscaped and well-drained; the ponds receive no surface runoff.

The total design population equivalent for the Gumeracha plant was 3,500 (domestic population 400). Design flows and organic loads represented in Table 2.1 show the composition of the design population. The biological filters remove 90% of the sewage BOD and the design load on the pond system was 35.9 Kg BOD/ha/day. Neither the cheese factory nor the fruit works is in operation and the slaughter

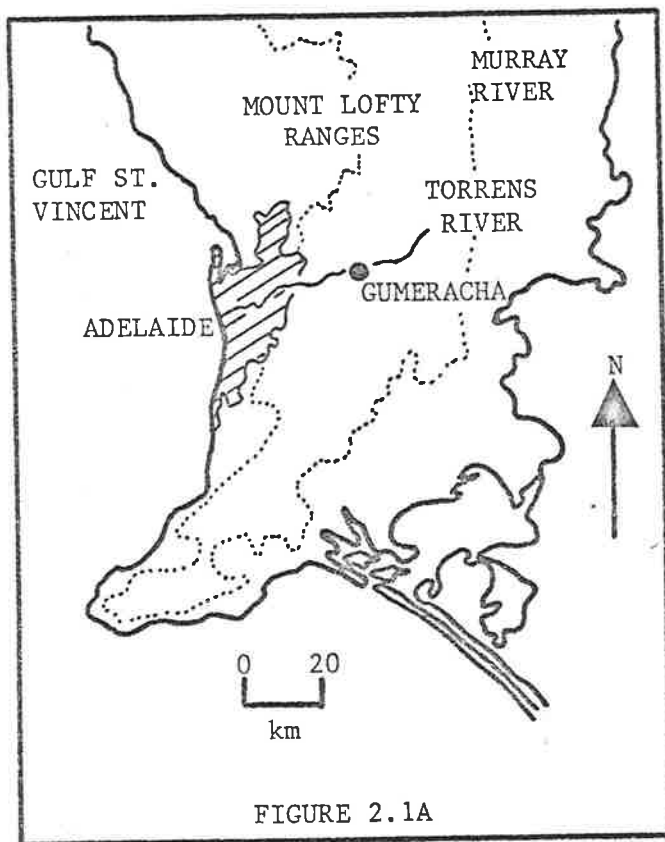


FIGURE 2.1A

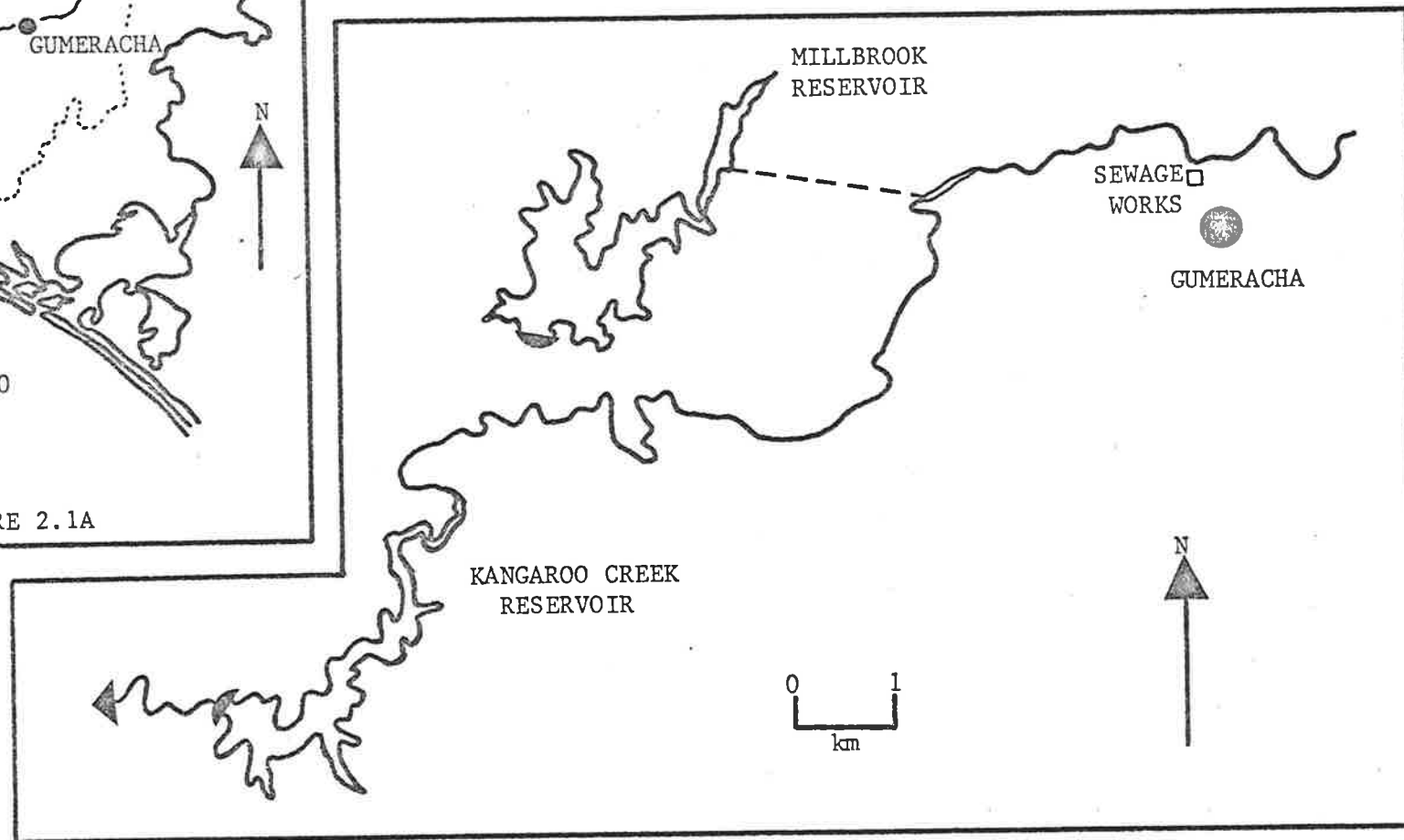


FIGURE 2.1B

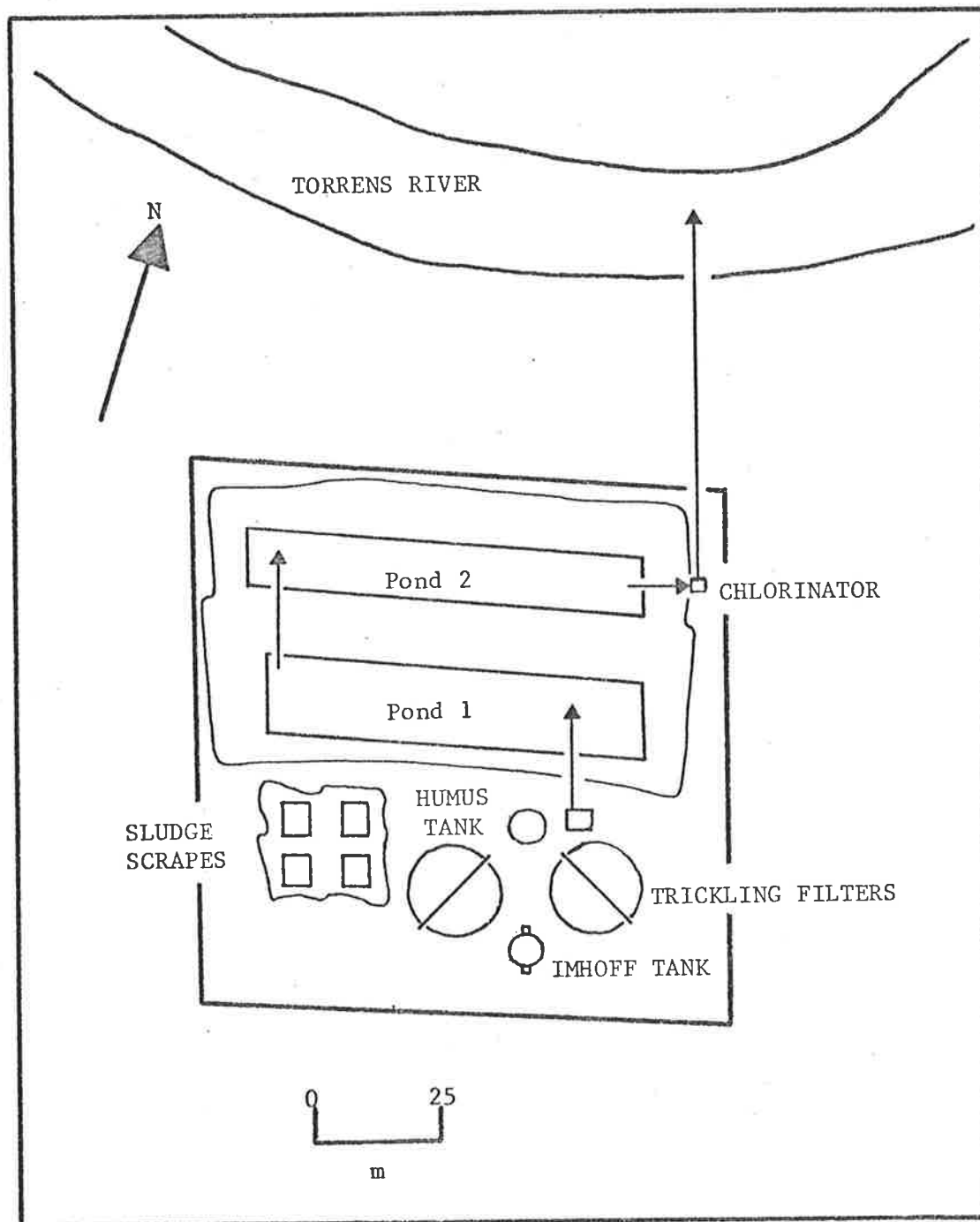


FIGURE 2.2 The Gumeracha treatment works.

Table 2.1

Design flows and organic loads for Gumeracha treatment works
(calculated from Engineering and Water Supply Dept.
information sheet).

	Working Flow (l/day)	Organic Load (Kg BOD/day)
Domestic	52,990 (158,990 Peak flow)	24.5
Cheese Factory	6,000 (pop ⁿ equivalent 1070)	68.0
Glace Fruit Works	3,000 (" " 1780)	113.4
Slaughterhouse	1,000 (" " 250)	15.9
Total	90,840 (196,820)	222.7

house contributes small, intermittent loads. The plant can be considered to treat solely domestic effluents and average operating characteristics for the ponds during 1977 are presented in Table 2.2. The Gumeracha ponds are currently operating at less than half design load (only one biological filter is in use).

The Gumeracha ponds are fully aerobic maturation ponds which receive influents relatively low in BOD and SS. The function of such ponds is the polishing of effluents via the reduction of SS, nutrients, and coliform bacteria (Ramani, 1976); BOD removal is not a primary requirement.

2.2 Physico-Chemical Characteristics

2.2.1 Methods. Physico-chemical parameters were measured fortnightly (sampled near 1200 hours) from January 1977 to October 1978. Discharge was measured over a "V" notched weir (Hynes, 1970). Water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/l) were measured at the surface and successive 10 cm depth intervals in the centre of each pond using a YSI Model 51B oxygen meter and a YSI Model 5739 temperature-oxygen probe calibrated for altitude. Noncomposite water samples were taken from the humus tank outflow (pond 1 influent), pond 1 outflow (pond 2 influent), and pond 2 outflow prior to chlorination. 1000 ml narrow-mouthed, glass-stoppered bottles were filled from a ladle taking care to avoid turbulence and entraining atmospheric oxygen; bottles were overflowed approximately 2 times their volume. Samples were kept in the dark and stored at 4°C within 2 hours. During summer, samples were placed on ice immediately after collection.

Prior to this study, pond 2 effluent quality had been monitored bimonthly. That programme did not permit comparison of the relative treatment efficiencies of pond 1 and pond 2 nor the determination of nutrient removal. The following parameters were determined during this study and all techniques followed APHA (1976): total and filtered

Table 2.2

Average operating characteristics for 1977.

	Pond 1	Pond 2
* Mean Daily Flow Rate (l/day)	90288	90288
** Retention Time (days)	17.5	15.2
*** Organic Loading (Kg BOD/ha/day)	10.9	5.5

* From discharge, see 2.2.1 .

** Pond volume/mean daily flow rate

*** $(\text{Mean influent BOD}) \times (\text{mean daily flow rate}) / \text{Pond surface area}.$

(0.45 μ m) 5-day biochemical oxygen demand (BOD); suspended solids (SS); pH (measured with an EIL Combination Electrode); total dissolved solids (TDS) (calculated from conductivity using Williams: 1966); total carbon (TC) and total inorganic carbon (TIC) (measured using a Beckman Carbon Analyser), total organic carbon (TOC) (calculated from the difference between TC and TIC); total Kjeldahl nitrogen (TKN); ammonia-nitrogen (NH_3) (measured by titration with sulphuric acid after distillation into a solution of boric acid); organic nitrogen (Org-N), particulate plus dissolved, (calculated from the difference between TKN and NH_3 after APHA, 1976, p. 437); nitrate-nitrogen (NO_3^-) (calculated from the difference between nitrite nitrogen and total oxidized nitrogen measured using Devarda's alloy reduction method. Nitrite contributed less than 2% total oxidized nitrogen and will not be considered.); total (filtrable plus nonfiltrable) orthophosphate (total $\text{PO}_4\text{-P}$) (measured colorimetrically after reaction with ammonium molybdate to form molybdophosphoric acid and reduction by stannous chloride to molybdenum blue); "soluble" (filtrable) orthophosphate (sol $\text{PO}_4\text{-P}$) (measured as above after filtration (0.45 μ m)). Chemical analyses were performed by the Bolivar Wastewater Laboratory of the Engineering and Water Supply Department of South Australia.

2.2.2 Results.

Retention time. Seasonal variation of instantaneous retention time (volume/daily flow rate) for the Gumeracha pond system overall during 1977 is shown in Figure 2.3. Retention time varied considerably throughout the year being longest during the warmer months (78 days) and shortest during mid-winter (5 days). Retention time in pond 2 would have been slightly shorter than in pond 1 due to the smaller volume of pond 2. Annual mean daily flow rates were of more value when considering pond function than individual instantaneous rates.

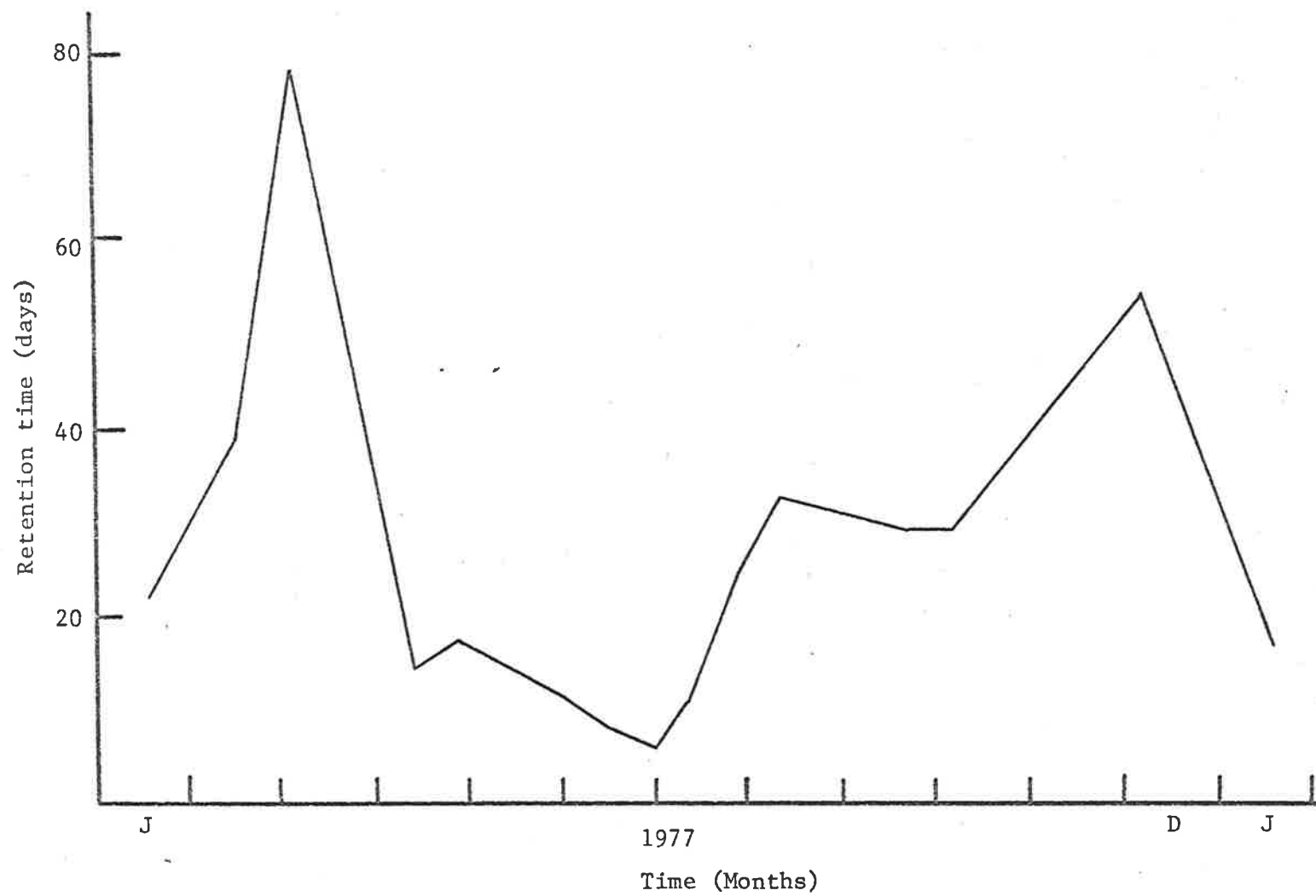


FIGURE 2.3 Overall retention time of the Gumeracha ponds.

Temperature. Surface water temperatures ($^{\circ}\text{C}$) and mean weekly maximum and minimum air temperatures (calculated from daily records at Mount Crawford, 13.3 km north-east of Gumeracha, same elevation) are shown in Figure 2.4. Annual fluctuations of surface temperature were similar in both ponds and closely followed air temperature. Surface temperature was generally higher than the average of maximum-minimum air temperature. Surface maxima recorded were 24.5°C on 16 February 1977 and 24.8°C on 15 March 1978 in pond 1, and 25.5°C on 16 February 1977 and 25.3°C on 15 March 1978 in pond 2. Surface minima recorded were 9.0°C on 1 June 1977 and 7.3°C on 9 August 1978 in pond 1, and 8.3°C on 15 June 1977 and 8.0°C on 9 August 1978 in pond 2. Temperature was recorded during mid-late morning and true surface maxima and minima would lie just outside the recorded range.

Depth-time isotherms for pond 1 and pond 2 from February 1977 to October 1978 are shown in Figure 2.5. For much of the study period both ponds were isothermal, or nearly so, and bottom water temperature varied from surface temperature by less than 1°C . At certain times, both ponds exhibited temporary thermal stratification with temperature differences up to 4.6°C between surface and bottom water. In pond 1 stratification occurred during May, August to September, and October to November in 1977, and during January to February, May, and August to September in 1978. Pond 2 exhibited a similar pattern with additional periods of stratification during February and December in 1977, and June to July in 1978. Stratification in both ponds occurred during all seasons and at temperatures spanning the annual range.

Temperature profiles taken in ponds 1 and 2 during periods of stratification are shown in Figure 2.6. On 15 March 1978, the stratification pattern observed in pond 1 was typical of a much deeper water body during summer (Wetzel, 1975; Hutchinson, 1975); the width of the thermal strata was, of course, much narrower. A thermally

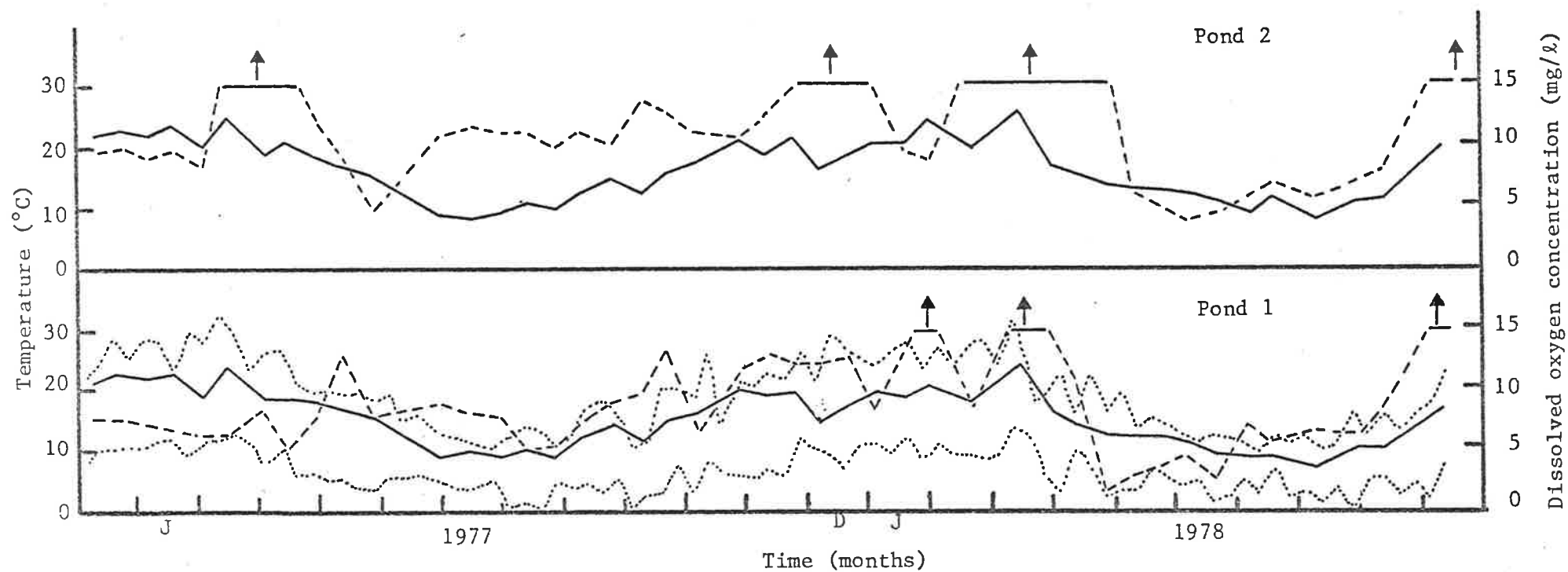


FIGURE 2.4 Surface water temperature (—), dissolved oxygen concentration (----) and mean weekly maximum-minimum air temperature (.....) for the Gumeracha ponds (arrows indicate oxygen readings off the meter scale).

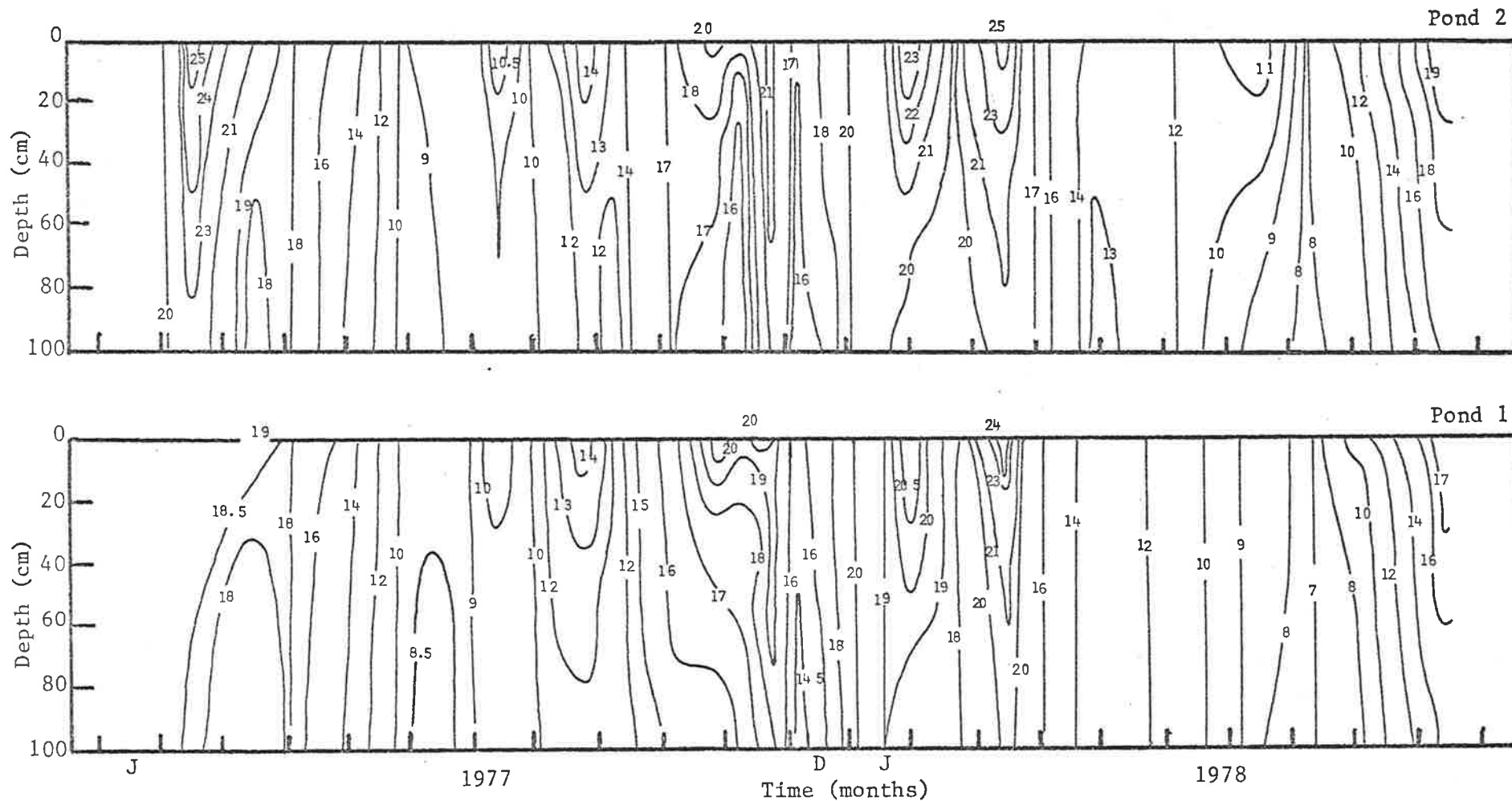


FIGURE 2.5 Depth-time isotherms ($^{\circ}\text{C}$) in the Gumeracha ponds.

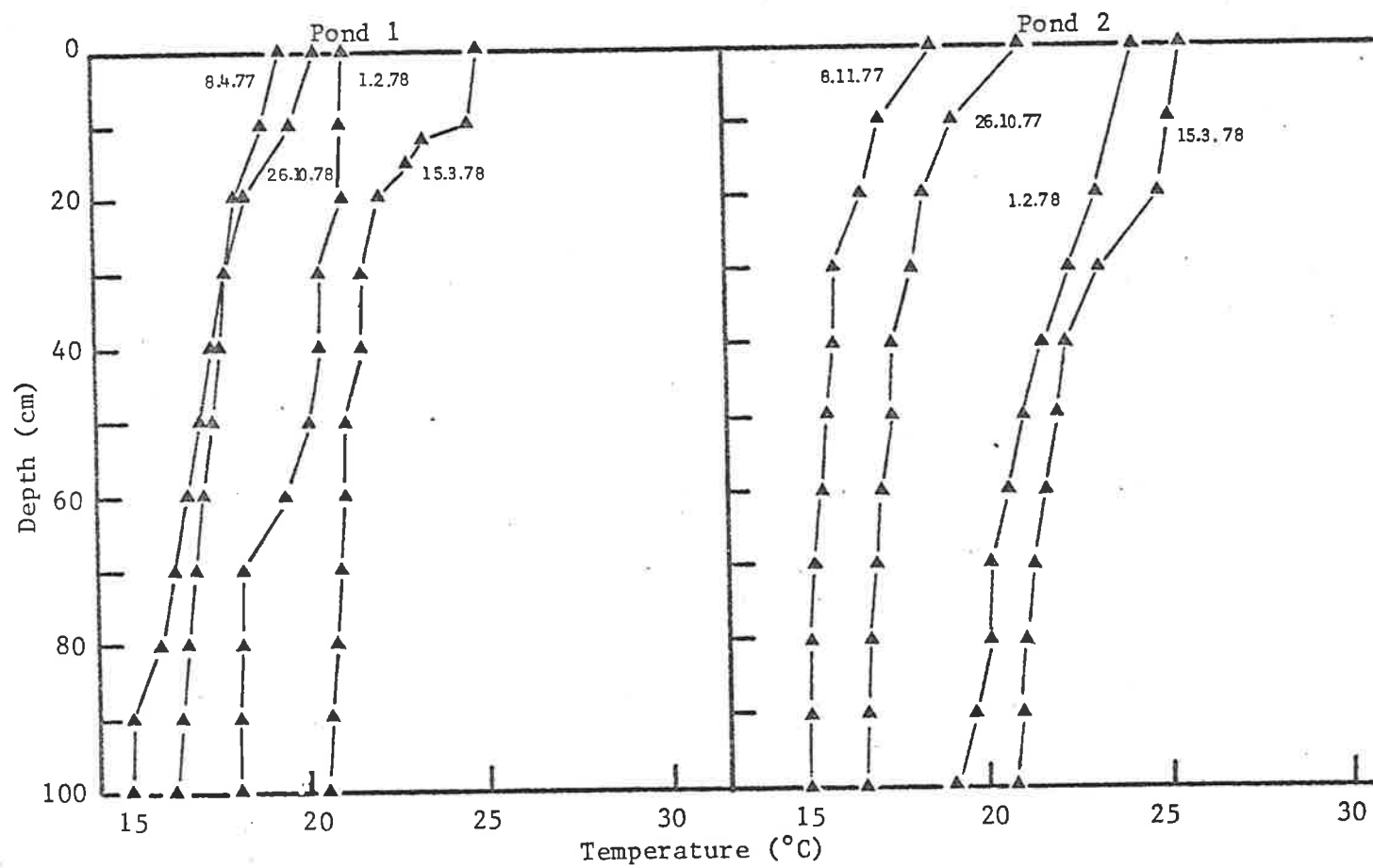


FIGURE 2.6 Temperature profiles in the Gumeracha ponds.

uniform epilimnion extended to 10 cm, a narrow metalimnion from 10-15 cm, and the hypolimnion from 15 cm to the bottom. A small, secondary thermal discontinuity occurred between 40 and 50 cm. "Diminutive" stratification (after Wetzel, 1975) was observed in pond 1 on 26 October and 8 November 1977; a poorly defined epilimnion (to 10 cm) was not clearly separated from the metalimnion which lacked a steep temperature gradient. A secondary discontinuity layer from 20 to 30 cm was observed in pond 1 on 1 February 1978. The epilimnion extended to 60 cm and the metalimnion from 60 to 70 cm. A typical deep-water summer stratification pattern was observed in pond 2 on 15 March 1978 with the epilimnion extending to 20 cm and the metalimnion from 20 to 36 cm. "Diminutive" stratification was observed in pond 2 on 26 October and 8 November 1977, and 1 February 1978, and secondary thermal discontinuities in the upper 10 cm of water on 26 October and 8 November 1977.

Diurnal depth-time isotherms from hourly readings in pond 2 on 13 and 14 December 1977, are shown in Figure 2.7. Thermal stratification was pronounced from 1300 to 1900 hours. After 2000 hours stratification broke down and the pond became isothermal by 2400 hours. At 0300 hours slight inverse stratification was exhibited.

Dissolved Oxygen. Surface absolute dissolved oxygen concentration (mg/l) is shown in Figure 2.4 (arrows indicate readings off the meter scale) and expressed as per cent saturation, calculated from the nomogram of Mortimer in Wetzel (1975, p. 666), in Figure 2.8.

Seasonal fluctuation in dissolved oxygen was similar in both ponds during 1978; events were dissimilar from January to November 1977. Pond 2 was supersaturated (>170%) from February to mid-March 1977, while pond 1 fluctuated from 68-96% saturation. Dissolved oxygen in pond 2 fell sharply to 49% saturation on 27 April 1977, but the extent of saturation steadily increased thereafter and reached 137% on 10 November 1977. After March 1977, saturation in pond 1 rose briefly to 143% on

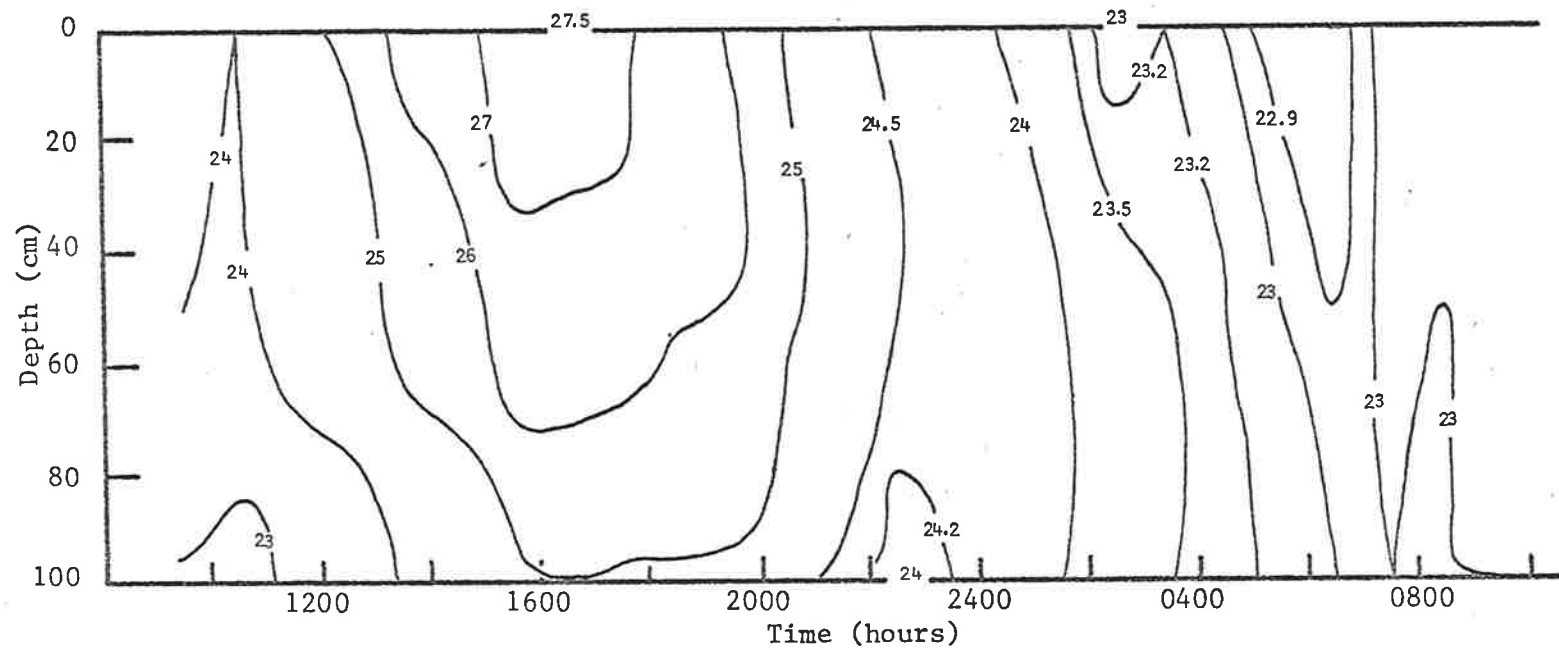


FIGURE 2.7 Diurnal depth-time isotherms ($^{\circ}\text{C}$) in Pond 2, 13.12.77-14.12.77

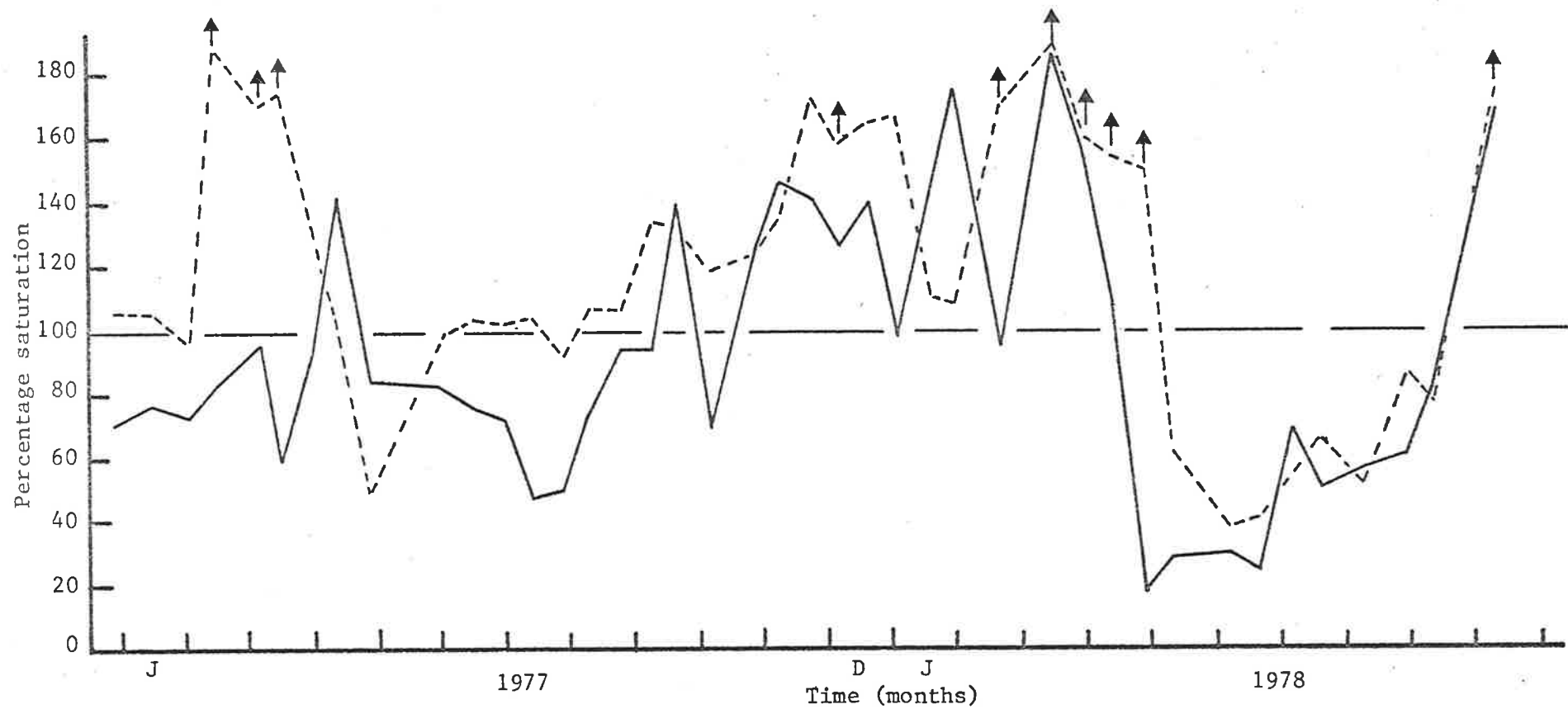


FIGURE 2.8 Surface dissolved oxygen concentration in the Gumeracha ponds expressed as percentage saturation (arrows indicate oxygen readings off meter scale). Pond 1 (—), pond 2 (---).

12 April, fell to 84% on 27 April, and gradually decreased to 48% on 12 July 1977. Both ponds were supersaturated during late 1977 and early 1978. Dissolved oxygen declined drastically in pond 1 after 29 March 1978 and reached 1.90 mg/l (19% saturation) on 27 April. In pond 2 dissolved oxygen declined after 27 April 1978, and reached 2.95 mg/l (38% saturation) on 10 May. Saturation in both ponds increased steadily during the winter of 1978 and exceeded 168% on 10 November. Diurnal observations during a phytoplankton bloom in December 1977, showed that dissolved oxygen did not fall below 130% saturation during the early morning oxygen sag, and exceeded 180% saturation for most of the night.

Depth-time oxygen isopleths for ponds 1 and 2 during 1977 and 1978 are shown in Figure 2.9. Vertical dissolved oxygen distribution was homogeneous in both ponds for much of the study. Stratification of dissolved oxygen occurred in both ponds during periods of thermal stratification. Oxygen stratification was most pronounced in pond 1 during February to March, May, and October to December, 1977, and during February to March and October, 1978. In pond 2 stratification was most pronounced during February to March, 1977 and 1978, and during October, 1978.

Dissolved oxygen profiles from ponds 1 and 2 during stratification are shown in Figure 2.10. Within each pond profiles were similar on 26 October and 8 November 1977, indicating that oxygen stratification persisted while thermal stratification was stable. Oxygen profiles were clinograde or weakly positive heterograde on the above dates with marked hypolimnetic depletion. A fairly marked metalimnetic maximum was observed in pond 1 on 26 October 1977, although water was supersaturated down to 70 cm. Oxygen profiles from pond 2 on 26 October and 8 November 1977, were orthograde; dissolved oxygen increased with depth as temperature decreased.

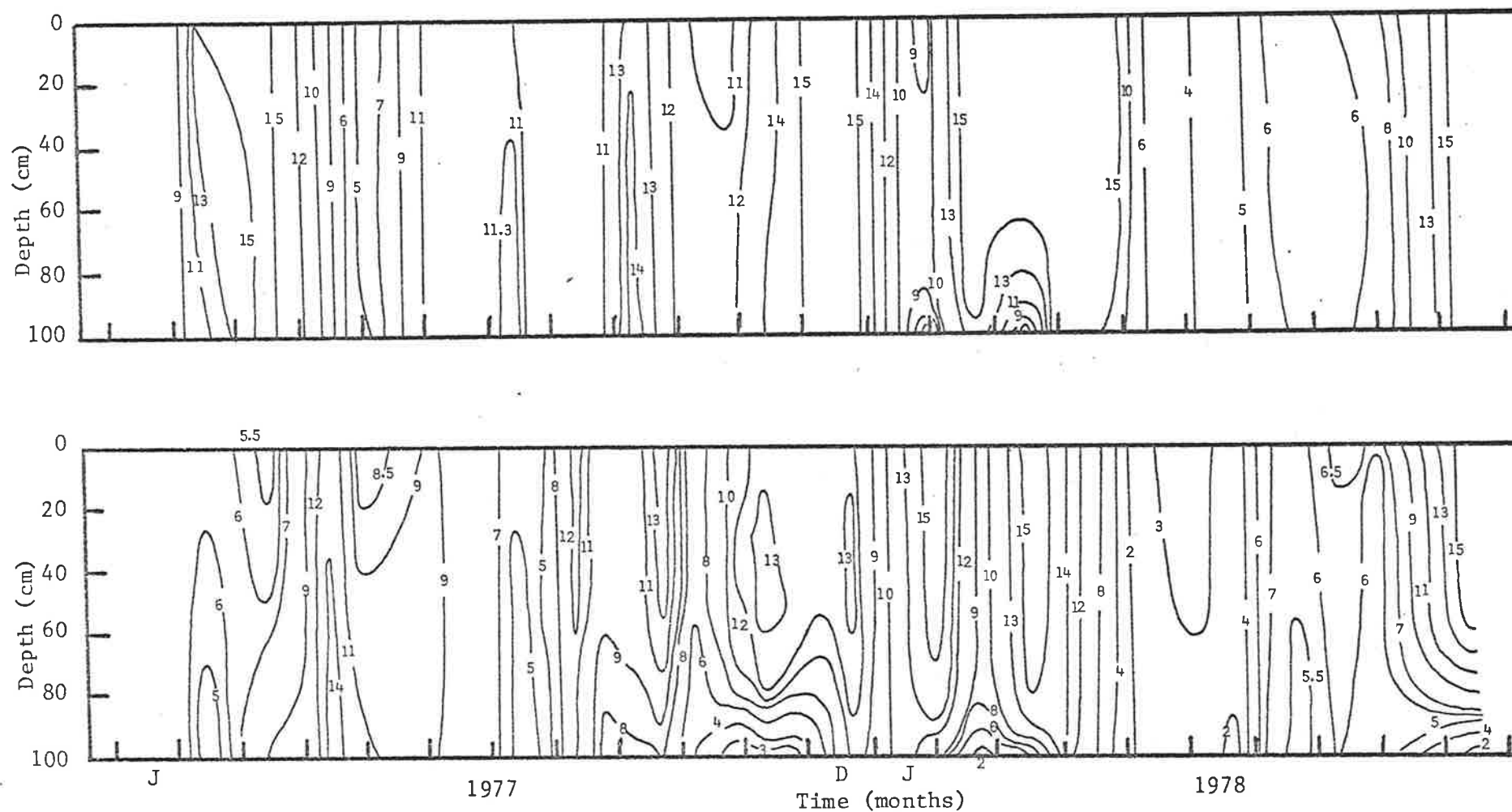


FIGURE 2.9 Depth-time oxygen isopleths (mg/l) in the Gumeracha ponds.

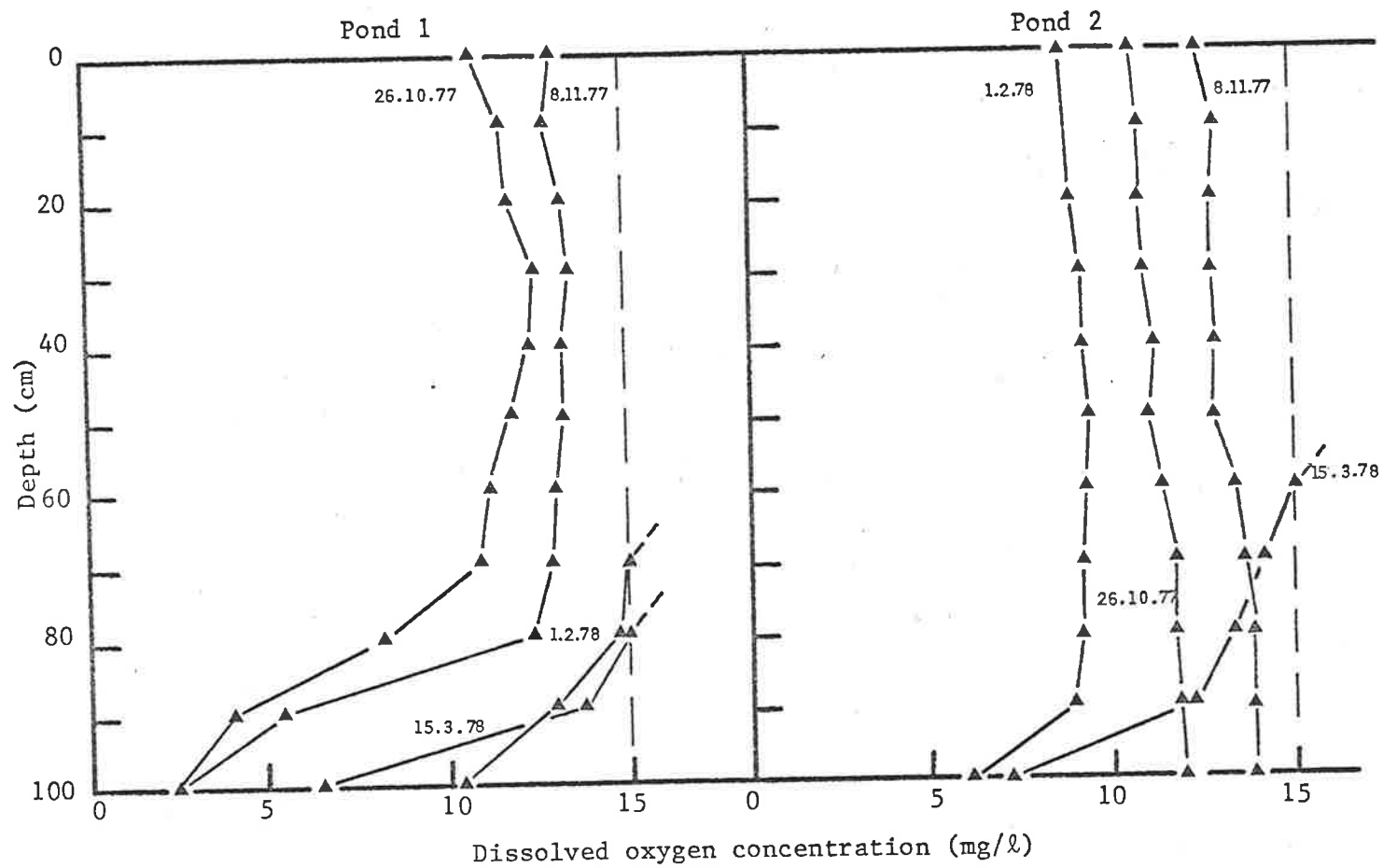


FIGURE 2.10 Dissolved oxygen concentration profiles in the Gumeracha ponds.

Profiles from pond 2 on 1 February and 15 March 1978, ranged from weak to strong clinograde.

Diurnal dissolved oxygen isopleths from hourly readings in pond 2 on 13 and 14 December 1977, are shown in Figure 2.11. Dissolved oxygen was inversely stratified from 1000 to 1600 hours. Readings were off the scale from 1800 hours until 0100 hours; at 0100 hours dissolved oxygen was homogeneous (15 mg/l). Slight stratification occurred from 0300 hours.

Temperature, dissolved oxygen and per cent saturation profiles beneath floating algal mats in ponds 1 and 2 on 19 July 1978, are compared with open water profiles in Figure 2.12. Algal mats consisting of an upper, dense layer of *Stigeoclonium* sp. (10 cm thick) and a lower layer of thin trailing filaments of *Ulothrix* sp. enclosures used in a fish introduction experiment (20 cm long), formed on the floating mesh covers of (see chapter 5). Thermal stratification was pronounced beneath algal mats and surface water was up to 1.9°C warmer than open water. Water 10 to 20 cm beneath the mats was cooler than open water due to absorption of heat by the *Stigeoclonium*. Pond 2 exhibited a well defined epilimnion (to 5 cm) and metalimnion (to 15 cm) below the mat. In pond 1 dissolved oxygen concentration and per cent saturation decreased gradually with depth beneath the mat exceeding open water values above 25 cm. In pond 2 the oxygen profile beneath the mat was clinograde; surface water was supersaturated down to 5 cm and dissolved oxygen concentration exceeded open water by 8 mg/l. Saturation declined to 68% at 10 cm beneath the mat in pond 2 and below this depth oxygen concentration was less than in open water. Oxygen depletion below 25 cm in pond 1 and 10 cm in pond 2 probably resulted from respiration of *Ulothrix* under low light conditions. After 19 July 1978, enclosure covers were raised above the water surface and the algae died off.

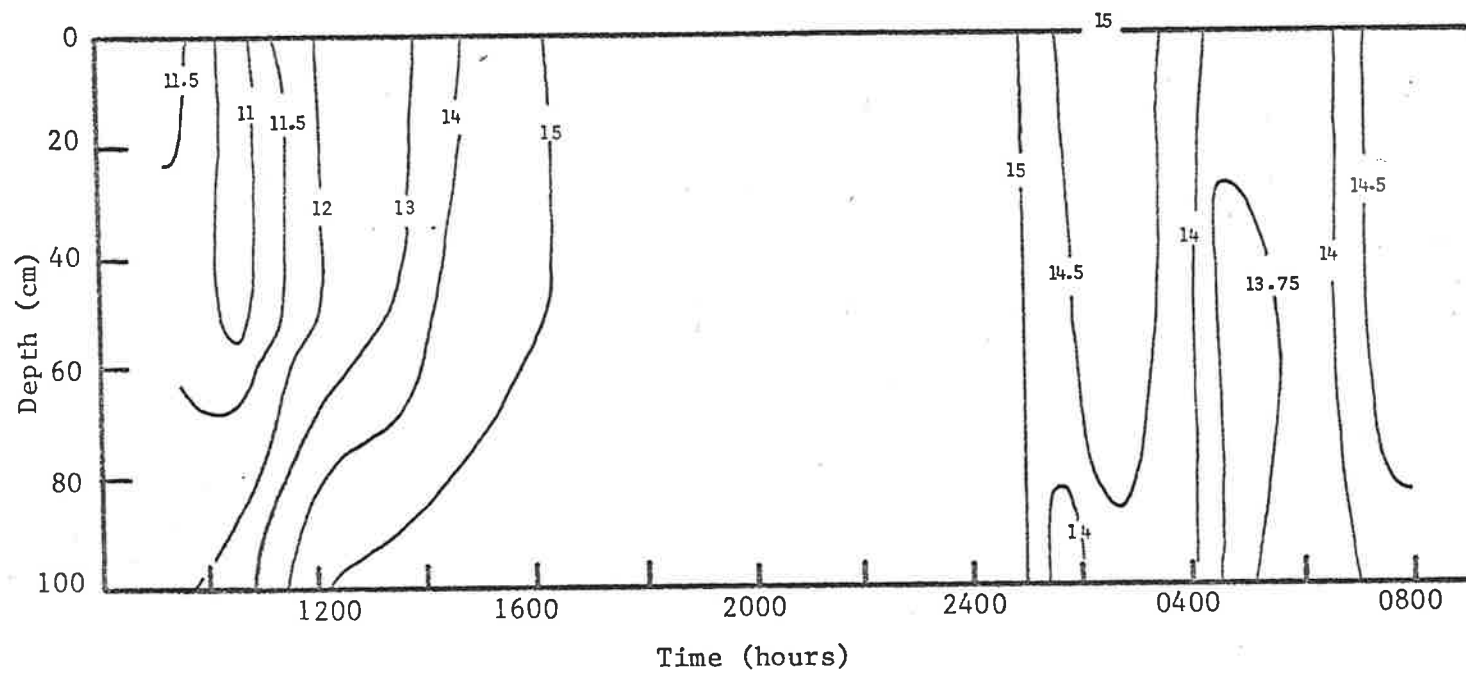


FIGURE 2.11 Diurnal depth-time oxygen isopleths (mg/l) in pond 2, 13.12.77-14.12.77

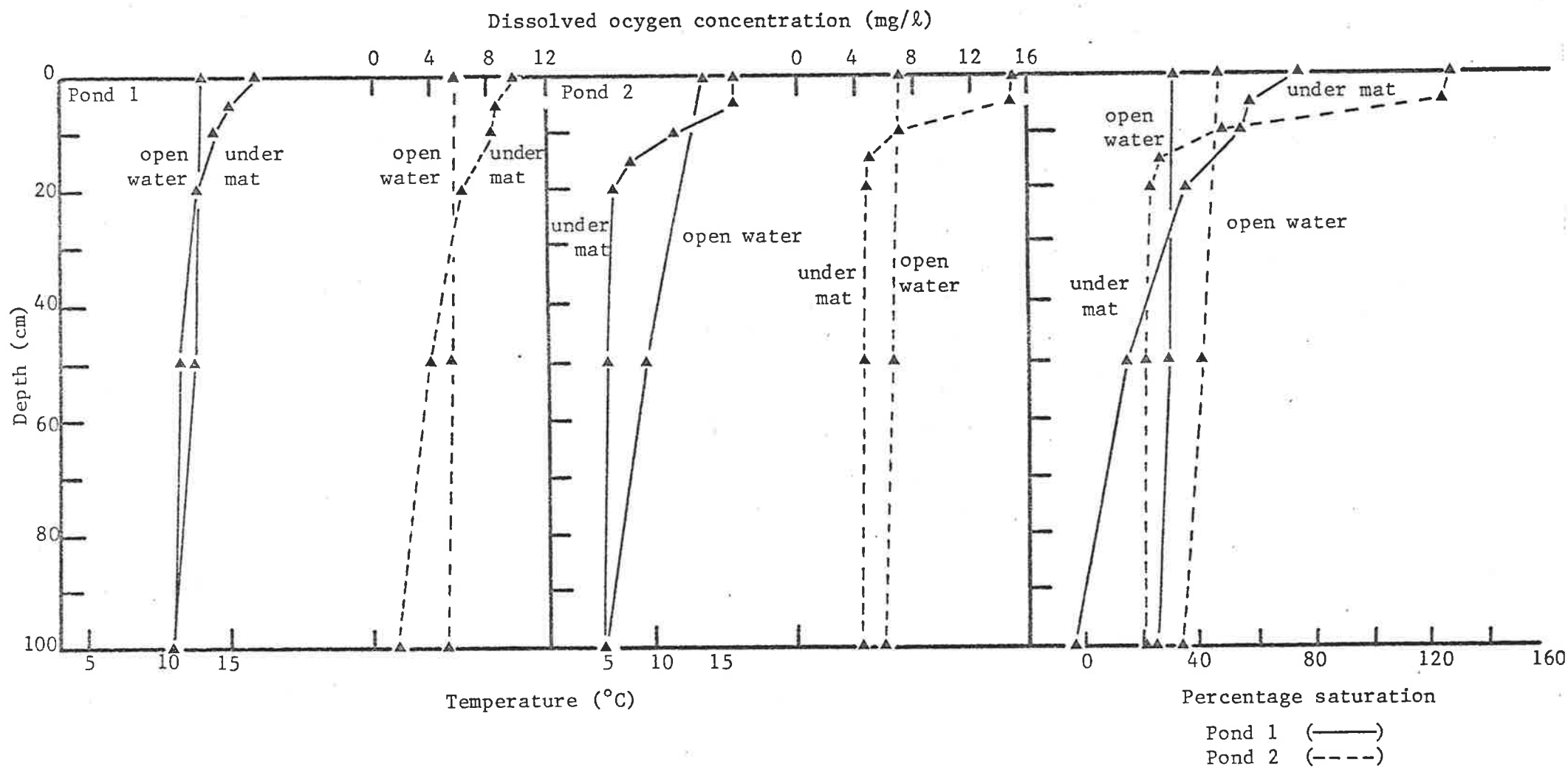


FIGURE 2.12 Water temperature and dissolved oxygen (concentration and percentage saturation) profiles in open water and under floating algal mats in the Gumeracha ponds on 19.7.78.

pH and Total Dissolved Solids. Seasonal fluctuations in pH and TDS (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.13. Pond 1 influent pH fluctuated erratically between 6 and 7.5 throughout the study. Pond 1 effluent and pond 2 effluent pH increased during the summer months (December to May). Pond 1 effluent pH fluctuated between 7 and 10.5 and pond 2 effluent pH between 7 and 11.2. pH increases of pond 2 effluent were similar during the summer of 1977 and 1978 while the increase of pond 1 effluent pH during the summer of 1978 was 1.5 units higher than during 1977. pH increased progressively through ponds 1 and 2. Pond 2 effluent pH exceeded pond 1 effluent pH by a maximum of 3.4 units during the summer of 1977 but by only a maximum of 2.1 units during the summer of 1978.

Pond 1 effluent and pond 2 effluent TDS were similar and both generally less than pond 1 influent except during March to May, 1978. Pond 1 influent TDS increased markedly from November 1977. Pond 1 effluent and pond 2 effluent TDS increased accordingly during the summer of 1978; the increase during the summer of 1977 was slight.

Biochemical Oxygen Demand. Seasonal fluctuations in BOD (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.14. Pond 1 influent BOD fluctuated widely but was generally between 10 and 24 mg/l. Pond 1 effluent BOD was less than influent BOD during 1977 (2 to 5 mg/l) but increased during January 1978 (6 to 21 mg/l) and exceeded influent BOD on some occasions. Pond 2 effluent total BOD exceeded pond 1 effluent and influent from January to March, 1977, was similar to pond 1 effluent from April to November of that year, and increased from November 1977 to April, 1978, exceeding pond 1 effluent and influent on some occasions. Pond 2 effluent filtered BOD was equivalent to 20 to 30% total BOD from January to March, 1977, and 1978, and to 60 to 100% total BOD from May to October, 1977. Pond 2 effluent filtered BOD was similar to pond 1 effluent (total) BOD during the

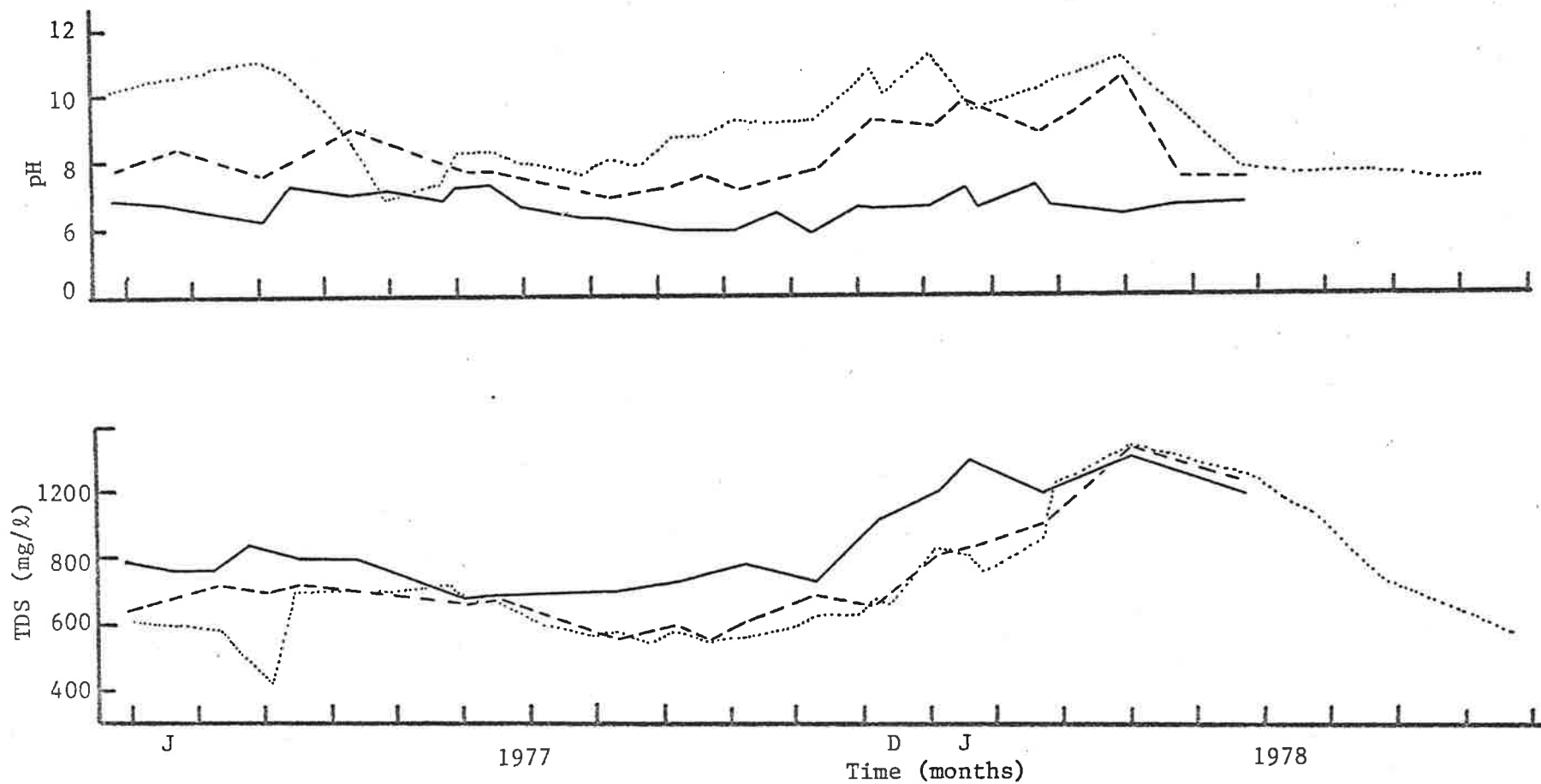


FIGURE 2.13 pH and TDS in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....).

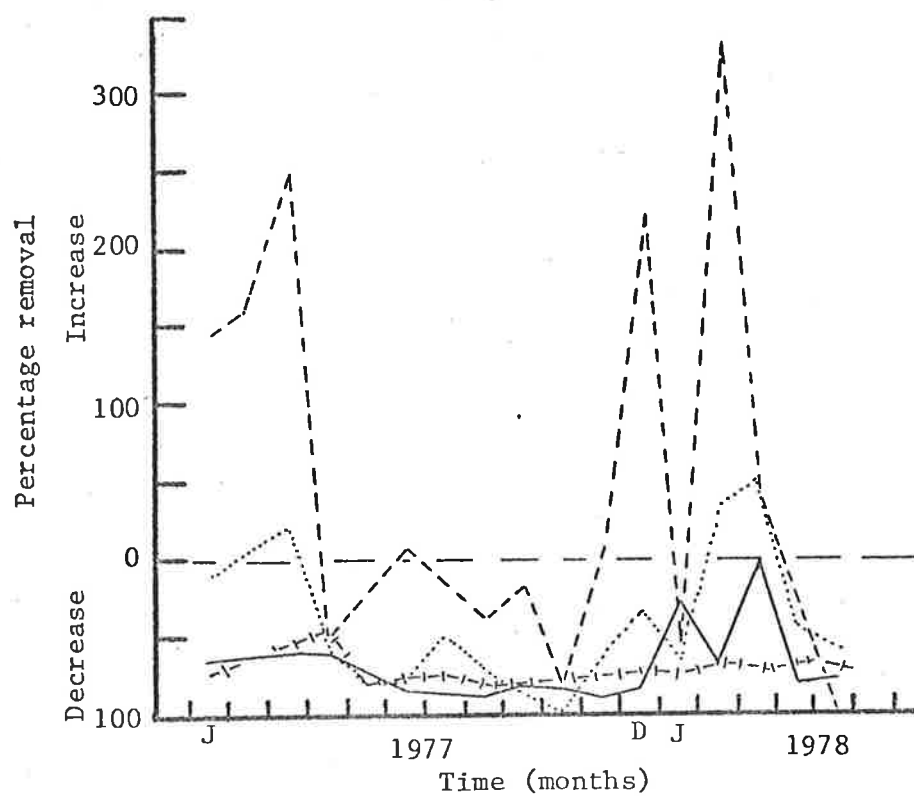
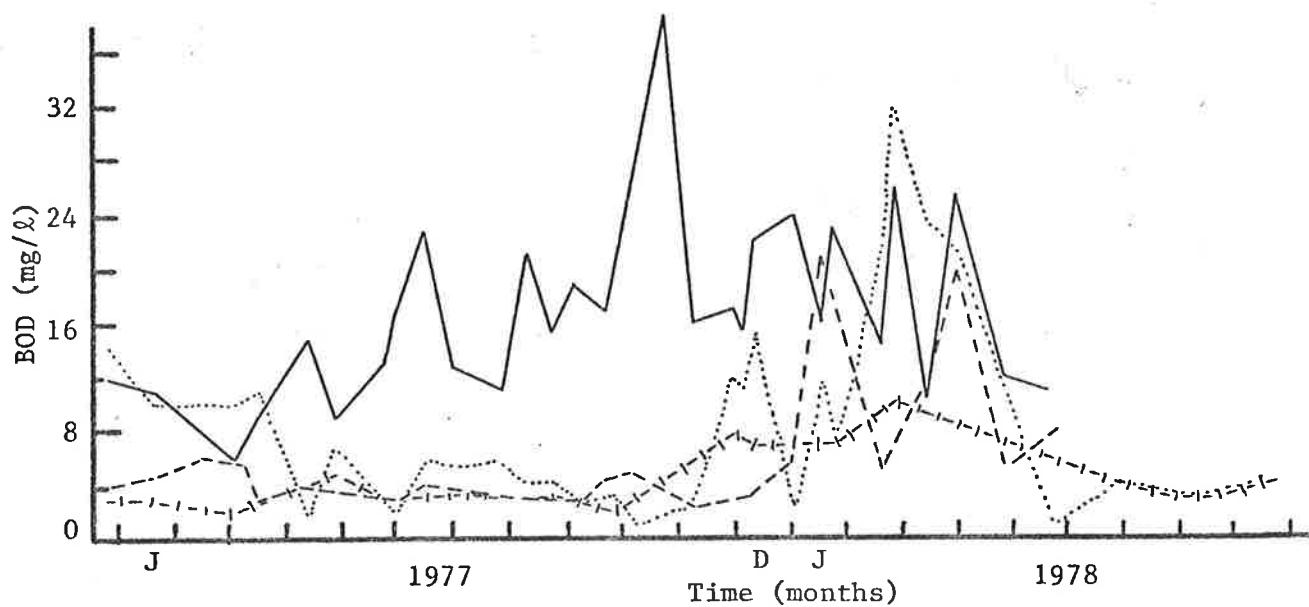


FIGURE 2.14 BOD in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (total, ...; filtered, - · - · -), and mean monthly percentage removal of BOD in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (total, ...; filtered, - · - · -).

winter of 1977 (April to October).

The efficiency of a WSP in stabilizing organic matter is measured by the per cent reduction in wastewater characteristics as wastewater passes through the pond. A negative reduction (increase) results if effluent values exceed influent values. A reduction of less than 30% will be considered "low", greater than 70% "high" and between these limits "medium".

Mean monthly per cent reductions of BOD by ponds 1 and 2 and the pond system overall are compared in Figure 2.14. Pond 1 reduced BOD by 60% until April, 1977, and by 80 to 90% from May to November, 1977. Pond 1 effected only 21% removal in late December, 1977, and no removal in April, 1978. Pond 2 reduced BOD by less than 50% from April to November, 1977, and during the summer of 1977 and 1978 increased BOD by over 200%. Overall, BOD (filtered) was reduced by 70% throughout the study. Total BOD was reduced by 70 to 80% during winter but increased by 20 to 50% during summer. Low summer removal overall was due to the pejorative effects of pond 2 in 1977, and both ponds in 1978. That is, pond 1 effected high removal during 1977 (summer and winter) but removal was low during the summer of 1978. Pond 2 increased BOD during the summers of 1977 and 1978 and although removal improved during the winter of 1977 it was still low.

Suspended Solids. Seasonal fluctuations in SS (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.15, and mean monthly per cent reduction of SS by the ponds are shown in Figure 2.15. Pond 1 influent SS fluctuated randomly (up to 48 mg/l) during the study. Pond 1 effluent SS was less than influent during 1977 but increased in January 1978 and exceeded influent during March and April (up to 105 mg/l). Pond 2 effluent SS exceeded pond 1 influent and effluent from January to April, 1977, was similar to pond 1 effluent SS from May to October, 1977, and again exceeded pond 1

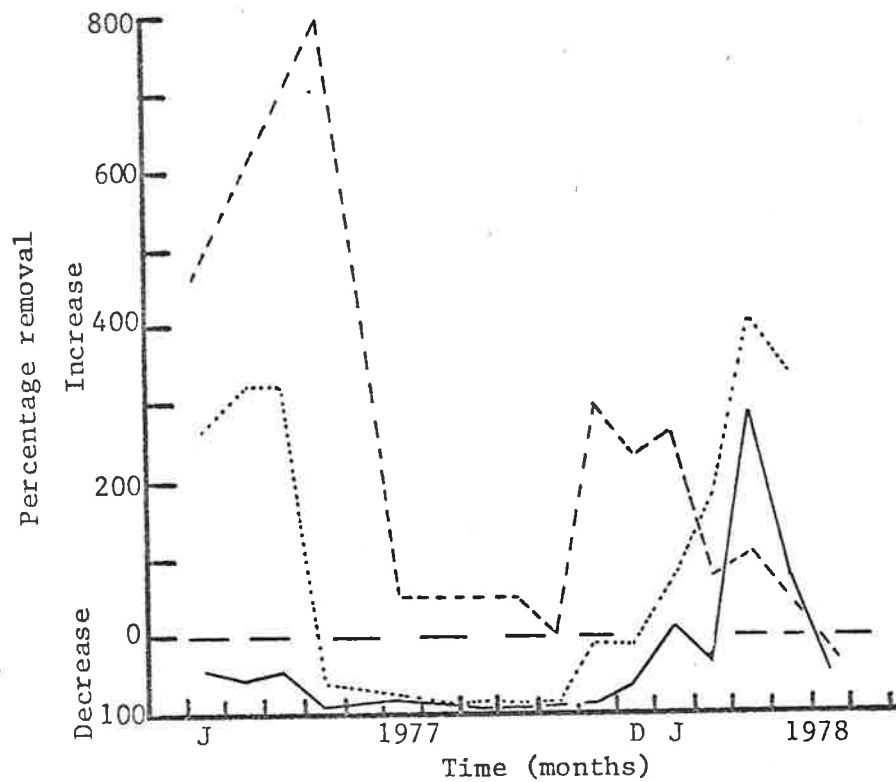
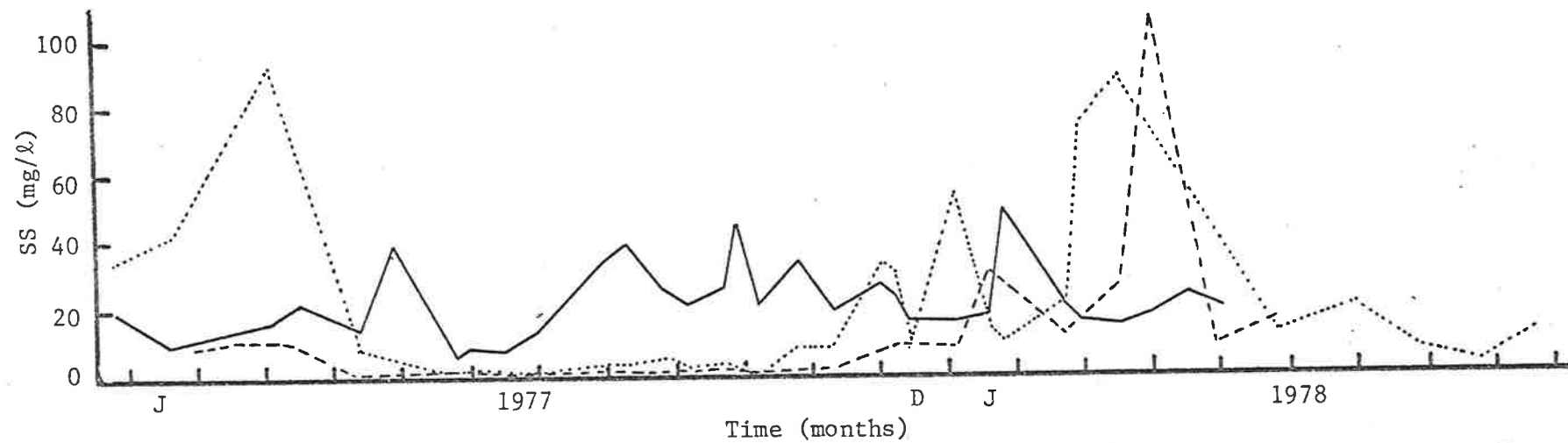


FIGURE 2.15 SS in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....), and mean monthly percentage removal of SS in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

influent SS from December, 1977, to April, 1978 (up to 88 mg/l).

Pond 1 effluent and pond 2 effluent SS both declined dramatically after March-April, 1978.

Pond 1 reduced SS by 90% from April to October, 1977.

Removal decreased steadily from December, 1977, and during March, 1978, pond 1 increased SS by 288%. Pond 2 increased SS by up to 800% from January to April, 1977, and effected no reduction of SS throughout the remainder of that year. Pond 2 increased SS up to 300% from November, 1977 to March, 1978. The pond system overall reduced SS by 70 to 90% from April to November, 1977. During the summer of 1977 and 1978 SS was increased over 300% by the system overall. Overall increases were due to pond 2 during 1977 and both ponds during 1978. That is, pond 1 effected medium to high SS removal during 1977 (summer and winter) but increased SS during the summer of 1978. Pond 2 increased SS throughout the study, summer and winter.

Total Carbon and Total Organic Carbon. Seasonal fluctuations in TC (mg/l) and TOC (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.16. From January to March, 1977, pond 1 effluent TC was less than pond 2 effluent TC and both exceeded pond 1 influent TC. Pond 1 effluent TC and pond 2 effluent TC were similar from April to December, 1977, and both were less than pond 1 influent TC. Pond 1 influent TOC was generally between 20 and 40 mg/l and pond 1 effluent TOC (13-22 mg/l) was less than influent throughout 1977. Pond 1 effluent TOC increased in January, 1978, and exceeded influent during March and April. Pond 2 effluent TOC exceeded pond 1 influent and pond 1 effluent from January to March, 1977 and 1978 and was similar to pond 1 effluent TOC from June to November, 1977.

Mean monthly per cent reduction of TC and TOC in ponds 1 and 2 are shown in Figure 2.17. Pond 1 increased TC up to 29% from January to March, 1977, and by 2% during February, 1978. From

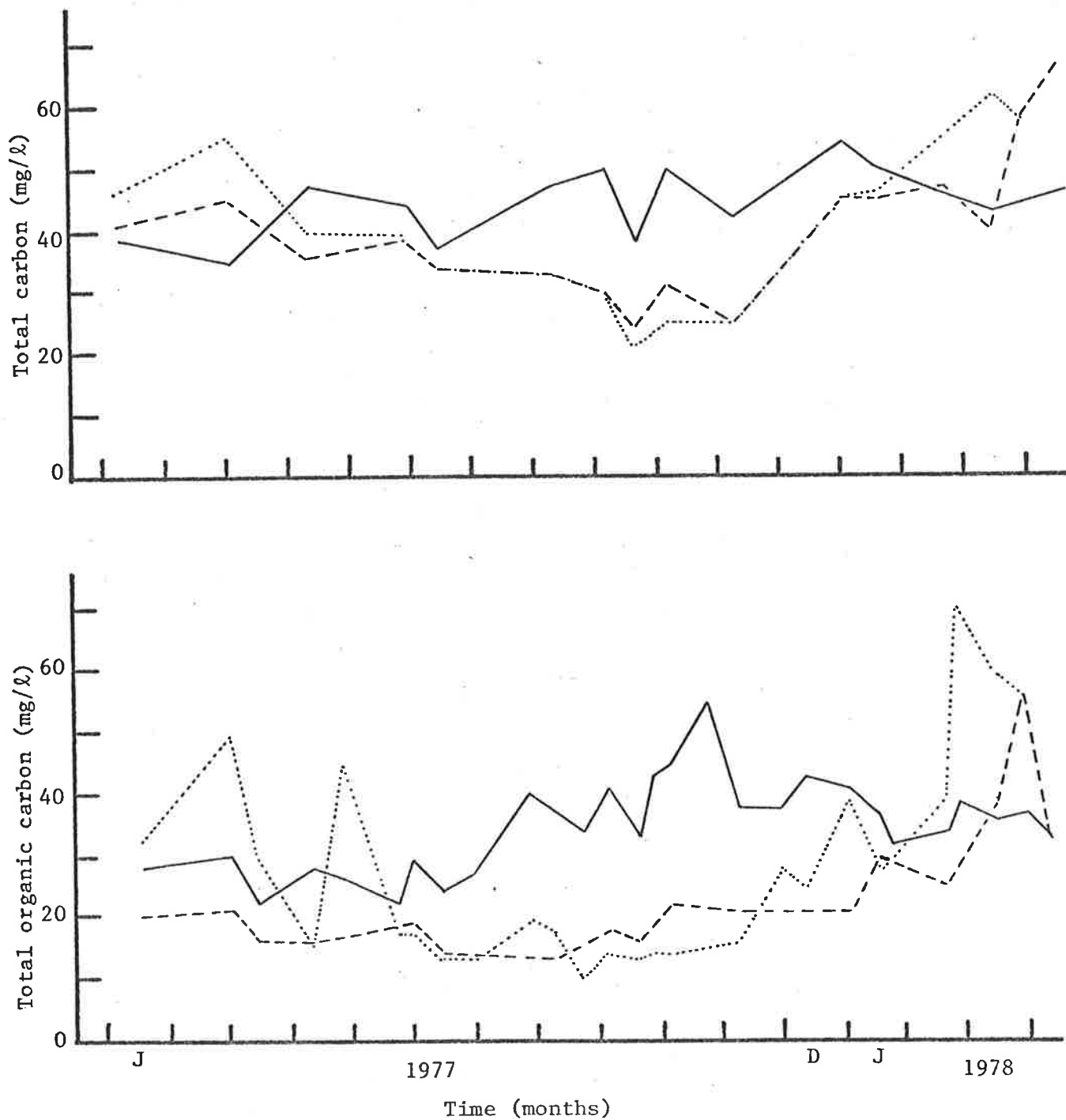


FIGURE 2.16 Total carbon and total organic carbon in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....).

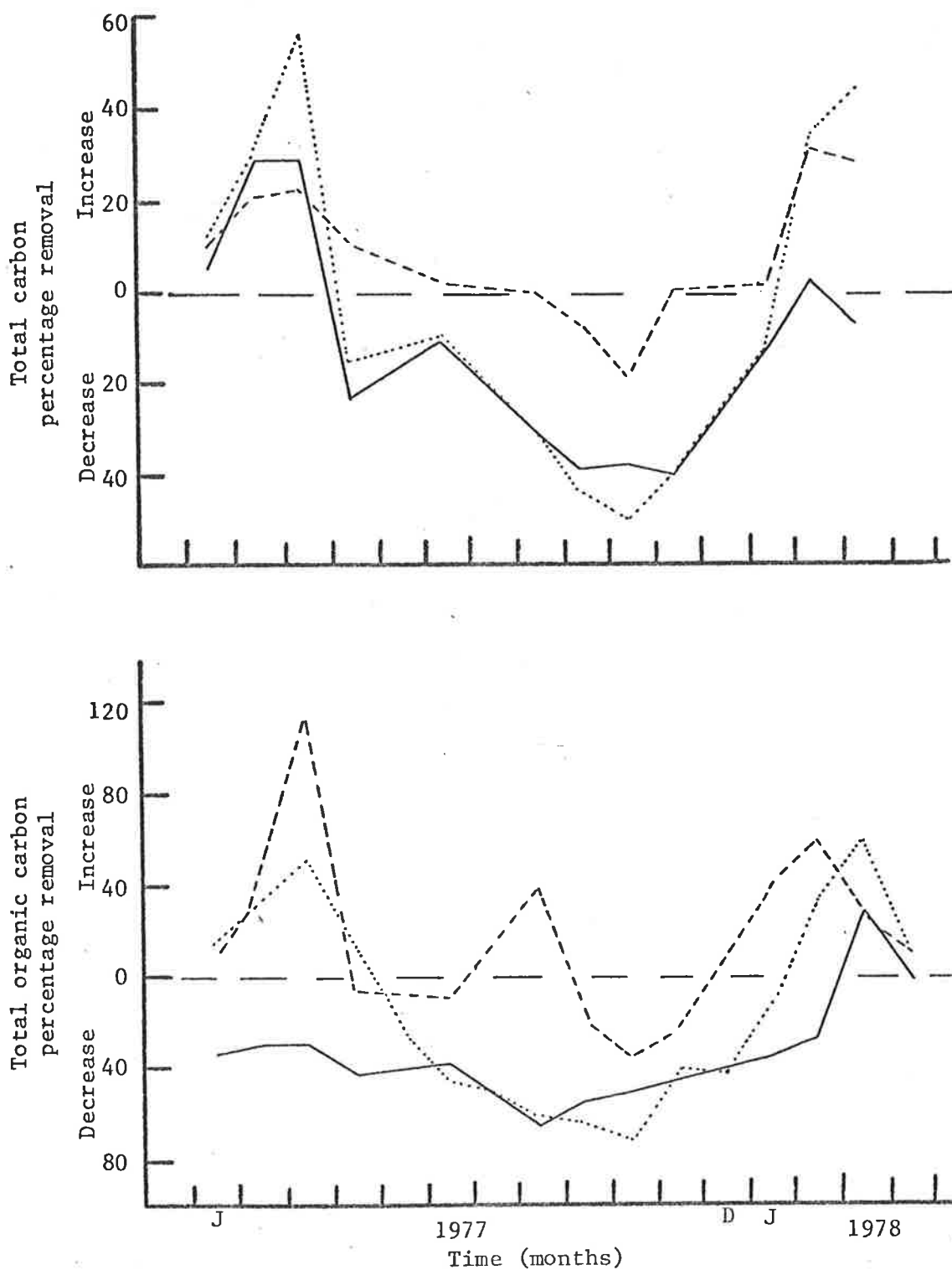


FIGURE 2.17 Mean monthly percentage removal of total carbon and total organic carbon in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

April to November, 1977, pond 1 reduced TC by 20 to 40%. Pond 2 increased TC 20 to 30% from January to March, 1977 and 1978, and only effected removal during September and October, 1977. The system overall reduced TC by 50% at best, and increased TC up to 57% from January to March, 1977 and 1978. Both ponds contributed to summer increases in TC. Pond 1 reduced TOC 30 to 65% throughout 1977. Removal decreased steadily from January, 1978, and TOC increased 29% during March. Pond 2 increased TOC up to 113% from January to March, 1977 and 1978, and July to August, 1977. Removal was less than 40% from April to November, 1977. The system overall reduced TOC up to 71% from May to December, 1977, and increased TOC up to 60% from January to April, 1977 and 1978. Overall summer increases were due to pond 2 in 1977 and both ponds in 1978. That is, pond 1 effected medium to high removal during 1977 (summer and winter) but increased TOC during the summer of 1978. Pond 2 increased TOC during the summers of 1977 and 1978; removal increased during the winter of 1977 but was still low.

Mean annual per cent reduction in BOD, SS, TC, and TOC during 1977 by ponds 1 and 2, and the pond system overall are compared in Table 2.3. Pond 1 effected high BOD and SS removal, medium TOC removal, and low TC removal. Pond 2 actually increased all parameters during 1977, most notably SS. Overall BOD removal was medium but removal for other parameters was low; SS was increased overall. Low overall removal during 1977 was thus due to the pejorative influence of pond 2 although pond 1 also contributed to decreased performance in 1978. That is, pond 1 performed efficiently during 1977 while pond 2 was inefficient, particularly during the summer. The efficiency of pond 1 decreased during the summer of 1978 and performance was similar to pond 2.

Total Inorganic Carbon. Seasonal fluctuations in TIC ($\text{CO}_2 + \text{HCO}_3^- + \text{CO}_3^{=}$) (mg/l) of pond 1 influent, effluent, and pond 2 effluent are

Table 2.3

Mean annual percentage reduction of organic parameters
in the Gumeracha ponds during 1977.

	Pond 1	Pond 2	Overall
BOD	77.1	-40.1	52.5 - Total 70.0 - Filtered
SS	82.1	-271.5	-6.0
TC	21.7	-1.3	18.7
TOC	46.4	-7.9	28.9

shown in Figure 2.18. Pond 1 effluent TIC exceeded influent throughout the study, except during March, 1978. Pond 2 effluent TIC was much lower than pond 1 effluent from January to February, 1977. During February and March, 1978, pond 1 effluent and pond 2 effluent TIC were similar; in late May, 1978, pond 1 effluent and pond 2 effluent TIC were both very low (2 mg/l) and less than pond 1 influent TIC.

Ammonia. Seasonal fluctuations in NH_3 (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.19, and mean monthly per cent reduction by ponds 1 and 2 are shown in Figure 2.19.

Pond 1 influent NH_3 varied considerably (0.8 to 9.8 mg/l). Pond 1 effluent NH_3 (0.1 to 1.2 mg/l) was much less than influent and pond 2 effluent NH_3 (0.1 to 3.9 mg/l) was similar to pond 1 effluent except during May, 1977 and January, 1978.

Pond 1 reduced NH_3 by 40% from January to March, 1977, and by 80 to 90% from April until December, 1977. Removal decreased slightly during January, 1978. NH_3 removal by pond 2 varied dramatically. Pond 2 reduced NH_3 by 78% during October, 1977, but increased NH_3 250 to 300% from April to June, 1977, and during January, 1978. The system overall reduced NH_3 by 70 to 90% during 1977 and 40% during January, 1978. Overall removal decreased when pond 2 increased NH_3 .

Total Kjeldahl and Organic Nitrogen. Seasonal fluctuations in TKN (mg/l) and org-N (mg/l) of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.20. Pond 1 effluent TKN (1.94 to 14.10 mg/l) was less than influent TKN (1.98 to 61.50 mg/l) throughout 1977 but increased markedly during February, 1978 and exceeded influent. Pond 2 effluent TKN was similar to pond 1 effluent TKN during 1977, except on June 15th, and also increased during February, 1978 when it exceeded pond 1 influent TKN.

Org-N followed a similar pattern to TKN, differences resulting

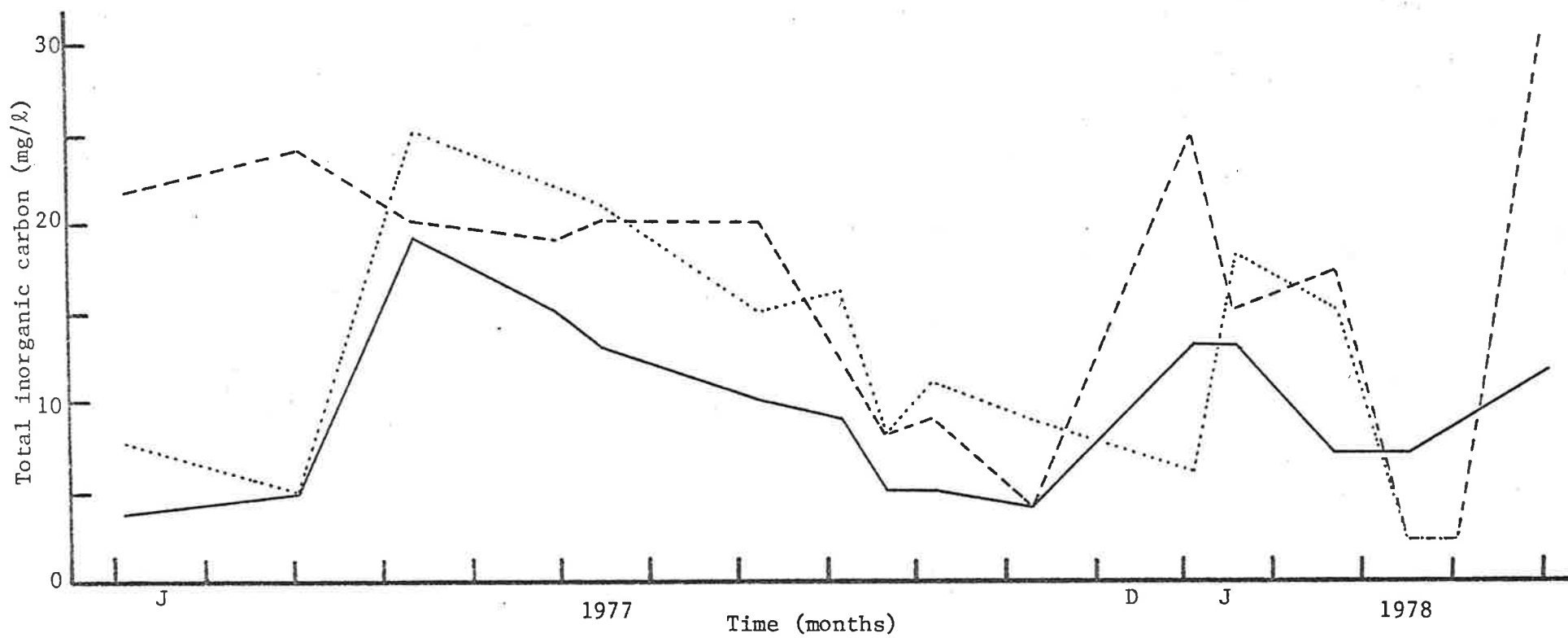


FIGURE 2.18 Total inorganic carbon in pond 1 influent (—), pond 1 effluent (----), and pond 2 effluent (.....).

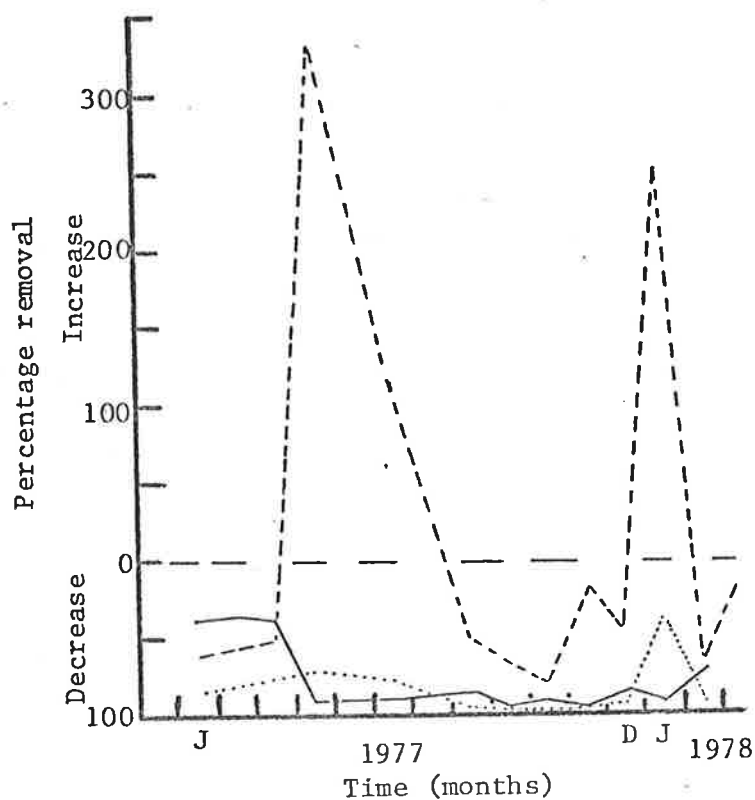
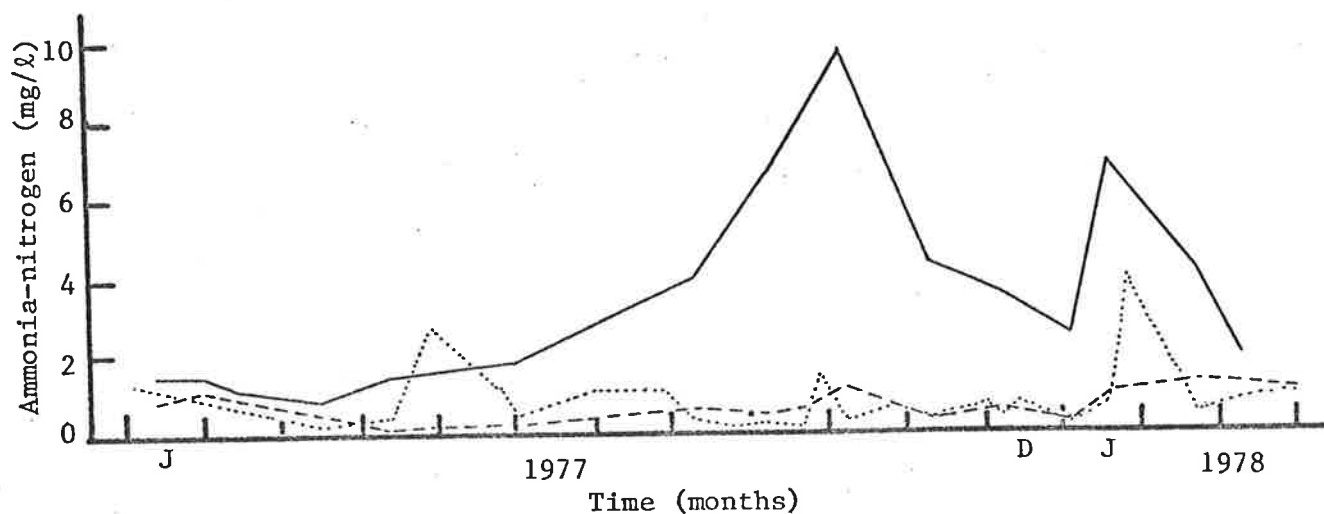


FIGURE 2.19 Ammonia-nitrogen in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....), and mean monthly percentage removal of $\text{NH}_3\text{-N}$ in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

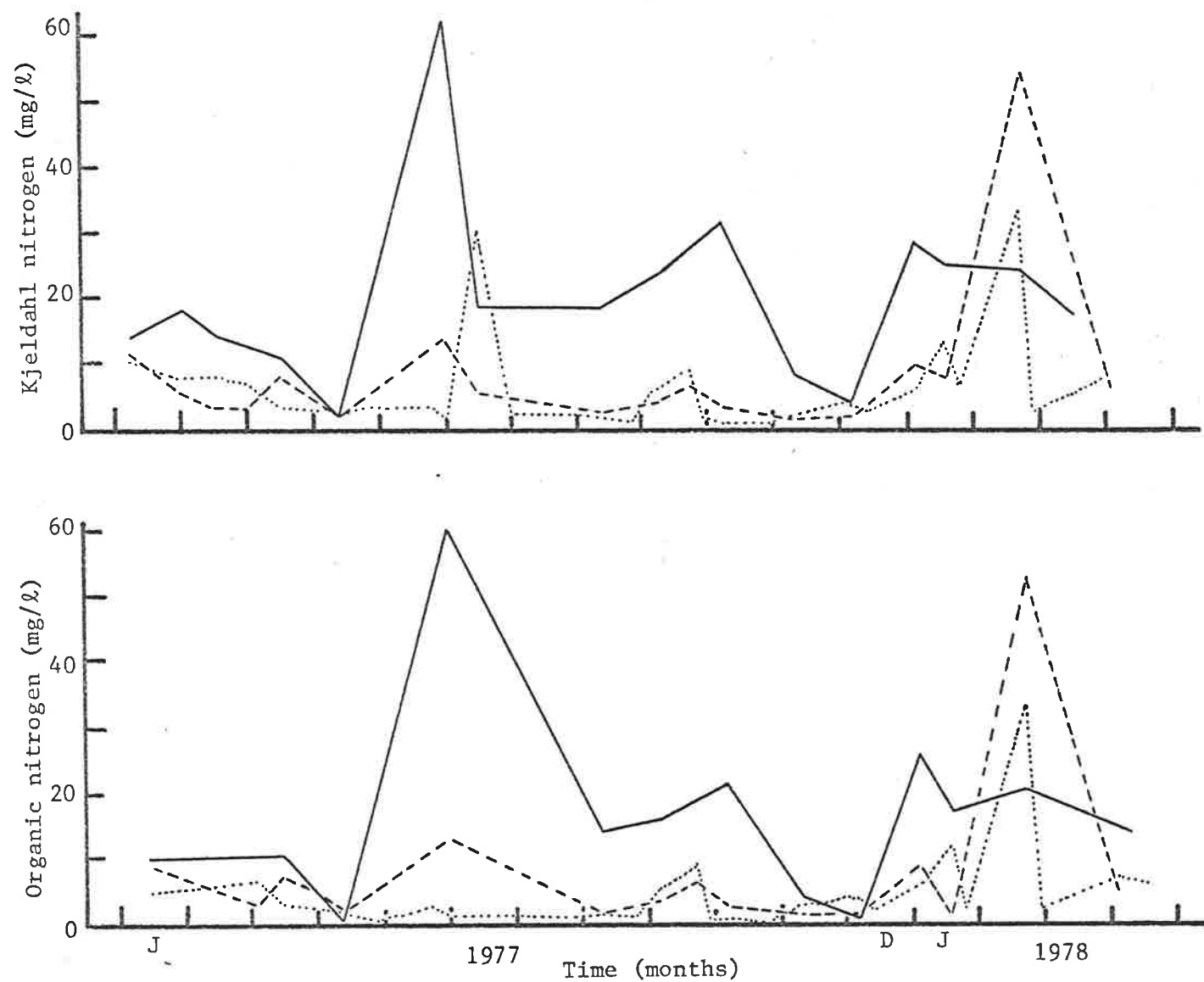


FIGURE 2.20 Total Kjeldahl nitrogen and organic nitrogen in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....).

from fluctuations in NH_3 concentration. Pond 2 effluent org-N was, however, considerably lower than pond 1 effluent org-N from May to July, 1977.

Mean monthly per cent reduction of TKN and org-N by pond 1 and pond 2 are shown in Figure 2.21. Removal of TKN by pond 1 was less than 50% from January to March, 1977, and 75 to 85% from June to November, 1977. Pond 1 increased TKN over 100% during February and March, 1978. TKN removal by pond 2 was low throughout the study except in October, 1977 (73%). Pond 2 increased TKN during most of 1977. The system overall increased TKN in April, 1977, and during February and March, 1978. Overall removal exceeded 70% only from August to October, 1977. Low overall TKN removal was due mainly to pond 2 during 1977, and mainly to pond 1 during 1978. That is, removal by pond 1 was low during the summer of 1977 and high during winter; pond 1 increased TKN during the summer of 1978. Pond 2 generally increased TKN except during the summer of 1978.

Pond 1 reduced org-N by 77 to 88% from June to October, 1977, but increased org-N during April (260%) and December, 1977, and February, 1978. Pond 2 reduced org-N over 70% in June and October, 1977, but increased org-N during March, September, November, and December, 1977, and January, 1978. The system overall reduced org-N by 65 to 98% from June to October, 1977, but increased org-N over 200% in April and December, 1977. Pond 1 and pond 2 both contributed to low overall org-N removal during 1977 and 1978.

Nitrate. Seasonal fluctuations in NO_3^- concentration (mg/l) pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.22, and mean monthly per cent removal by ponds 1 and 2 are shown in Figure 2.22. The relative concentrations of NO_3^- and NH_3 in pond 1 influent indicated that nitrification reactions in the trickling filter had proceeded to a considerable extent. Pond 1 influent NO_3^-

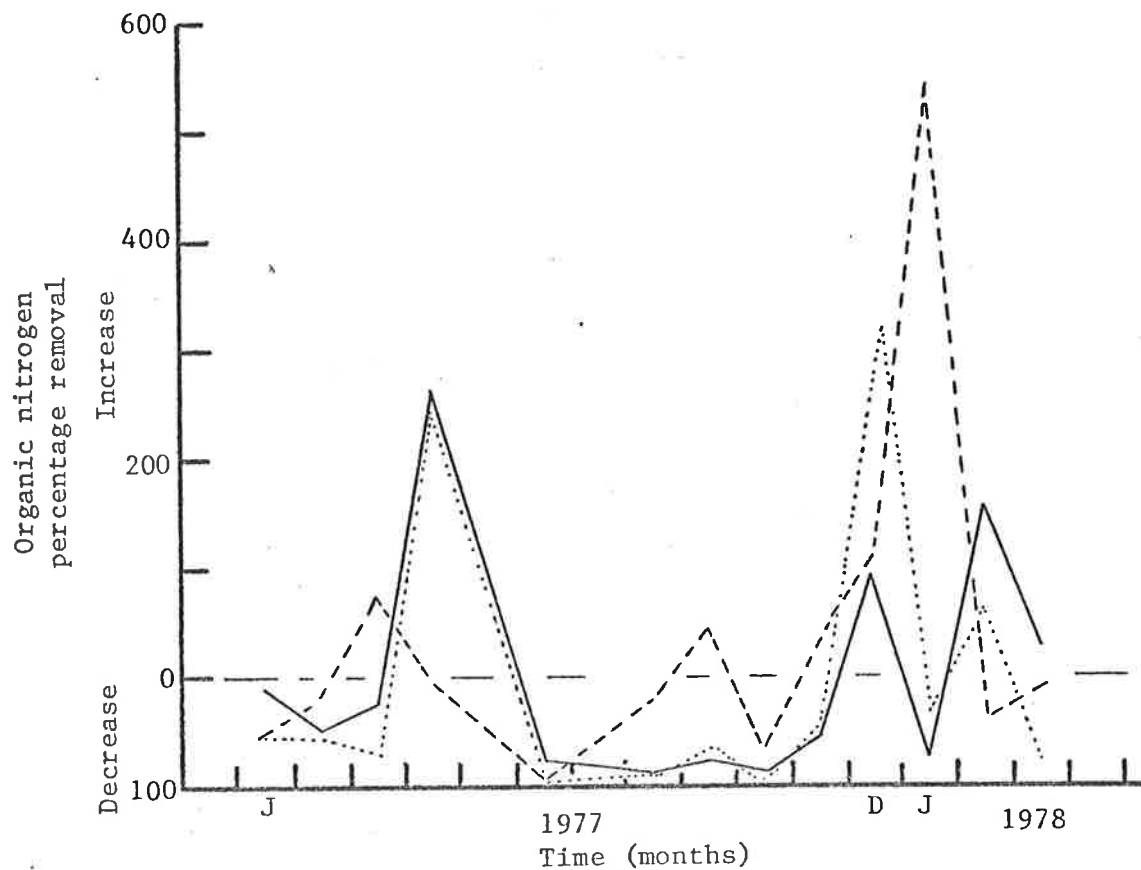
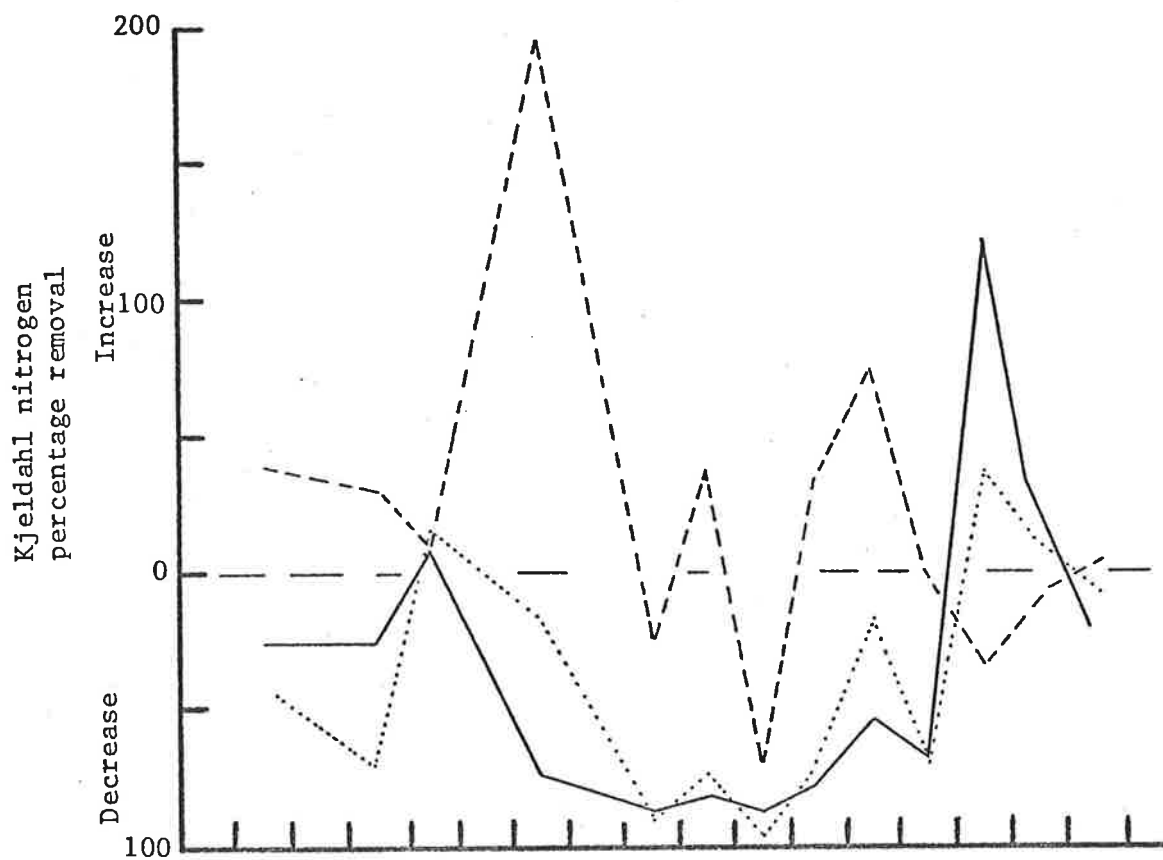


FIGURE 2.21 Mean monthly percentage removal of Kjeldahl and organic nitrogen in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

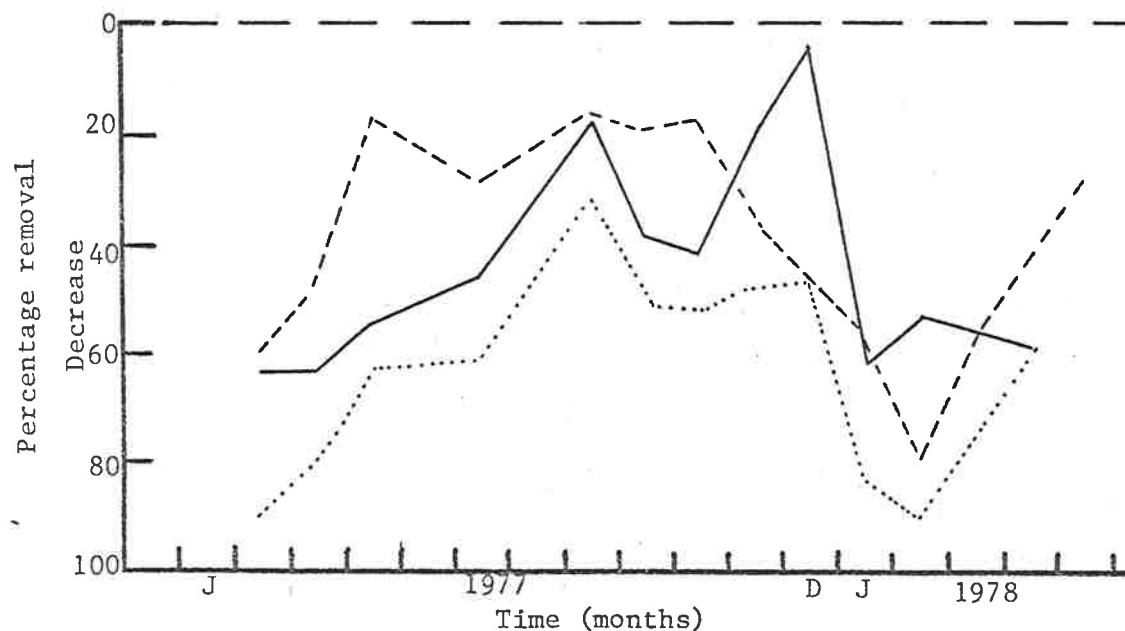
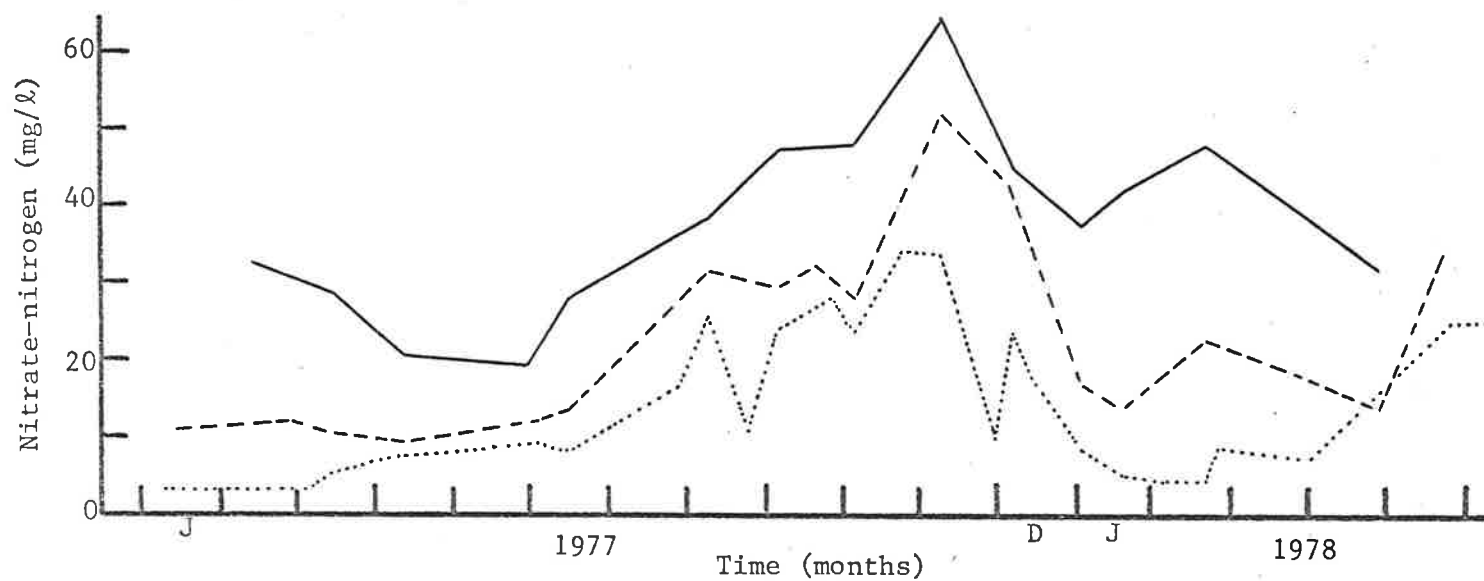


FIGURE 2.22 Nitrate-nitrogen in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....), and mean monthly percentage removal of nitrate-nitrogen in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

varied from 19.5 to 64.6 mg/l. Pond 1 effluent NO_3^- was consistently lower than pond 1 influent and pond 2 effluent NO_3^- consistently lower than pond 1 effluent. Pond 1 effluent and pond 2 effluent NO_3^- minima occurred from January to April during 1977 (pond 1 effluent, 9.5 to 13.1 mg/l; pond 2 effluent, 3.5 to 9.6 mg/l) and 1978 (pond 1 effluent, 13.4 to 22.5 mg/l; pond 2 effluent, 4.5 to 8.9 mg/l).

Both ponds reduced NO_3^- throughout the study period. Removal by pond 1 was highest from February to March, 1977 (maximum 63%) and from January to February, 1978 (maximum 68%). Removal was poor (4 to 53%) from May to December, 1977. NO_3^- removal by pond 2 was highest during February, 1977 (maximum 60%) and 1978 (maximum 80%). Removal by pond 2 from April to November, 1977, was low and less than pond 1. Overall NO_3^- removal was 80 to 90% during February and March, 1977, and January and February, 1978, but decreased from April to December, 1977. That is, removal by pond 1 was medium during 1977 (except November and December) and summer, 1978. Removal by pond 2 was medium during summer, 1977, low during winter, and high during summer, 1978.

Orthophosphate. Seasonal fluctuations in total (unfiltered) and soluble (filtered) $\text{PO}_4\text{-P}$ of pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.23. Pond 1 effluent total $\text{PO}_4\text{-P}$ exceeded influent from January to March, 1977, decreased during March and April, and was less than influent until November. Pond 1 effluent total $\text{PO}_4\text{-P}$ exceeded influent briefly during November, 1977, and thereafter fell dramatically being less than influent (by a maximum of 8.47 mg/l) from December, 1977 until March, 1978. Pond 2 effluent total $\text{PO}_4\text{-P}$ was less than pond 1 influent and effluent from January to March, 1977, but exceeded pond 1 effluent from April to July. From August, 1977, pond 2 effluent total $\text{PO}_4\text{-P}$ decreased steadily and was considerably lower than pond 1 effluent. Pond 2 effluent total $\text{PO}_4\text{-P}$

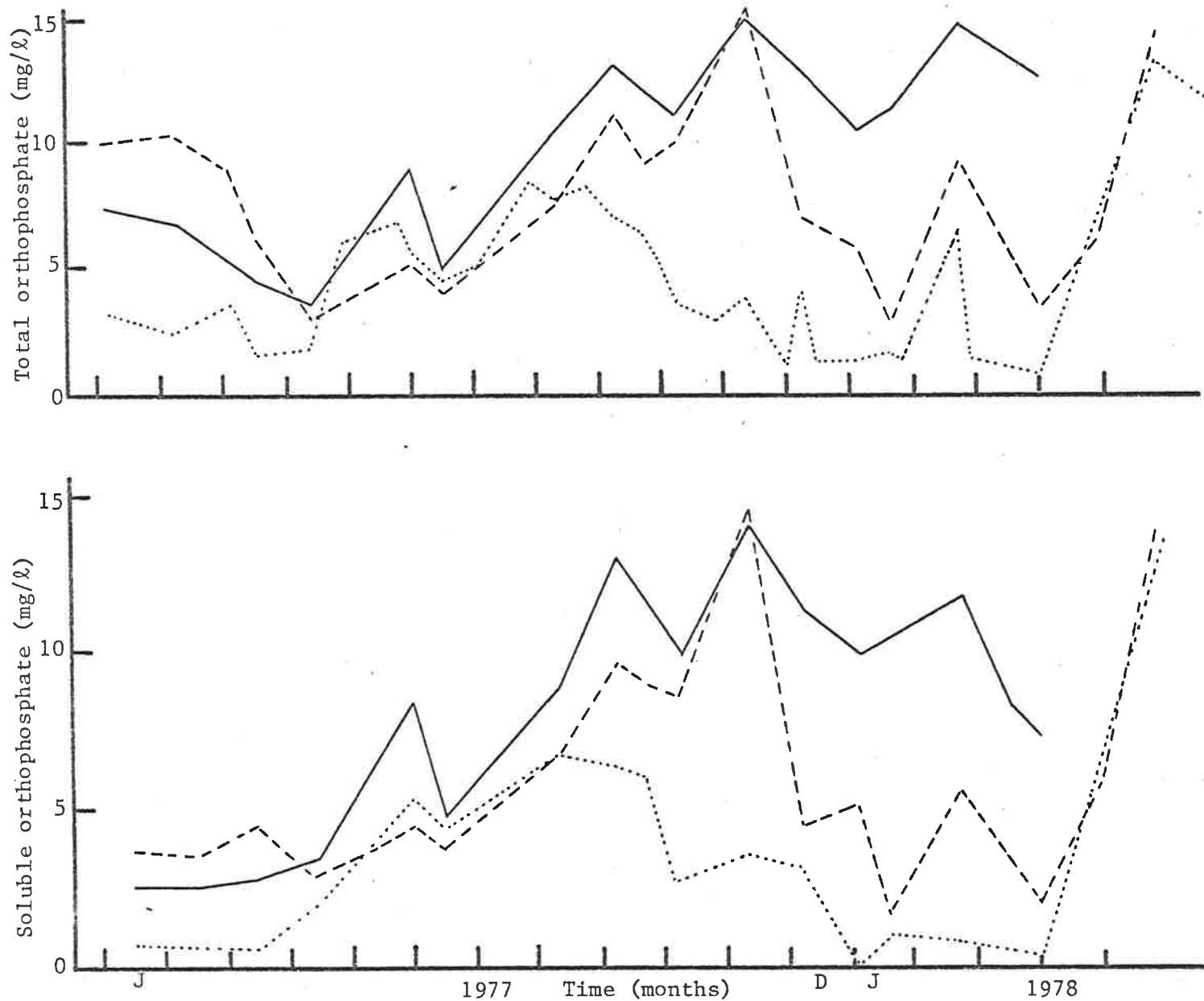


FIGURE 2.23 Total (unfiltered) and soluble (filtrable) orthophosphate-phosphorus in pond 1 influent (—), effluent (---), and pond 2 effluent (.....).

remained lower than pond 1 effluent until March, 1978; thereafter pond 2 effluent total $\text{PO}_4\text{-P}$ increased and was similar to pond 1 effluent total $\text{PO}_4\text{-P}$.

Soluble $\text{PO}_4\text{-P}$ varied in a similar manner, apart from minor variations; of course, concentrations were less than total $\text{PO}_4\text{-P}$. Seasonal fluctuations in soluble $\text{PO}_4\text{-P}$ expressed as a percentage of total $\text{PO}_4\text{-P}$ for pond 1 influent, effluent, and pond 2 effluent are shown in Figure 2.24. Soluble $\text{PO}_4\text{-P}$ was less than 40% of total $\text{PO}_4\text{-P}$ in pond 1 influent and effluent during January and February, 1977, but contributed 80 to 95% of total $\text{PO}_4\text{-P}$ from April to November, 1977. Per cent soluble $\text{PO}_4\text{-P}$ in pond 1 effluent declined during December, 1977 and fluctuated between 65 and 75% until February, 1978. Soluble $\text{PO}_4\text{-P}$ was less than 30% of total $\text{PO}_4\text{-P}$ in pond 2 effluent until March, 1977, contributed 75 to 90% of total $\text{PO}_4\text{-P}$ from April until November, and declined markedly from December, 1977, until February, 1978 (14%). Percentage soluble $\text{PO}_4\text{-P}$ in pond 2 effluent increased to 95% by April, 1978. Particulate $\text{PO}_4\text{-P}$ thus increased during the summer months (January to March).

Mean monthly percentage reductions of total and soluble $\text{PO}_4\text{-P}$ by pond 1 and pond 2 are shown in Figure 2.25. Pond 1 increased total $\text{PO}_4\text{-P}$ by 50% from January to March, 1977; removal increased thereafter, reaching 31% in June, but declined during the second half of 1977. Removal increased from December, 1977, and reached 70% in March, 1978. Pond 2 reduced total $\text{PO}_4\text{-P}$ by up to 75% from January to March, 1977, but removal declined thereafter and pond 2 increased total $\text{PO}_4\text{-P}$ by 13% during June, 1977. Removal increased from September, 1977, and reached 75% during November, 1977, and 78% during March, 1978. Removal declined after March and was only 8% during May, 1978. The pond system overall reduced total $\text{PO}_4\text{-P}$ by 65 to 89% from January to March, 1977 and 1978, but by only 23-47% from April to September, 1977.

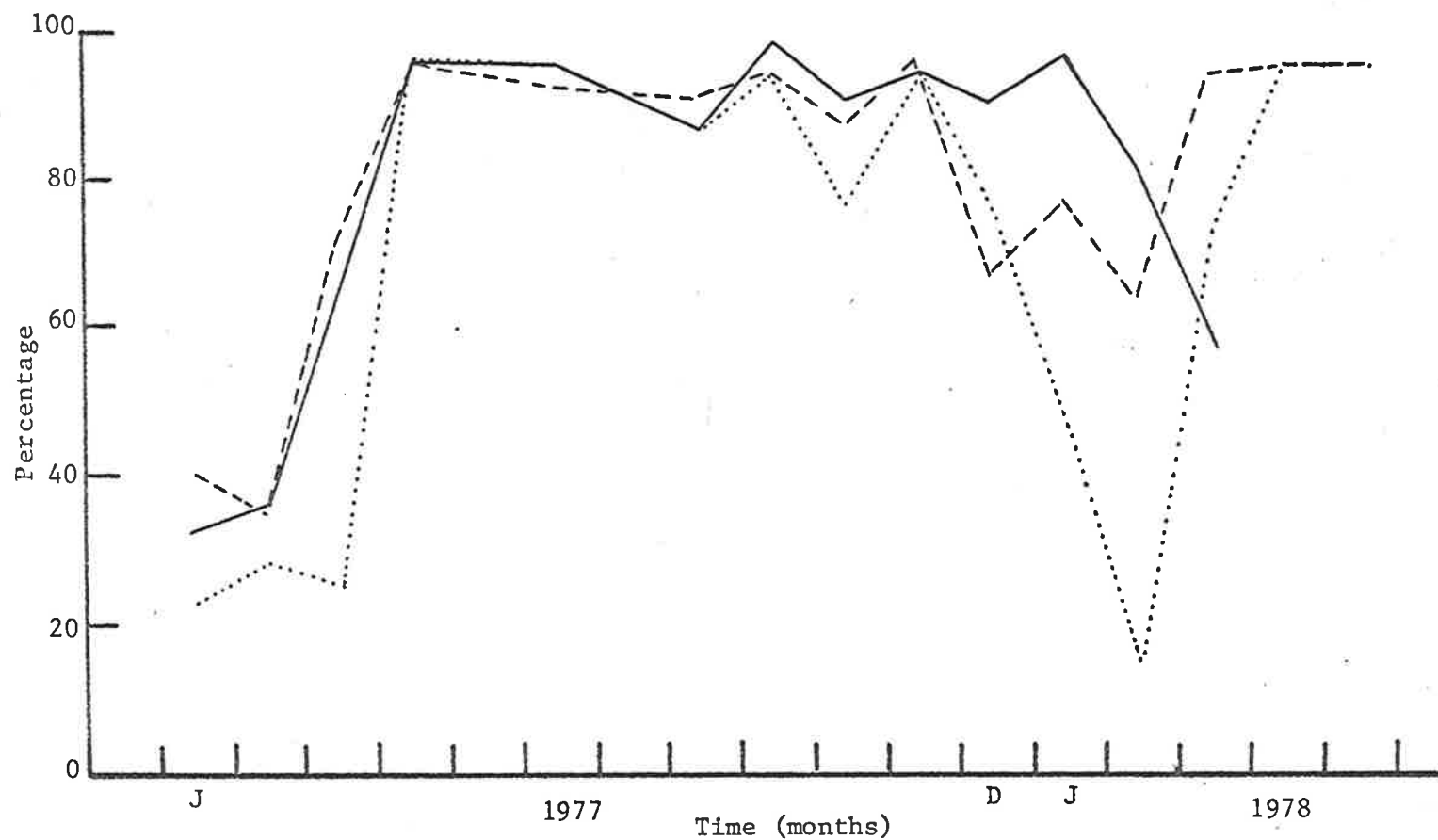


FIGURE 2.24 Soluble orthophosphate-phosphorus (expressed as a percentage of total orthophosphate) in pond 1 influent (—), pond 1 effluent (---), and pond 2 effluent (.....).

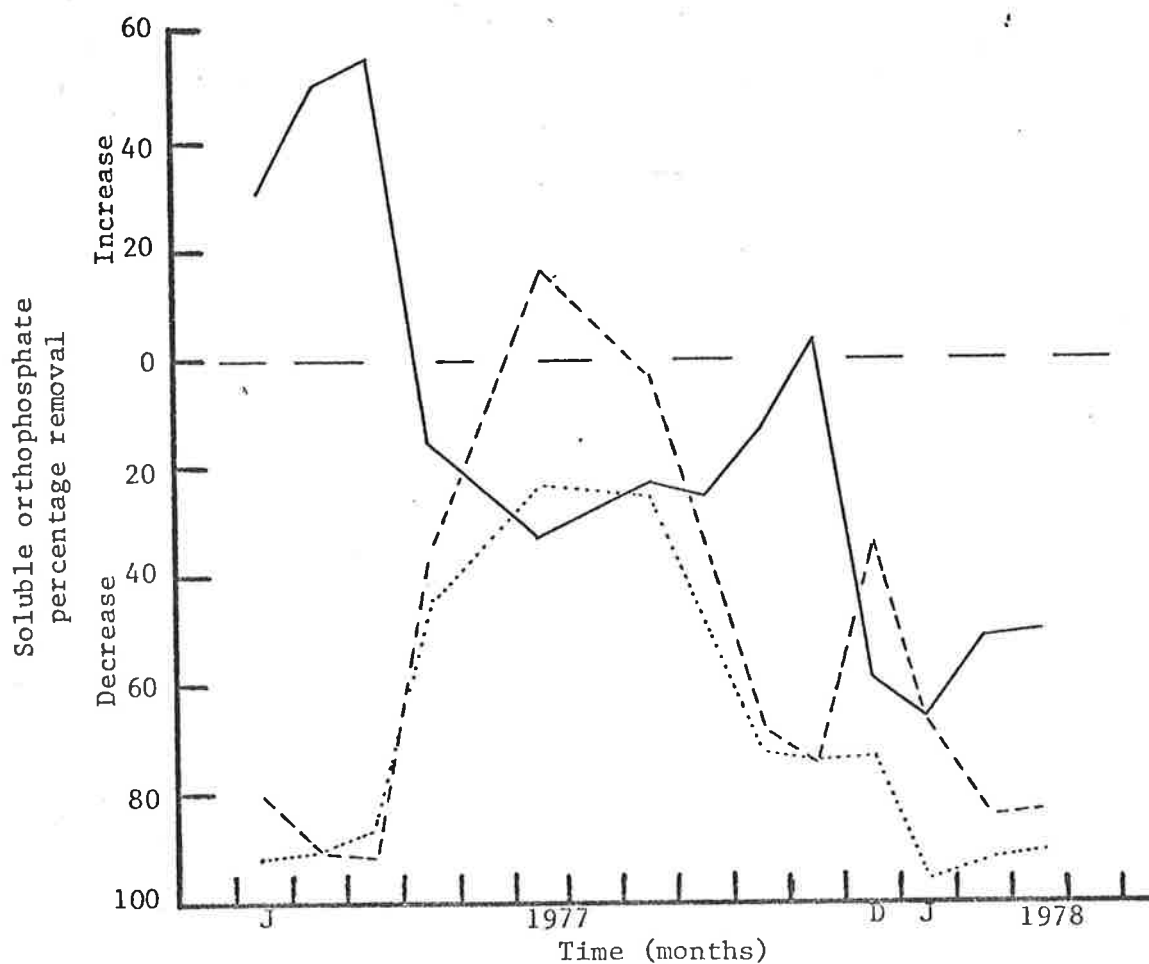
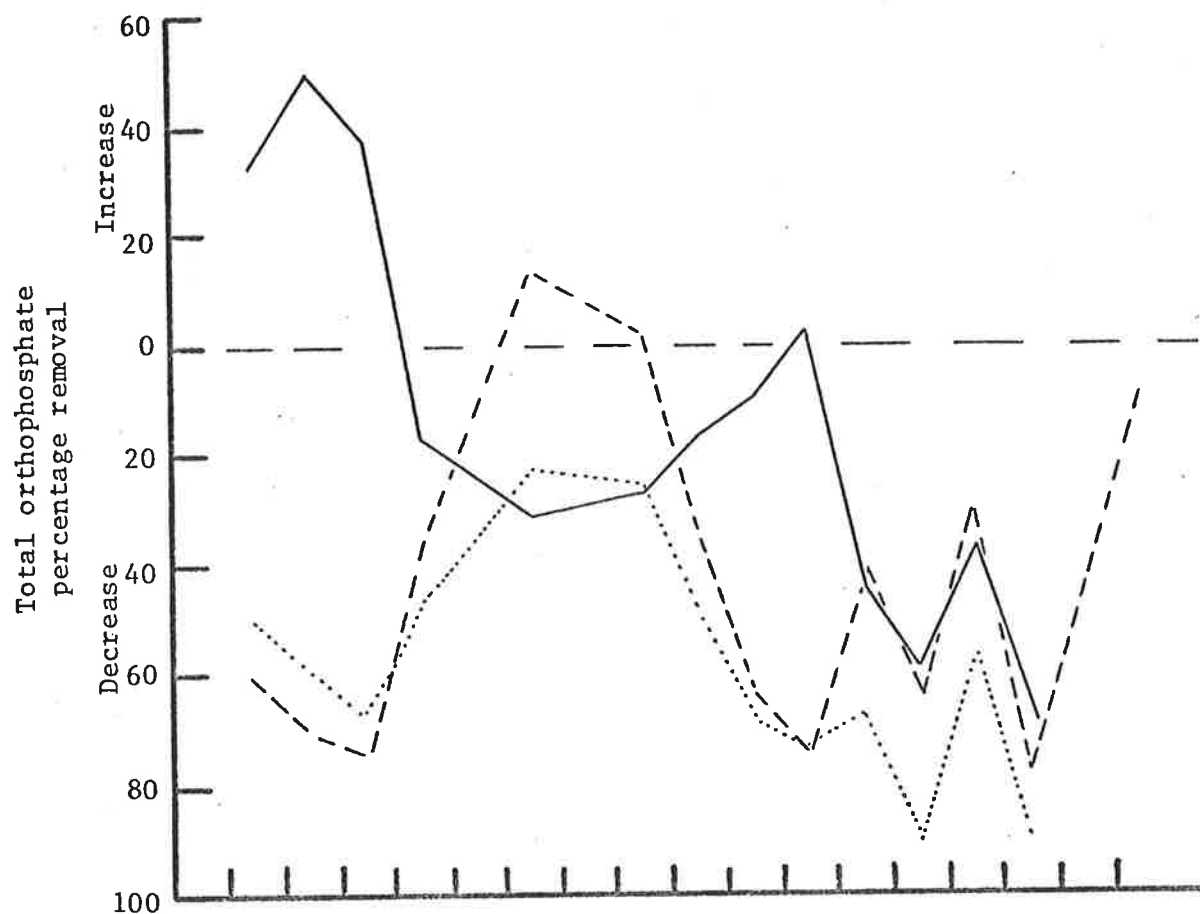


FIGURE 2.25 Mean monthly percentage removal of total and soluble orthophosphate phosphorus in pond 1 (—), pond 2 (---), and the Gumeracha pond system overall (.....).

Removal of soluble $\text{PO}_4\text{-P}$ followed a similar seasonal cycle to total $\text{PO}_4\text{-P}$. Pond 1 increased soluble $\text{PO}_4\text{-P}$ during the summer of 1977; soluble $\text{PO}_4\text{-P}$ removal increased to 33% during the winter of 1977 and again to 66% during the summer of 1978. Pond 2 reduced soluble $\text{PO}_4\text{-P}$ by 80 to 90% during the summers of 1977 and 1978 but removal was low during the winter of 1977. Pond 2 increased soluble $\text{PO}_4\text{-P}$ by 17% during June, 1977. The system overall reduced soluble $\text{PO}_4\text{-P}$ by 85 to 95% during the summers of 1977 and 1978, but by only 23 to 51% during the winter of 1977.

Pond 1 increased total and soluble $\text{PO}_4\text{-P}$ during summer, 1977, while removal by pond 2 was high. Removal by pond 1 increased (low to medium) during winter, 1977, but pond 2 increased total and soluble $\text{PO}_4\text{-P}$ during that period. Removal by both ponds was medium to high during summer, 1978.

Mean annual percentage reductions of nitrogen and phosphorus compounds by ponds 1 and 2, and the pond system overall during 1977 are shown in Table 2.4. Pond 2 removed a higher percentage of influent phosphorus than pond 1. Pond 1 removed a higher percentage of influent nitrogen than pond 2 and the latter increased NH_3 , TKN, and org-N. Org-N removal by pond 1 was low. The system overall reduced total $\text{PO}_4\text{-P}$, TKN, and NO_3^- by over 50%, and reduced NH_3 by over 80%. The system overall increased org-N by 29%. Pond 1 reduced overall phosphorus removal, and pond 2 caused a deterioration in effluent quality, reducing nitrogen removal. $\text{PO}_4\text{-P}$ and NO_3^- removal was highest during the summer months while NH_3 , TKN, and org-N removal was highest in winter.

Nitrogen and Phosphorus Retention. Annual nitrogen and phosphorus retention in pond 1 and pond 2 for 1977 (Table 2.5) were calculated from the difference between influent and effluent concentrations and daily flow rate. Annual retention of total $\text{PO}_4\text{-P}$ was similar for

Table 2.4

Mean annual percentage nitrogen and phosphorus removal
in the Gumeracha ponds during 1977.

	Pond 1	Pond 2	Overall
Soluble $\text{PO}_4\text{-P}$	13.6	40.4	56.1
Total $\text{PO}_4\text{-P}$	13.5	38.8	52.0
$\text{NO}_3\text{-N}$	35.9	28.1	54.1
$\text{NH}_3\text{-N}$	82.8	-16.5	86.8
TKN	60.1	-35.8	52.0
Organic-N	7.3	-11.3	-29.1

Table 2.5

Annual nutrient retention in the
Gumeracha ponds during 1977.

	Pond 1			Pond 2		
	Total PO ₄ -P	NO ₃ -N	TKN	Total PO ₄ -P	NO ₃ -N	TKN
Mean Daily Loading (g/day)	134.006	965.412	1432.000	143.359	422.702	-295.920
Annual Loading (Kg/yr)	48.912	352.375	522.728	52.326	154.286	-108.011
Annual Areal Loading (g/m ² /yr)	33.967	244.705	363.005	42.029	123.925	-86.756

pond 1 and pond 2. Removal by pond 1 was lower than by pond 2 and similar retention resulted from higher influent concentrations to pond 1. Pond 2 had higher areal retention due to its smaller surface area. Annual areal NO_3^- retention in pond 1 was 1.97 times that in pond 2. NO_3^- removal by both ponds was similar and the higher retention in pond 1 reflected higher influent concentrations. Pond 2 had a negative TKN retention; TKN increased on passage through pond 2. Pond 2 had a net positive nitrogen retention as NO_3^- was numerically greater than TKN but this pond, in effect, exported org-N. This contrasted with pond 1 where org-N contributed the major nitrogen load.

Phosphorus Retention Coefficients. Models for the determination of lake trophic status and critical phosphorus loading (e.g. Dillon, 1975; Dillon and Rigler, 1975, 1974; Kirchner and Dillon, 1975; Vollenweider, 1975) provide equations for the calculation of a phosphorus retention coefficient, R. These models regard phosphorus changes over time as the result of supply added per unit volume minus losses through sedimentation (retention) and outflow. R is thus a measure of annual phosphorus removal. If phosphorus removal in WSPs is qualitatively the same process as in natural water bodies, R should be equivalent to mean annual per cent reduction. Strictly speaking, R values refer to the retention of total phosphorus (organic and inorganic). However, most organic phosphorus compounds and polyphosphates are converted into soluble orthophosphate during the passage of wastewater through trickling filters (Nesbitt, 1973). In maturation ponds, R will refer to the retention of total (soluble plus particulate) inorganic orthophosphate.

R values for pond 1 and pond 2 are compared with mean annual per cent removal of total $\text{PO}_4\text{-P}$ in Table 2.6. R^2 corresponded well with per cent total $\text{PO}_4\text{-P}$ removal in pond 2 and the system overall. R^2 overestimated removal by pond 1. R^3 corresponded well with per cent removal of total $\text{PO}_4\text{-P}$ by pond 1 but considerably underestimated

Table 2.6

Phosphorus retention coefficients, R,
for the Gumeracha ponds during 1977.

	L (g/m ² /yr) ¹	R ²	R ³	ρ (yr ⁻¹) ⁴	Mean % Removal Total PO ₄ -P
Pond 1	33.967	0.46	0.20	20.9	14
Pond 2	42.029	0.45	0.17	24.0	39
Overall (Pond 1 + Pond 2)	75.996	0.51	0.31	11.2	52

¹ Areal retention of total PO₄-P.

² Calculated using the model of Kirchner and Dillon (1975).

³ Calculated using the model of Vollenweider (1975).

⁴ Flushing rate (number of times volume replaced per year).

removal by pond 2 and the system overall.

Summary. While pond 1 and pond 2 functioned quite differently during 1977, performance was similar during the summer of 1978. Pond 1 reduced BOD, SS, TOC, and NO_3^- during summer, 1977, but increased TC, org-N, and $\text{PO}_4\text{-P}$. During the same period, pond 2 reduced NO_3^- and $\text{PO}_4\text{-P}$ but increased BOD, SS, TOC, and org-N. While pond 1 effected medium to high removal of BOD, SS, TC, TOC, and org-N during the winter of 1977, removal of all parameters was low in pond 2. During summer, 1978, both ponds reduced NO_3^- and $\text{PO}_4\text{-P}$ but increased BOD, SS, TOC, and org-N (as pond 2 had done during summer, 1977).

2.2.3 Discussion

Although it is often assumed that small, shallow water bodies are generally well-mixed and do not stratify (e.g. George, 1961), small ponds may exhibit extreme temperature stratification (Ruttner, 1963). The propensity of a small water body to stratify will depend upon many factors including morphometry, turbidity, and wind exposure. Stable stratification has been observed in wind-sheltered ponds 3-4 m deep (Haphey, 1970; Moss, 1969; Welch, 1968; Ahl, 1966) but not in wind-exposed ponds of similar depth (Macan and Maudsley, 1966). Both ponds at Gumeracha were thermally stratified at a variety of air temperatures during this study. This suggested that stratification arose in response to a peculiar set of climatic conditions. Solar radiation may be important in determining water temperature even when air temperature is low (Macan and Maudsley, 1966) and it is, likely that stratification in the wind-exposed ponds at Gumeracha during winter arose as a result of calm, cloudless days (high solar radiation). Stratification in shallow, turbid pools can arise as a result of light absorption by suspended material (Eriksson, 1966). Although stratification occurred in the Gumeracha ponds when the

standing crop of phytoplankton, and therefore biogenic turbidity, was high (the euphotic zone in WSPs during algal blooms may vary between 10 and 70 cm in depth (Bartsch and Allum, 1957; Towne et al. 1957)), ponds were also stratified when light penetration was high (bottom visible). Thermal stratification was pronounced beneath floating algal mats.

"Diminutive" stratification, exhibited in both ponds, is common in shallow lakes or shallow, protected areas of large lakes (Wetzel, 1975). This type of profile arises when water depth is insufficient to maintain a typical epi- and hypolimnion or when inflow causes turbulence (Wetzel, 1975). The Gumeracha ponds have retention times of 15 to 17 days and influent volume is therefore large relative to epilimnetic volume. Turbulence may be responsible for the occurrence of "diminutive" profiles at Gumeracha. Thermal discontinuities, exhibited in both ponds, occur in larger water bodies when high temperatures alternate with periods of intensive mixing (Wetzel, 1975). This results in the formation of an epilimnetic thermocline, and if the epilimnion is thin the metalimnion curve extends to the surface (Hutchinson, 1957). Such an effect may have been observed in pond 1 on 15 March, 1978, after a period of isothermy in late February. The true metalimnion may have been between 40 and 50 cm, the discontinuity at 10 cm representing epilimnetic stratification at high air temperatures.

From Figure 2.6, stratification in the Gumeracha ponds appeared to be stable for up to 6 weeks. It is more likely that the phenomenon was short-lived and that the apparent pattern reflected sampling interval. Thermal profiles with secondary discontinuities are characteristically short-lived (Wetzel, 1975). Diurnal events (Figures 2.9 and 2.13) showed that stratification was established on a daily basis. The metalimnion was broken down during the evening-early morning and isothermy resulted from surface cooling (conditions were

calm during the 24 hour study and inverse stratification occurred during early morning). Daily patterns of stratification have been shown to be more important for shallow water bodies than seasonal events (Erikssen, 1966; Young and Zimmerman, 1956; Vaas and Sachlan, 1953). Stratification of the Gumeracha ponds may have occurred diurnally but over an extended period while conditions were calm with high incident solar radiation. Diurnal stratification, following the same sequence of events as in natural shallow water bodies, has been observed in many WSPs (Uhlmann, 1979; Dodakundi et al., 1973; Oswald, 1968; Wachs and Berend, 1968; Drews, 1966; Marais, 1966; Bartsch and Allum, 1957). In deeper ponds, the thermocline may be stable for several weeks during summer (Hartley and Weiss, 1970; Oswald, 1968; Wachs and Berend, 1968; Marais, 1966). Thermal stratification in facultative ponds may be self-maintaining; fundamentally different biochemical processes above and below the thermocline result in the accumulation of dissolved substances (e.g. HCO_3^- and NH_3) in the anaerobic hypolimnion (Boksil and Agrawal, 1977; Dodakundi et al., 1973). Density differences between epi- and hypolimnetic water would magnify the effects of small temperature changes at the surface thus maintaining stratification in a manner analogous to biogenic meromixis.

Stratification in WSPs has special implications for the stabilization process. During summer stratification, pond influent, generally with a lower temperature than epilimnetic water, will form a layer on the pond bottom. Sediment deposition occurs below the thermocline and higher loadings may occur near the pond inlet (Oswald, 1968). During winter, pond influent may have a higher temperature than pond surface water resulting in streaming or sheet-spreading; settleable solids are distributed over a wider area (Oswald, 1968; Marais, 1966). Uhlmann (1979) has demonstrated that low organic

substrate removal efficiency can occur in WSPs due to variations in flow pattern as a result of thermal stratification. The polymictic behaviour of diurnally stratifying WSPs, such as those at Gumeracha, means oscillation between plug flow during isothermal conditions and bypassing (vertical gradients) during stratification.

The concentration of dissolved oxygen in a body of water is the result of the balance between gain from the atmosphere, photosynthetic production, animal and plant respiration, bacterial respiration during the decomposition of organic matter in the sediments, and chemical oxidation of dissolved organic matter (Hutchinson, 1957). Photosynthesis by phytoplankton and macrophytes was the most important influence upon oxygen concentration in the Gumeracha ponds. The effects of population fluctuations of these groups upon the dissolved oxygen regime of the ponds will be more fully discussed in chapter 3. While dissolved oxygen concentration during a phytoplankton bloom in facultative ponds may vary from ≤ 1 to ≥ 30 ppm diurnally (Hussainy, 1978; King, 1976, 1972; Williford and Middlebrooks, 1967; Bartsch and Allum, 1957; Towne *et al.*, 1957), it was more constant in the Gumeracha ponds. Diurnal fluctuations of dissolved oxygen concentration are generally small in maturation ponds (Drews, 1966).

In stratified facultative ponds oxygen production is confined to the euphotic zone above the thermocline; the epilimnion becomes supersaturated and the hypolimnion oxygen depleted (see data in Oswald, 1968; Wachs and Berend, 1968; Marais, 1966). Consequently, oxygen profiles in facultative ponds are characteristically clinograde or positive heterograde. The Gumeracha ponds displayed both types of profile, although hypolimnetic water was not anaerobic. The reestablishment of stratification diurnally will mean that over 24 hours oxygen profiles change from uniform (with varying degrees of

hypolimnetic depletion) to clinograde to positive heterograde (at the height of stratification) to clinograde and back to uniform as the pond is mixed (see data in Marais, 1966). Oxygen profile differences between the Gumeracha ponds on the same day may have resulted from ponds being at different points in the daily cycle when sampled. Positive heterograde curves may have been the result of oxygen loss from a supersaturated epilimnion to the atmosphere or light inhibition and subsurface aggregation of phytoplankton. Vertical stratification of algae has been observed in facultative ponds (Dodakundi *et al.*, 1973; Hartley and Weiss, 1964; Sless and Samsonov, 1964; Bartsch and Allum, 1957).

The pH of WSPs is mainly influenced by CO_2 uptake from the carbonate-bicarbonate alkalinity system by algae during photosynthesis (King, 1976, 1972). At Gumeracha, pH increased through pond 1 and pond 2 and maxima occurred during summer when retention time was longest. This is common in maturation ponds (Ramani, 1976; Drews, 1966). CO_2 produced by bacterial degradation may be insufficient to meet photosynthetic demand when algal standing crop is high. Additional CO_2 is extracted from the $\text{CO}_3^{=}$ - HCO_3^{-} system; pH rises due to the precipitation of Ca CO_3 and then the formation of OH^{-} ions as a result of the dissociation of $\text{CO}_3^{=}$ and HCO_3^{-} (Cole, 1975; Wetzel, 1975). CO_2 is depleted during the day and recharged by nighttime respiratory release. During summer, pH increases progressively as free CO_2 declines. Algae may become limited by CO_2 availability (King, 1976; 1972; Meron *et al.*, 1965; Bartsch, 1961).

During March, 1977 and 1978, pond 2 effluent TIC was low and pH exceeded 10.2. Free CO_2 would have been absent and inorganic carbon would have been in the form of HCO_3^{-} and $\text{CO}_3^{=}$ (Wetzel, 1975, p.168). Carbon limitation of algae might have occurred at those times. From pH and TIC variations it was predicted that in pond 1

during the summer of 1977 CO_2 was abundant and respiration exceeded photosynthesis while in pond 2 CO_2 was reduced and photosynthesis predominated. In both ponds during the summer of 1978 CO_2 was low and photosynthesis predominated. It will be shown in chapter 3 that phytoplankton cycles matched these predictions.

Quality criteria for domestic wastewater effluents after 1977 (in the United States) are: pH, upper limit 9; 5 day BOD, upper limit 30 mg/l; SS, upper limit 30 mg/l (Boatwright and Lawrence, 1977). Pond 2 effluent pH exceeded the upper limit from January to April, 1977, and from October, 1977 to April, 1978. Pond 1 effluent pH exceeded the upper limit after December, 1977. Pond 2 effluent BOD met quality requirements throughout the study. BOD removal by the overall system was only 52.5% during 1977. If the ponds were fully loaded, pond 2 effluent BOD would exceed the upper limit during summer. The Gumeracha ponds are maturation ponds and advanced wastewater treatment BOD requirements may be as low as 5 mg/l (Anon., 1978). Pond 2 effluent met this requirement only from August to October, 1977. During low flow periods in the Torrens River, the Gumeracha plant contributed up to 0.54 mg BOD to each litre of river water. Flowing waters are of suspect quality if BOD exceeds 5 mg/l (Hart, 1974). Wastewater treatment plants export varying proportions of their organic load and effluent quality criteria may need to vary between plants taking into consideration the assimilative capacities of the receiving water bodies.

Pond 2 effluent SS exceeded the upper limit for domestic wastewaters from January to March, 1977, and from December, 1977 to May, 1978. Pond 1 effluent SS exceeded the upper limit during March and April, 1978. Advanced treatment criteria for SS may be as low as 5 mg/l (Anon., 1978). Pond 2 effluent SS met this requirement from May to October, 1977. The pejorative effects of pond 2 upon

effluent SS make it unlikely that the Gumeracha plant would meet the domestic wastewater SS criteria if subjected to full design load.

Despite the extensive use of maturation ponds for tertiary treatment, both in Australia and in other countries, very little operational data documenting the treatment capabilities of this type of WSP have been published. The relative performance of the Gumeracha maturation ponds is, therefore, difficult to assess. BOD removal varies generally from 13 to 35% and SS removal from 8 to 50% (Carpenter *et al.*, 1976; Ramani, 1976). Dinges (1978, 1976) reported 80 to 90% BOD removal and 90-95% SS removal in ponds culturing *Eichhornia crassipes*. Loadings in these studies were similar to those at Gumeracha. Overall BOD removal at Gumeracha was reasonable but SS were increased. Pond 1 performed noticeably better than most maturation ponds almost reaching the extremely high removals reported by Dinges (1978, 1976). Pond 2 increased BOD and SS. BOD removal in facultative ponds ranges from 58 to 97% (most in the range 75-85%) while SS removal ranges from 85% in winter to 550% increase during summer (Carpenter *et al.*, 1976; Goulden, 1976; Rodgi and Kanabur, 1971; Bopardikar, 1969; Williford and Middlebrooks, 1967; Meron *et al.*, 1965; Nemerow and Bryson, 1963; Neel *et al.*, 1961; Fitzgerald and Rohlich, 1958; Bartsch and Allum, 1957; Merz *et al.*, 1957; Towne *et al.*, 1957; Malchow-Møller *et al.*, 1955). BOD and SS removal by pond 1 was similar to that in facultative secondary ponds.

Removal of NO_3^- and $\text{PO}_4\text{-P}$ at Gumeracha was highest during the summer when org-N, BOD, SS, and TOC were increased during the passage of wastewater through the ponds. It will be shown in chapter 3 that changes in chemistry during summer were correlated with high standing crops of phytoplankton. This was reflected by an increase in particulate $\text{PO}_4\text{-P}$ in effluents during summer (Fig. 2.24). Particulate $\text{PO}_4\text{-P}$ also increased in the trickling filter effluent (pond 1 influent)

during summer probably due to sloughing off or washout of the zoogloal growth (algae and photosynthetic Protozoa) from the surfaces of stones in the filter (McKinney, 1971; Bartsch, 1961; Usinger and Kellen, 1955). Turnover of these populations would be higher during summer.

Pond 1 and pond 2 effluent TKN exceeded advanced wastewater treatment requirements (3 mg/l: Anon., 1978) during most of the study. Pond 1 effluent NO_3^- exceeded safe drinking levels (10 mg/l, 1 mg/l for infants: Hart, 1974) throughout the study but pond 2 effluent met this requirement during summer. During periods of low flow in the Torrens River, the plant contributed up to 0.15 mg NO_3^- to each litre of river water. This is 50% of the critical load for eutrophication (0.3 mg/l: Stewart and Rohlich, 1967). The lability of nitrogenous compounds makes the total nitrogen pool a more important measure of pollution load than any one form of nitrogen. The Gumeracha plant contributed up to 0.14 mg TKN to each litre of river water during low flow. The total nitrogen contribution from the plant to the river was as high as 0.29 mg/l during summer.

Pond 1 and pond 2 effluent total $\text{PO}_4\text{-P}$ alone exceeded advanced wastewater treatment requirements for total phosphorus (1 mg/l: Anon., 1978) throughout the study. Pond 1 and pond 2 effluent soluble $\text{PO}_4\text{-P}$ exceeded the safe drinking level (0.2 mg/l: Hart, 1974) throughout the study. During low flow the plant contributed up to 0.019 mg of soluble $\text{PO}_4\text{-P}$ per litre of water in the Torrens River. This exceeded the critical level for eutrophication (0.015 mg/l: Stewart and Rohlich, 1967). Phosphorus loading is the most significant factor determining lake trophic state (Dillon and Rigler, 1975; Shannon and Brezonik, 1972; Schindler et al., 1971) and it has been demonstrated that phosphorus control is an effective primary step in preventing eutrophication (Schindler and Fee, 1974;

Vallentyne et al., 1970). Overall $\text{PO}_4\text{-P}$ removal by the ponds was 52%, removal by pond 2 being 3 times that of pond 1. The latter effected higher removal of nitrogenous compounds; overall mean removal of all nitrogenous compounds was 41%.

Nitrogen and phosphorus removal is a fundamental requirement of maturation pond function, and ponds are used widely throughout Australia and other countries ostensibly for this purpose. Yet, remarkably, few studies actually report nutrient removal efficiencies for functional maturation ponds. The following removal efficiencies have been directly reported or calculated from primary data: TKN, 2 to 66% (Carpenter et al., 1976; Drews, 1966); org-N, 0 to 72% (Dinges, 1978, 1976; Drews, 1966); NH_3 , 29 to 71% (Dinges, 1978, 1976; Ramani, 1976); $\text{PO}_4\text{-P}$, 31% (Dinges, 1978, 1976); total phosphorus, 25% (Carpenter et al., 1976). Overall removal of nitrogen and phosphorus by the Gumeracha plant was high, except for the production of org-N. Removal of NO_3^- , NH_3 , and TKN by pond 1 was high but org-N and $\text{PO}_4\text{-P}$ removal was poor. $\text{PO}_4\text{-P}$ removal by pond 2 was above average but this pond increased NH_3 , TKN, and org-N. Nutrient removal by facultative secondary ponds varies considerably. Phosphorus removal ranges from 0 to 96% (Meron et al., 1965; Neel et al., 1961; Fitzgerald and Rohlich, 1958), and total nitrogen removal from 9 to 93% (Hussainy, 1978; Meron et al., 1965; Wuhrmann, 1964; Neel et al., 1961); org-N and NH_3 removal has been reported at less than 60% (Fitzgerald and Rohlich, 1958; Malchow-Møller et al., 1955) and 80 to 95% (Neel et al., 1961). In high rate oxidation ponds, nitrogen removal from 44 to 94% has been reported (Shelef et al., 1978; Caldwell-Connell, 1976; Wuhrmann, 1964) while phosphorus removal has been reported at 20% (Shelef et al., 1978). Under current operational practices, nutrient removal by maturation ponds appears not to be superior to that effected by other pond types. The polishing of effluents in maturation

ponds depends upon lower influent nitrogen and phosphorus concentrations.

Dillon (1975) has shown that Vollenweider's (1975) model of phosphorus retention is inapplicable to lakes with high flushing rates (i.e. low retention times). The Gumeracha ponds obviously fall into this category. This explains why phosphorus retention coefficients calculated using Vollenweider's model do not correspond with measured phosphorus removal. Kirchner and Dillon's (1975) model predicted phosphorus removal by pond 2 and the overall system well but over-estimated removal by pond 1. It will be shown in chapter 3 that this resulted from fundamental biological differences between pond 1 and pond 2 during 1977. During 1978, when biological conditions were similar in both ponds, mean monthly removal of total $\text{PO}_4\text{-P}$ from January to May was 48% for pond 1 and 45% for pond 2.

The applicability of Kirchner and Dillon's (1975) model to the Gumeracha ponds suggested that phosphorus removal was influenced greatly by flushing rate. Drews (1966) has also suggested that NO_3^- removal in maturation ponds is a function of retention time. Nutrient removal in maturation ponds thus appears to be qualitatively the same as in natural water bodies. R values for lakes with low flushing rates ($\rho = 0.001$ to 0.96) vary from 0.95 to 0.53 while lakes with high flushing rates ($\rho = 1.75$ to 18.5) have R values from 0.49 to 0.01 (Dillon, 1975; Dillon and Rigler, 1974). R decreases as flushing rate increases. $\text{PO}_4\text{-P}$ removal by pond 2 ($\rho = 24.0$) and the pond system overall ($\rho = 11.2$) was very high compared to natural lakes with similar flushing rates (and vastly reduced loadings). The relationship of R to flushing rate suggests that nutrient removal in WSPs could be increased by increasing retention times. This relationship had, in the past, only been guessed at by pond designers based upon the role of algae in nutrient removal and the observation that high algal standing crops developed at increased retention times.

Increasing retention time in maturation ponds may, however, generate operational problems. Excessive retention time can lead to carbon limitation of green algae and the dominance of blue-green algae (King, 1976). Blue-greens form floating mats which block light penetration resulting in anaerobic conditions (McKinney, 1976). Long retention times result in increases of the algal fraction of SS (Meron *et al.*, 1965). The oxygen required for algal respiration may exceed the BOD of incoming sewage (Bartsch, 1961). Water loss by seepage and evaporation will raise TDS causing problems if water reclamation is involved (Ramani, 1976). Increased retention time also increases areal requirements and therefore plant cost. This study has shown that nutrient removal in the Gumeracha ponds is not compatible with other aspects of pond function, particularly SS, BOD, TOC, and org-N reduction. Manipulation of retention time to increase nutrient removal is finely tuned to algal requirements and has limits if effluent quality in other areas is to be maintained. Alternative approaches to improving nutrient removal in maturation ponds are important and information concerning nutrient partitioning within pond ecosystems is vital.

The aquatic phosphorus cycle is a dynamic system; phosphorus is constantly incorporated into organisms and simultaneously released via excretion and decay. Exchange between water and the sediments is a major component of the phosphorus cycle in natural waters, and in most lakes there is a net movement of phosphorus into the sediments (Schindler *et al.*, 1975; Wetzel, 1975; Hesse, 1973). The sedimentation of suspended organic matter and the precipitation of phosphates at high pH in WSPs (Ramani, 1976; Lewin, 1973) would suggest that phosphorus loss to the sediments is also important in these ponds. Phosphorus exchange across the sediment interface is regulated by oxygen concentration at the sediment surface (Wetzel, 1975; Kramer *et al.*, 1972) and

phosphorus release from the sediments is likely to be low in fully aerobic WSPs. This suggests that the sediments are the major phosphorus pool in WSPs. Nutrient removal schemes incorporating algal harvest from WSPs assume that the incorporation of soluble inorganic phosphorus into algal cells is the most important avenue of phosphorus removal. The implication is that events in maturation ponds resemble the epilimnion of lakes where phosphorus is incorporated rapidly into the seston (Rigler, 1973; Wetzel, 1975).

The nitrogen cycle is also highly dynamic. The major nitrogen transformations in natural waters are the removal of NH_3 by nitrifying bacteria which produce NO_3^- (the major nitrogen source for algae and macrophytes: Wetzel, 1975), and NH_3 release via the decomposition of organic material and zooplankton excretion. The sediments are a major nitrogen store (Frink, 1967) and the presence of an oxidized surface layer prevents NH_4^+ release (Barica, 1974; Brezonick, 1972). However, the major avenue of nitrogen removal in maturation ponds is (as for phosphorus) assumed to be incorporation into the seston. Nitrogen, unlike phosphorus, can become limiting in WSPs as a result of NH_3 loss to the atmosphere at high pH (King, 1976).

The model presented in Figure 1.2 indicates alternative avenues of nutrient uptake in maturation ponds. Algal ^{crop}standing may not be high in some maturation ponds (Ramani, 1976) suggesting that organisms other than algae are responsible for nutrient removal. The most significant groups are likely to be macrophytes, zooplankton, and fish. No account of nutrient partitioning in any type of WSP has, as yet, been published and the importance of these groups for nutrient removal from the Gumeracha ponds is subsequently investigated in this study.

Chapter 3. Algae and Macrophytes

3.1 Introduction

The role of algae in facultative and maturation WSPs includes the uptake of stabilized nitrogen and phosphorus compounds and the production of oxygen during photosynthesis. The detrimental effects of algae upon effluent quality mean that the use of algae for effluent polishing is dependant upon removal prior to discharge. A conflict arises between the need to maximize algal standing crop for nutrient removal and the need to prevent algae from entering the receiving water body. The high financial and energetic investments required for mechanical algal harvest offset the advantages of WSPs for waste treatment. This problem may be overcome by the utilization of in-pond methods of algal control. Ponds with differing treatment requirements may be connected in series, the final pond performing an algal removal function. Understanding the factors controlling algal numbers in maturation ponds is thus important for effective pond management.

The seasonal cycle of chlorophyll a concentration in maturation ponds has^{only} been described in the studies of Shillinglaw and Pieterse and White (1975). (1977)

Generally, little attempt has been made to correlate seasonal fluctuations in algal abundance with pond performance, or to examine the factors controlling population fluctuations under operational conditions. Algal studies in WSPs to date have been restricted to:

- a) extensive species lists (Goulden, 1976; Benson-Evans and Williams, 1975; Ahmed, 1974; Singh and Saxena, 1969; Malchow-Møller *et al.*, 1955),
- b) descriptions of succession during blooms (Patil *et al.*, 1975; King, 1972; Haughey, 1965; Singh and Saxena, 1969; De Noyelles, 1967; Fitzgerald, 1964; Neel *et al.*, 1961),

- c) the examination of short-term yields in mass-culture situations where conditions for algal growth are optimized (Goldman, 1979a, b; Shelef *et al.*, 1978, 1973; Uhlmann, 1978; McGarry *et al.*, 1973; Oswald and Golueke, 1968), and,
- d) nutrient removal experiments in laboratory-simulated WSPs (Fitzgerald and Rohlich, 1964) or on a short-term field scale (Paelinck and Maeseneer, 1978; Hemens and Stander, 1969; Hemens and Mason, 1968).

Algal productivity may be limited by factors which suppress reproductive rate (nutrients, light, temperature), or which remove individuals from the population (predation, flushing, sedimentation, and disease). It has been suggested that the factors responsible for the seasonal variation of algal numbers in WSPs are those operating in natural waters, in particular, light, temperature, and grazing (White, 1975; Rodgi and Patil, 1971; De Noyelles, 1967). Additionally, phytoplankton productivity in WSPs may be limited by carbon availability (King, 1976, 1972); this is unlikely in natural lakes (Schindler, 1971a). High flushing rate can also reduce phytoplankton productivity (O'Connell and Andrews, 1977; Dickman, 1969) and may be important in WSPs during periods of low retention time.

The seasonal cycle of chlorophyll *a* concentration (an indicator of algal biomass) was followed in the temperate Gumeracha ponds to correlate algal standing crop with pond function (and effluent quality) and to identify the physico-chemical factors controlling algal fluctuations. The influence of biotic factors, such as zooplankton and fish, upon algal populations is examined in subsequent chapters.

Phytoplankton is generally regarded as the major contributor to primary production in natural lakes. A greater proportion of the nitrogen and phosphorus retained in such a lake would be incorporated into phytoplankton biomass than into other components of the autotrophic

community. In some lakes, however, a high proportion of the total carbon fixed annually may be contributed by macrophytes and periphyton (Huntsinger and Maslin, 1976; Gak et al., 1972; Rich et al., 1971; Davies, 1970; Wetzel, 1964). Standing crops of aquatic vascular plants may thus represent significant nutrient stores. Macrophyte harvest could possibly provide a useful pathway for nutrient removal from maturation ponds. Unlike unicellular algae, which must be removed from effluents continuously, nutrient removal using macrophytes could be achieved in a single, annual harvest provided this occurred prior to plant senescence.

In this regard, the wastewater treatment capabilities of the floating vascular plant *Eichhornia crassipes* have been extensively studied (Wolverton and McDonald, 1979; Wolverton et al., 1976; Anon., 1978; Dinges, 1978, 1976; Corwell et al., 1977; Wooten and Dodd, 1976; Boyd, 1970). Although nitrogen and phosphorus removal during growth of *E. crassipes* may be above 80%, studies have generally been of short duration and have computed nutrient removal by comparison of influent and effluent concentrations. The effectiveness of macrophyte harvest as a pathway for nutrient removal is more properly determined by a comparison of the nutrient pool represented by annual plant production with the total amount of nutrient retained annually in the water body (Carpenter and Adams, 1977). Although values for the production of floating plants generally exceed those of submerged species (Mitchell, 1978; Davies, 1970) the use of *E. crassipes* for effluent polishing is restricted to the warmer part of the year in temperate areas (Wolverton and McDonald, 1979). Evaporation and transpiration by the plant may increase the TDS of pond water and nitrogen may become limiting before the desired reduction of orthophosphate has been achieved (Wooten and Dodd, 1976). Additionally, *E. crassipes* prevents light penetration resulting in anaerobic effluents (Wolverton and

McDonald, 1979; Corwell et al., 1977; Culley and Epps, 1973) which may have high BOD (Boyd, 1971).

Other aquatic vascular plants studied include the emergents *Scirpus* and *Phragmites* which can reduce BOD, SS, and coliforms in effluents (De Jong, 1976; Seidel, 1976). BOD and bacterial removal appears to be effected largely by attached microorganisms (De Jong, 1976; Spangler et al., 1976). De Jong (1976) has shown that the phosphorus contained in *Scirpus* and *Phragmites* production may be equivalent to 50% of annual pond load. However, nitrogen and phosphorus removal ceases when the nutrient uptake capacity of the plant is exceeded (De Jong, 1976) and *Scirpus* may release orthophosphate at certain times of the year (Spangler et al., 1976; Whigham and Simpson, 1976). Generally, only small quantities of orthophosphate are removed by harvest of emergents, the remainder accumulating in the sediments with the unharvestable root-rhizome and microflora-substrate complexes. The phosphorus content of the sediments in reed or rush ponds may increase until equilibrium levels in effluents reach excessive amounts (Boyd, 1971). Rooted emergent plants obtain most mineral nutrient from the sediments (Mitchell, 1978; Hutchinson, 1975) and may thus mine nitrogen and phosphorus from the substrate. Nutrient budgets for these plants (e.g. De Jong, 1976) are suspect, particularly as underground, unharvestable parts may represent a higher areal mass of nitrogen and phosphorus than aboveground parts. Provision must be made to control algae in reed or rush ponds (Seidel, 1976; Spangler et al., 1976) and the use of emergents for effluent polishing is likely to be accompanied by insect problems.

Despite considerable research effort, the value of floating and emergent macrophytes for effluent polishing remains to be demonstrated convincingly. Neither group is without its attendant problems. Study of the usefulness of submerged macrophytes for wastewater treatment has

been neglected. In natural ponds and lakes, low phytoplankton density is often associated with high standing crops of submerged macrophytes; macrophyte removal or decline is often followed by an increase in phytoplankton density, biomass, and productivity (Crawford, 1979, 1977; McCord and Loyacano, 1978; Kimball and Kimball, 1977; Brooker and Edwards, 1973; Nichols, 1973; Fitzgerald, 1969; Goulder, 1969; Hasler and Jones, 1949). Filamentous algae (e.g. *Cladophora*) may also have an inhibitory effect upon phytoplankton (Crawford, 1977; Boyd, 1973; Fitzgerald, 1969; Goulder, 1969). This type of interaction has not been described in WSPs but submerged macrophytes and/or filamentous algae could provide a simple, convenient, and inexpensive means of controlling algal levels in effluents.

Although submerged macrophytes are less productive than emergent species (Wetzel, 1975; Westlake, 1963), their harvest from natural lakes may remove significant proportions (16-37%) of annual total nitrogen and phosphorus retention (Carpenter and Adams, 1977; Wile, 1975). Submerged macrophytes may be more effective for the removal of dissolved nitrogen and phosphorus than rooted emergents. Although many submerged aquatic plants obtain nutrients from the sediments, vittate plants (with long stems, thin trailing leaves, and small underground parts), characteristic of eutrophic lakes, obtain most of their required nutrients from the water (Hutchinson, 1975). This is advantageous for effluent polishing. Within the genus *Potamogeton* dependence upon root absorption ranges from high in the thick-cuticled *P. thunbergii* (with thick, coriaceous floating leaves) to low in the submerged, ribbon-leafed *P. schweinfurthii* (Bristow and Whitcombe, 1971).

Naturally occurring populations of submerged macrophytes (including a thin-leafed *Potamogeton*) in maturation ponds have been studied by McNabb (1976). His study showed that submerged species

could concentrate nitrogen and phosphorus above the levels in wastewater and it was calculated that harvest could remove 20-25% of the total nitrogen load and 50-70% of the total phosphorus load during the growing season. However, the actual nutrient store of harvestable biomass was not compared directly with annual nutrient retention. Submerged macrophytes may also contribute to SS removal in maturation ponds as they reduce turbulence thereby increasing sedimentation rates. (Schiemer and Prosser, 1976).

Monospecific stands of *Potamogeton ochreatus* Raoul occurred in both the Gumeracha ponds during the present study. This submerged plant is vittate, hyphydate, and terete-branched in form with long, thin leaves and slender rhizomes. Leaf form and cuticle thickness in this species suggest that nutrients are obtained mainly from the water (c.f. Bristow and Whitcombe, 1971). No emergent vascular plants occurred at Gumeracha.

Dense mats of the filamentous alga *Cladophora* Kuetzing formed in both the Gumeracha ponds at various times during the present study. This genus exhibits extreme morphological variability (in branching pattern, chloroplast form, and relative development of intercalary and apical growth) in response to environmental conditions (Whitton, 1970; Prescott, 1968). Specific identification was not attempted but species most frequently encountered in eutrophic waters are *C. glomerata*, *C. rivularis*, and *C. fracta* (Whitton, 1970).

The effects of *P. ochreatus* and *Cladophora* upon algal standing crops and effluent quality at Gumeracha were monitored. The production of *P. ochreatus* in the Gumeracha ponds was measured and the production of *Cladophora* and phytoplankton in the Gumeracha ponds estimated. The nutrient stores represented by annual net production of *P. ochreatus*, *Cladophora*, and phytoplankton were compared with annual nitrogen and phosphorus retention in the Gumeracha ponds. In this manner, the

potential of submerged macrophytes and filamentous algae as tools for the management of maturation ponds was investigated.

3.2 Methods

3.2.1 Chlorophyll a. Surface water samples (600 ml) from the centre of each pond were taken fortnightly from January 1977 to October, 1978. During warmer months samples were also taken from depths of 50 and 100 cm with a "Chimp" hand pump. Water was filtered through 150 μm mesh to exclude herbivorous zooplankton. Samples were stored on ice in darkness. On each sampling date live material was examined in the laboratory and the algae identified using Fott (1971), Prescott (1970, 1968, 1951), Haughey (1969, 1968, 1965), Tiffany and Britton (1952), Smith (1950), and Chodat (1909).

Chlorophyll a and phaeophytin were determined after Strickland and Parsons (1968). Samples from different depths were pooled prior to filtration. Depending on algal density, a 50, 200 or 500 ml subsample was filtered using Gelman filtration flasks and a vacuum pump. Until March 1977 samples were filtered through 0.45 μm Millipore filter discs. Chlorophyll was extracted in 90% acetone and absorbance measured on a Perkin-Elmer 124 double beam spectrophotometer using 5 cm cells. The use of Millipore filters resulted in incomplete chlorophyll extraction at high cell densities due to poor cell disintegration. Chlorophyll a concentrations in pond 2 from January to March 1977 were therefore underestimated. After March 1977 samples were filtered through Whatman GF/C glass fibre filter discs (particle size retention of 1.2 μm : Whatman filter selection guide). Holm-Hansen and Riemann (1978)' have shown that concentrations of chlorophyll a recovered from Whatman GF/C filter discs and 0.45 μm membrane filters are equivalent. Chlorophyll was extracted in 90% acetone after disintegration of filter discs in a ground glass tissue grinder. Absorbance of pigment extracts was measured on a Varian Superscan 3 spectrophotometer at 750, 663, 645,

and 630 nm using 1 cm cells. Absorbance was also measured at 665 nm before and after acidification with 50% hydrochloric acid. Chlorophyll a concentration (mg/m^3) was calculated using the SCOR/UNESCO tri-chromatic equation (Strickland and Parsons, 1968, p. 189) and active chlorophyll a and phaeophytin concentration calculated using Lorenzen's equation (Strickland and Parsons, 1968, p. 194).

Autotrophic sulphur bacteria may be present in large concentrations in oxidation ponds (Hussainy, 1972). The contribution of this group to chlorophyll concentration can be determined from absorbance of pigment extracts at 720 nm (blank at 850 nm) (Hussainy, 1972). Sulphur bacteria did not contribute to chlorophyll concentrations in the Gumeracha ponds.

3.2.2 Algal Counts. Cell density in each pond was determined from the peak of the phytoplankton bloom in March 1978 until algae were virtually absent from the water column. 1 ml of fresh, agitated sample was placed into a Thomas C20 counting cell (No. 9851) and examined under 200 times magnification. Five random fields were examined, the algae identified and counted. Cell number per ml was calculated from the relative area of the ocular field. This technique may have failed to detect very small algae (less than $6\mu\text{m}$) and therefore underestimated total algal crop.

3.2.3 Filamentous Algal Mats. On each sampling date from July 1976 until October, 1978 percentage coverage of the water surface in each pond by floating *Cladophora* mats was estimated visually. Coverage was recorded as 0% (if mats were absent), less than 5% (plotted as 2.5%) if any mats were present, less than 10% (plotted as 5%), 10%, and multiples of 10 thereafter. This technique is subject to error arising from observer inaccuracy and variation in wind force and direction. Observer error could have been overcome by the actual measurement of mat dimensions. However, variation in the speed and direction of the wind was considered a more significant source of error. It was felt that the extra effort involved in measuring mats would have been largely wasted

in the absence of daily measurements of wind speed and direction.

3.2.4 Submerged Macrophytes. Visual observations on the abundance and shoot height of *Potamogeton ochreatus* were made throughout the study period. *P. ochreatus* beds were mapped on 15 June, 19 October, and 13 December 1977 and on 30 August 1978 from boat and bank observations. Per cent bottom coverage was estimated from these maps using a graphical square counting method.

Due to time and labour constraints, an approximate method was used to measure net production (excluding losses due to respiration) of *P. ochreatus* in both ponds during 1977. Biomass was measured in both ponds on 15 June 1977 when areal standing crop was judged (by observation) to be maximal. It is stressed that biomass was not sampled regularly throughout the growing season. Production was then calculated from published production to biomass ratios.

Areal standing crop was sampled from a boat using a dredge-rake sampler (Figure 3.1). One end of a 2.5 m steel pipe (2.5 cm diameter) was angled at 40° and welded to a steel frame (38 x 18 cm). The lower long side of the frame bore teeth with a 2 cm side length. A large bag of 1 cm plastic mesh was attached to the back of the steel frame. The sampling technique was similar to that of Swindale and Curtis (1957). The toothed-edge of the frame was pressed into the sediment and then dragged towards the boat (anchored to the shore) for a distance of approximately 0.5 m. This gave a quadrat size of 0.19 m^2 . Samples included underground parts; that is, standing crop was equivalent to biomass. Six representative samples within the area under plant coverage were taken from each pond. Sediment was washed from samples before return to the laboratory. Excess water was removed from each sample by spin drying and wet weight measured. Samples were then dried to constant weight in an oven at 60°C and stored in desiccators over silica gel.

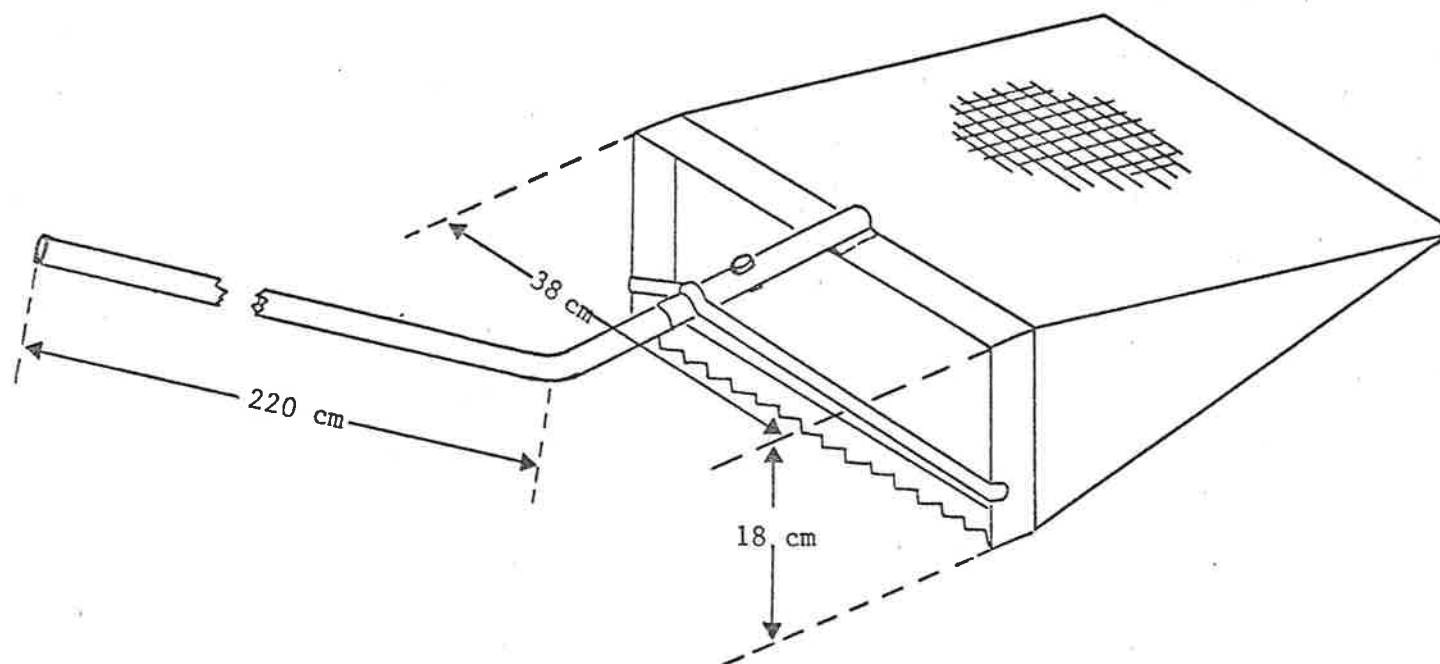


FIGURE 3.1 Dredge-rake macrophyte sampler

Critique of Production Estimate. In macrophyte populations showing a marked annual fluctuation in biomass, and in which losses during the growing season due to mortality and grazing are small, the increase in biomass up to its maximum is a measure of net production (Westlake, 1974a, 1965, 1963; Sculthorpe, 1967). In a harvest situation, such as for nutrient removal, net production is of more interest than gross production. If the initial biomass is negligible or lost before the seasonal maximum is attained, a determination of maximum biomass is alone sufficient to determine net production (Westlake, 1963). That is, if none of the previous year's growth remains by the time of maximum biomass initial biomass need not be determined (Westlake, 1974a).

P. ochreatus was absent from pond 2 at Gumeracha in early 1977. That is, summer die-off of aboveground parts had been complete. Maximum biomass in late 1977 therefore represented a single season's growth; *P. ochreatus* behaved as a true annual (Westlake, 1965) in pond 2. In pond 1, plants from the previous season (1976) were present during early 1977 (at the start of the current season's growth) but had disappeared by the time of maximum biomass. The method of estimating production from maximum biomass was applicable to the populations of *P. ochreatus* in both ponds at Gumeracha.

Species of *Potamogeton* are grazed by coots, ducks, grebes, herons, and plovers (Sculthorpe, 1967). Although these types of birds were recorded at Gumeracha, their numbers were low. Grazing losses, usually involving the removal of upper leaves (Jupp and Spence, 1977b), were not obvious and no attempt was made to estimate grazing intensity.

No estimate was made of mortality. In the morphologically similar *P. pectinatus*, shoots absorb water and collapse upon death (Howard-Williams, 1978). Shoots in this condition were not obvious at Gumeracha prior to the period of maximum biomass. It must be remembered that the time of maximum biomass reflects sampling interval

and may have occurred just prior to or later than the actual sample date. Losses over short periods may usually be neglected (Westlake, 1974a). Ideally, maximum biomass should be determined by frequent, regular sampling throughout the growing season. In the absence of more complete data, a single measurement of biomass (when judged to be maximal) might be expected to yield a reasonable, although approximate, estimate of net production.

The dredge-rake sampler used to measure biomass gave only an approximate quadrat size. This may have been the most significant source of error in the method of production estimation. However, Swindale and Curtis (1957) have shown that with practice this technique can approximate a quadrat of similar size with reasonable accuracy. The sampler used in this study was not tested against a quadrat of known size.

Nitrogen Content of *Potamogeton ochreatus*. Stem, leaf, and rhizome tissue of *P. ochreatus* collected on 15 June, 1977 was ground and homogenized. Total particulate nitrogen was determined using a Kjeldahl digestion technique after Major et al. (1972). Organic matter was digested in a mixture of potassium sulphate and sulphuric acid (mercuric chloride catalyst). Nitrogen was converted to ammonia and determined spectrophotometrically (absorbance at 640 nm) after reaction with phenol and hypochlorite under alkaline conditions (sodium nitroprusside catalyst) to produce indophenol blue (Stainton et al., 1974).

No analyses of tissue phosphorus content were conducted.

3.3 Results

3.3.1 Chlorophyll a. Chlorophyll a concentrations calculated using the SCOR/UNESCO equation included phaeopigments and exceeded values for active chlorophyll a calculated using Lorenzen's equation. Seasonal trends in chlorophyll concentrations calculated using both equations were identical. The tri-chromatic equation is no more accurate than that based upon a single reading at 665 nm (Vollenweider, 1974) and allowance

must be made for inactive chlorophyll in shallow, well-mixed water bodies where zooplankton grazing might be high. Seasonal variation of active chlorophyll a and phaeophytin (mg/m^3) in the Gumeracha ponds, calculated using Lorenzen's equation, is shown in Figure 3.2.

Field observations commenced in July 1976 and pond 1 remained very clear until the end of December 1976. Active chlorophyll a concentration increased from mid January to mid February 1977 (62 mg/m^3) although the transparency of pond 1 remained high (could see substrate).

Chlorophyll a concentration varied between 0 and 10 mg/m^3 from March until early November 1977 and the pond bottom was usually visible during this period. Chlorophyll a concentration increased steadily during December 1977 and early 1978 reaching a maximum of 988 mg/m^3 on 29 March, 1977. Thereafter, chlorophyll a concentration declined rapidly and was 13 mg/m^3 on 27 April 1978. Chlorophyll a concentration was less than 10 mg/m^3 until October 1978 when it again increased rapidly. The concentration of phaeophytin in pond 1 was generally less than 10 mg/m^3 but increased to 35 mg/m^3 in March and April 1977. Phaeophytin increased during the phytoplankton bloom in late 1977 - early 1978 and reached 115 mg/m^3 in April 1978 as active chlorophyll a was decreasing.

Pond 2 was very clear until 8 November 1976 when it became turbid and appeared quite green. Turbidity and the intensity of green colouration both increased during December 1976. Chlorophyll a concentrations in pond 2 from January until March 1977 were underestimated due to incomplete pigment extraction. The intensity of water colouration during this period suggested that chlorophyll concentrations during the peak of the phytoplankton bloom were similar to those from February to March 1978. Chlorophyll concentration decreased rapidly in

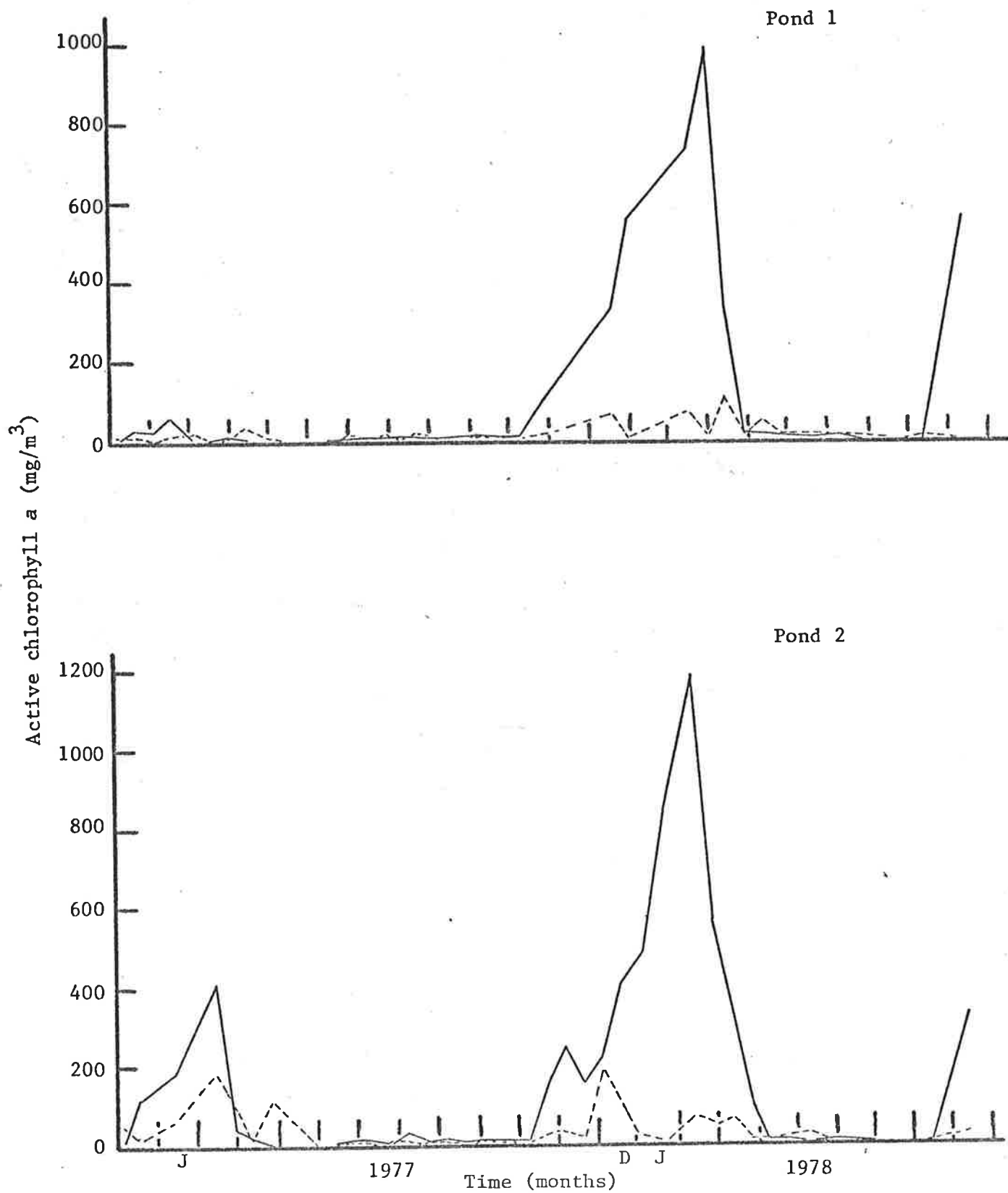


FIGURE 3.2 Active chlorophyll a concentration (—) and phaeophytin (----) in the Gumeracha ponds.

late March 1977 and remained low ($<10 \text{ mg/m}^3$) until November.

Chlorophyll a increased steadily during December 1977 and early 1978 reaching 1185 mg/m^3 on 15 March. Thereafter chlorophyll a concentration declined rapidly and was 5 mg/m^3 on 10 May 1978. Chlorophyll concentration remained low until October. Phaeophytin concentration in pond 2 was low in January 1977 (15 mg/m^3) but increased in March as the phytoplankton bloom declined. A secondary peak in phaeophytin concentration occurred on 27 April after the bloom had declined. Phaeophytin concentration remained low until January 1978 when it reached 180 mg/m^3 just after a decrease in active chlorophyll a. Phaeophytin decreased in February but reached $60\text{--}70 \text{ mg/m}^3$ during March and April as the phytoplankton bloom declined. Phaeophytin concentration remained low until October when it increased slightly as active chlorophyll a concentration increased.

In summary, a phytoplankton bloom developed and continued in pond 2 from early November 1976 until March 1977. A bloom did not develop in pond 1 during this period and water remained very clear until November 1977. Phytoplankton blooms occurred in both ponds from early November 1977 until March 1978. Chlorophyll a concentration maxima were similar in both ponds. Maximum chlorophyll concentration in pond 2 occurred 2 weeks earlier than in pond 1, although chlorophyll concentration declined to very low levels in pond 1 earlier than pond 2. Phytoplankton blooms developed in both ponds in October 1978.

A plot of chlorophyll a concentration (mg/m^3) versus mean water temperature in both ponds on each sampling date from September 1977 until the peak in chlorophyll concentration (mid March 1978) is shown in Figure 3.3,A. The curve (fitted by eye) showed a rapid increase in chlorophyll a concentration at water temperatures above about 18°C . Phytoplankton blooms occurred during late 1976 and late 1978 when water temperature exceeded $17\text{--}18^\circ\text{C}$. However, while maximum chlorophyll a concentration in pond 2 (1186 mg/m^3) occurred at a mean water temperature

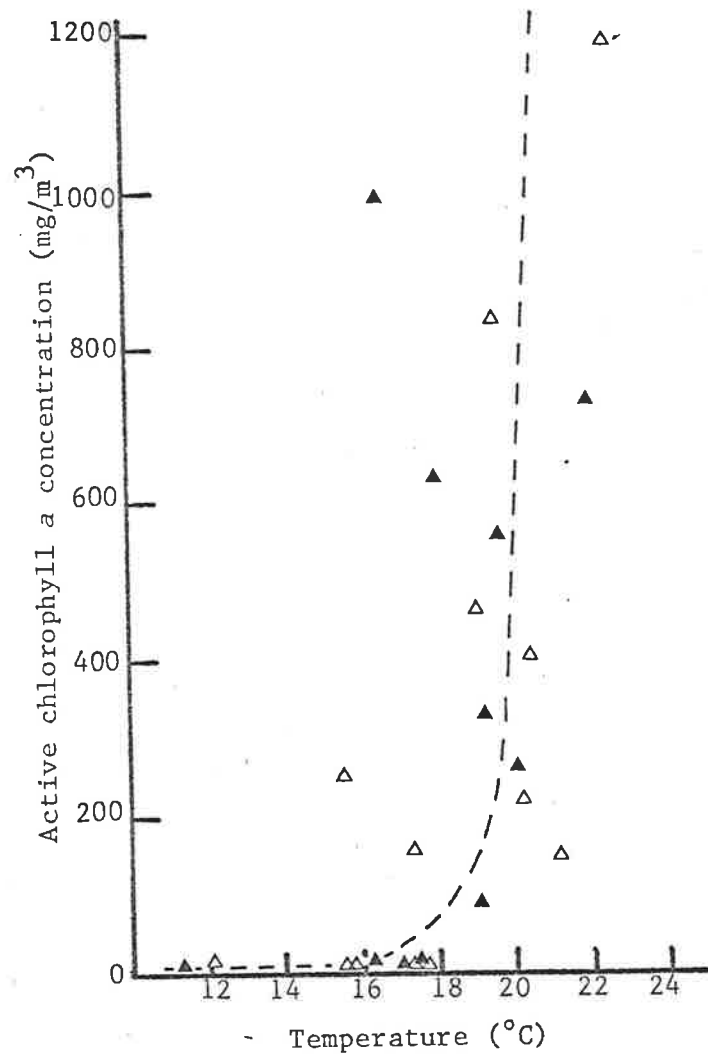


FIGURE 3.3A Active chlorophyll a concentration versus depth-averaged water temperature. Pond 1 (▲), pond 2 (△).

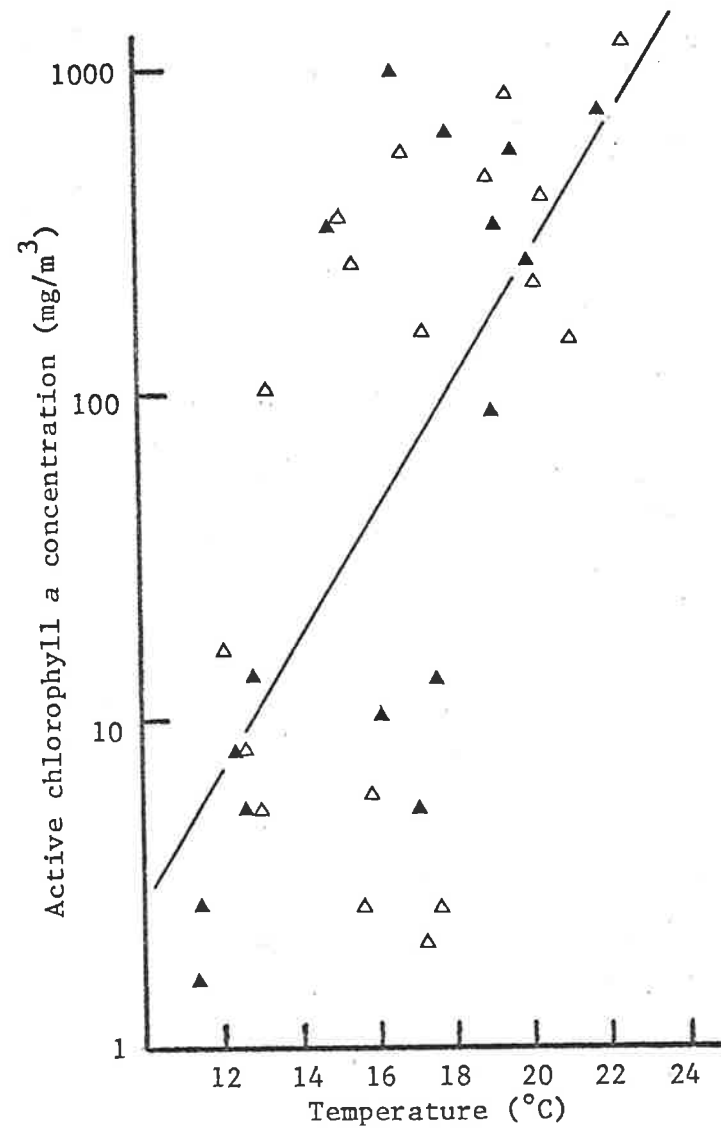


FIGURE 3.3B Active chlorophyll a concentration versus depth-averaged water temperature. Pond 1 (▲), pond 2 (△).

of 22.5°C, maximum concentration in pond 1 (988 mg/m³) occurred at 16.6°C. A semilog plot of chlorophyll a concentration versus mean water temperature in both ponds on each sampling date from September 1977 until late May 1978 is shown in Figure 3.3,B. This graph includes all data presented in Figure 3.3,A. A linear regression of log chlorophyll a on temperature yielded a relationship of the form $\log \text{chlorophyll a} = -1.50 + 0.20 (\text{temperature})$, $r^2 = 0.42$. That is, variation in temperature accounted for only 42% of the variance in chlorophyll a concentration. The regression line intercepted 100 mg/m³ chlorophyll a (concentrations above this constitute a "bloom") at 17.7°C, although chlorophyll concentrations above this also occurred at water temperatures as low as 13.2°C. Most of these values occurred during the decline of the phytoplankton bloom.

Seasonal variation of phaeophytin, expressed as percentage of the total chlorophyll a pool, in ponds 1 and 2 is shown in Figure 3.4. Phaeophytin was low (<30% total chlorophyll) in the early stages of phytoplankton blooms as the number of actively growing cells increased. As blooms progressed, the proportion of inactive chlorophyll in the total chlorophyll a pool increased. Phaeophytin constituted over 90% of total chlorophyll a as phytoplankton blooms declined and senescent cells predominated. From May until November 1977 phaeophytin fluctuated markedly but was generally less than 50% of total chlorophyll. Total chlorophyll a concentrations were very low during this period. During the same period in 1978 phaeophytin constituted more than 60% of the total chlorophyll a pool.

3.3.2 Composition of Algal Communities. Phytoplankton blooms in both ponds at Gumeracha were dominated by species of *Scenedesmus* Meyen. *S. quadricauda* (Turpin), *S. opoliensis* (Richter), *S. acutiformis* (Schroeder), *S. dimorphus* (Turpin), *S. pannonicus* (Hortobagyi), *S. acuminatus* (Lagerheim), and *S. abundans* (Kirchner) were recorded. Species of this

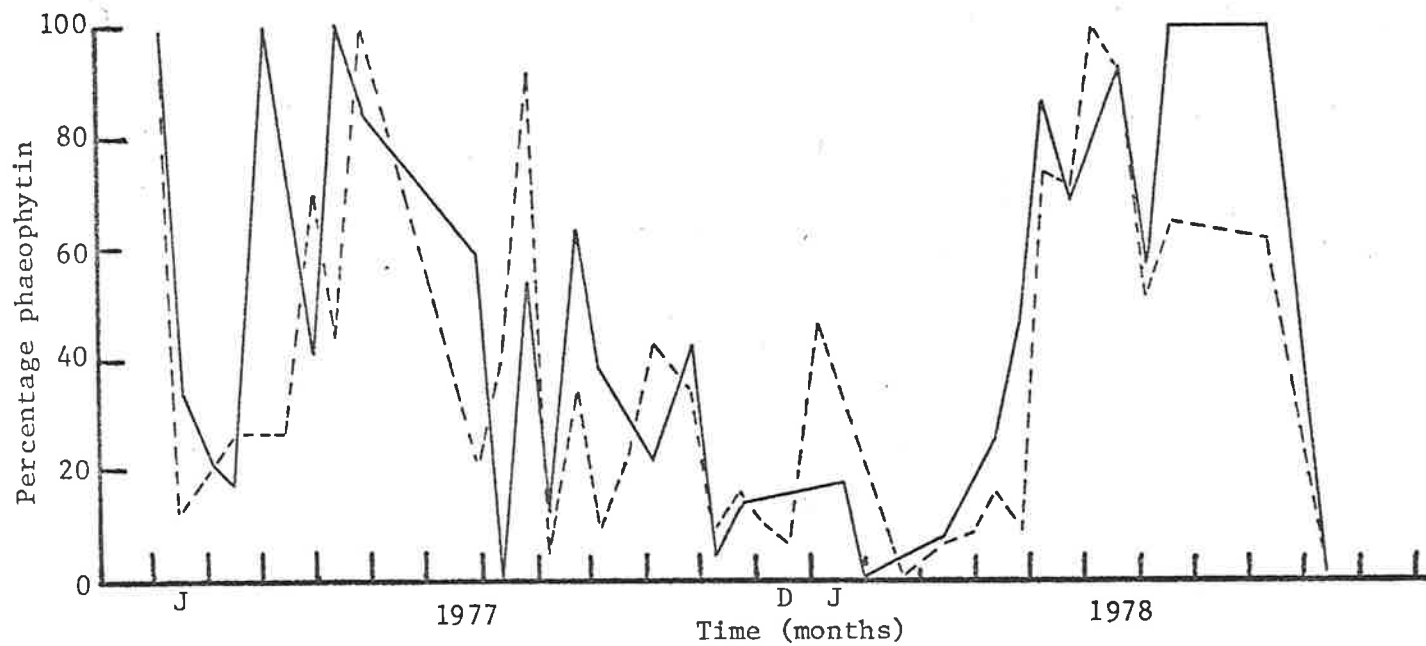


FIGURE 3.4 Concentration of phaeophytin, expressed as a percentage of total chlorophyll a, in pond 1 (—) and pond 2 (----)

genus have generally been described on the basis of cell shape and size, the number and position of spines on coenobia, and the presence of lateral ridges or teeth on cell walls (Chodat, 1909). Several species exhibit extreme phenotypic plasticity with respect to spine distribution and wall ornamentation, and both coenobe formation and spine lengths are affected by the nature of the culture medium (particularly the presence of organic material and bacteria) (Trainor and Roskosky, 1967; Trainor, 1966, 1964, 1963; Trainor and Hilton, 1963). These species, including *S. dimorphus* and *S. acuminatus* (Trainor, 1964), can mimic several different coenobial types and pure culture studies are necessary for identification. Other species, including *S. quadricauda*, *S. acutiformis*, and *S. abundans*, are morphologically stable (Trainor, 1966, 1964). In the absence of pure culture studies, the identification of *S. opoliensis*, *S. acuminatus*, *S. dimorphus*, and *S. pannonicus* from the Gumeracha ponds must remain tentative.

From November 1977 until mid-February 1978, the phytoplankton of both ponds was dominated by a small (7-10 μm long, approximately 2 μm across), crescent-shaped, unicellular green alga most like *Ourococcus* or *Selenastrum* (Dr. G. Ganf, Botany Department, University of Adelaide, pers. comm., 1978). *Scenedesmus* became dominant by 22 February 1978, although several species had been present in low numbers prior to this. During the summer blooms of *Scenedesmus* several other species of algae were present. These included *Ankistrodesmus* sp., *Closterium acerosum* (Schränk), *C. moniliferum* (Bory), *Schroederia setigera* (Schröder), ? *Cryptomonas* sp., ? *Microspora* sp., *Characiochloris* sp. (epiphytic on filamentous algae), *Micractinium* sp., and one or more species of the diatoms *Navicula*, *Cephalomonas*, *Cocconeis*, and *Nitzschia*.

Several genera were recorded from surface water samples during winter periods of low chlorophyll *a* concentration (May to October 1977 and May to September 1978). Diatoms were most abundant and included

species of *Cyclotella*, *Surirella*, *Navicula*, *Nitzschia*, *Cymbella*,
 ? *Denticula*, ? *Amphora*, ? *Fragilaria*, ? *Frustulia*, *Synedra*, and
Diatoma. Green algae, generally less abundant, included *Scenedesmus*,
Ankistrodesmus, *Chlamydomonas*, *Closterium*, ? *Cryptomonas*, ? *Raciborskiella*,
Palmella ? *mucosa* (Kuetzing) (epiphytic on filamentous algae), and
Gyrosigma. Active chlorophyll a generally constituted more than 50% of
 total chlorophyll a during these winter and spring periods. That is,
 most algal cells present in the water column were live.

Periphytic growths formed on the concrete aprons of both ponds
 during most of the year. These growths consisted mainly of *Scenedesmus*
 and diatoms on filaments of the blue-green alga, *Phormidium* sp. Short-
 trichome blue-green algae were recorded rarely from Gumeracha pond water.

3.3.3 Algal Counts. Some counts of algal cell density were made
 during the present study. Counts were undertaken during the course of
 a fish introduction experiment (chapter 5) over a short time interval.
 In the absence of more complete records the most useful information gained
 concerned the succession of *Scenedesmus* species. The density (number of
 cells/ml) of *Scenedesmus* species in both ponds during the decline phase of
 phytoplankton blooms (March to June 1978) is shown in Figure 3.5. In
 both ponds *S. opoliensis* was numerically dominant at maximum chlorophyll
 a concentrations. *S. acuminatus* was recorded in pond 2 on 15 March 1978
 but was not present when counts commenced on 29 March. The order of
 disappearance in both ponds was therefore *S. acuminatus*, *S. acutiformis*,
S. opoliensis, and finally *S. quadricauda*. *S. quadricauda* reached
 maximum density on 13 April in pond 1 and 27 April in pond 2. *S.*
quadricauda increased in density as *S. opoliensis* declined; maximum
 density of *S. quadricauda* was much lower than for *S. opoliensis*.
Scenedesmus declined to very low density in pond 1 about 4 weeks earlier
 than in pond 2.

3.3.4 Phytoplankton Production. The production of phytoplankton in

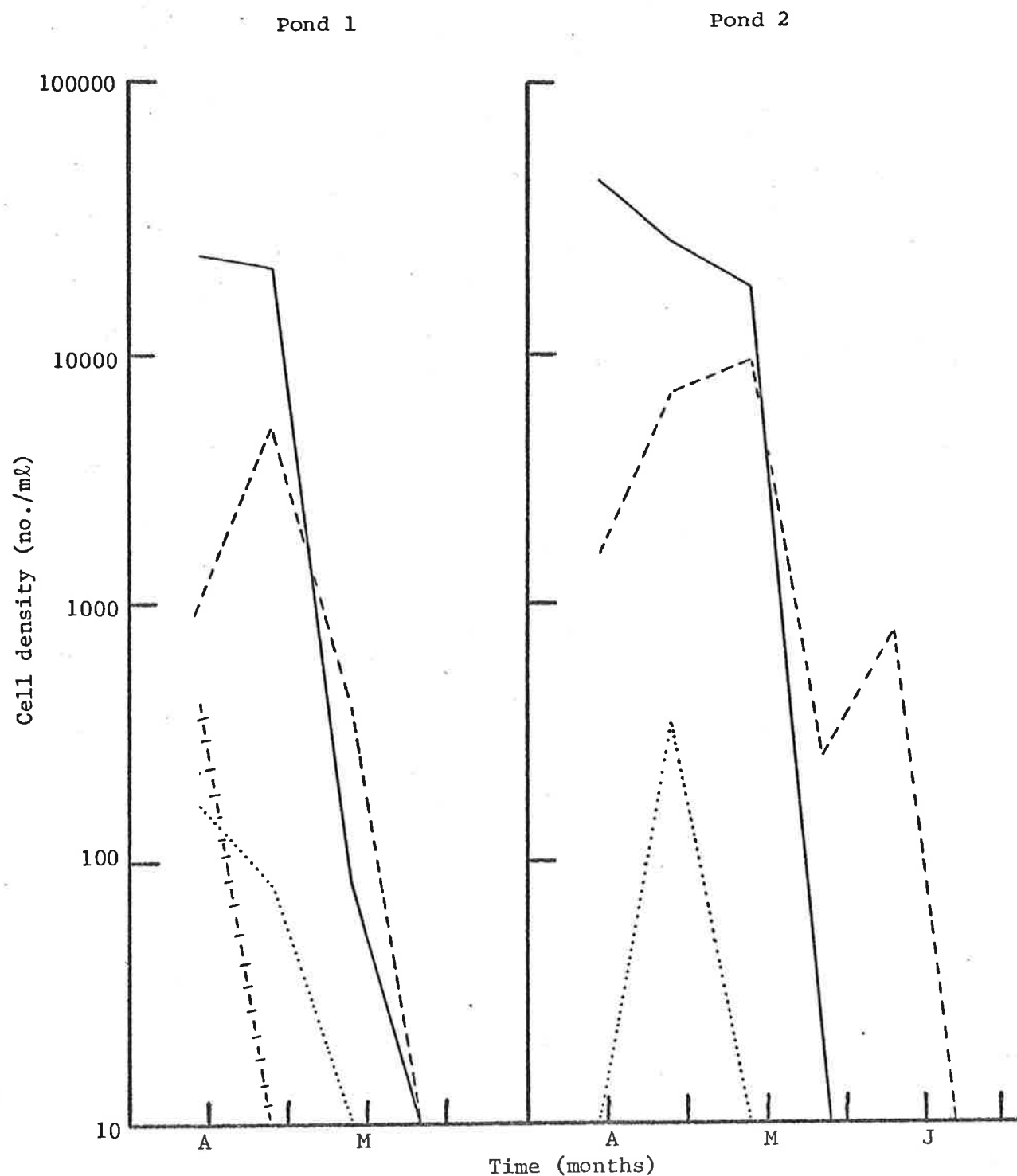


FIGURE 3.5 Succession of *Scenedesmus* species in the Gumeracha ponds

S. opoliensis (—)
S. quadricauda (---)
S. acutiformis (.....)
S. acuminatus (-|-|-)

the Gumeracha ponds was measured indirectly. Estimates of production were calculated on the basis of the correlation between chlorophyll a concentration and gross phytoplankton productivity (Brylinsky and Mann, 1973; Anderson and Banse, 1965; Ryther, 1956). Obviously, in situ productivity is dependant upon many factors (e.g. nutrients, light, temperature, and physiological state), not simply chlorophyll content, and there is not always close correspondence of chlorophyll a concentration and productivity (Hickman, 1979, 1973). Ideally, the degree of correlation should be established individually for each water body. Chlorophyll a concentrations in pond 2 during early 1977 were underestimated due to incomplete pigment extraction. Chlorophyll a concentrations during early 1978 were considered more representative of algal events in pond 2 and have been used in the following calculations.

Two methods were used to approximate net phytoplankton production. The first was based upon the relationship of average chlorophyll a concentration (mg/m^3) and gross phytoplankton production (Kcal/m^2) during the growing season presented by Brylinsky and Mann (1973, p.10, graph B). Mean chlorophyll a concentration in pond 1 during the 1977 growing season was $37.4 \text{ mg}/\text{m}^3$ ($\pm$ standard error equal to 36.0% of the mean) and gross production during the growing season was estimated to be $8750 \text{ Kcal}/\text{m}^2$. Mean chlorophyll a concentration in pond 2 during the equivalent growth period (late 1977 and early 1978) was $359.0 \text{ mg}/\text{m}^3$ ($\pm 26.3\%$) and gross production during the growing season was estimated to be $84,000 \text{ Kcal}/\text{m}^2$. To calculate gross annual production ($\text{gC}/\text{m}^2/\text{year}$), production during the growing season was assumed to be 85% of annual production and 1g Carbon assumed to be equivalent to 9.4 Kcal (Brylinsky and Mann, 1973). Net annual production was taken as 50% of gross production after Westlake (1974b) and Likens (1971). It was assumed that *Scenedesmus* was responsible for total phytoplankton production. The carbon content of *Scenedesmus* was taken as 46% of dry weight

(Strickland, 1960). Net annual production or yield was calculated as 1,190 g dry weight/m²/year ($\pm$ standard error equal to 36.0% of the mean) in pond 1 and 11,427 g dry weight/m²/year ($\pm$ 26.3%) in pond 2. From these values average daily net production rate was 3.26 g dry weight/m²/day in pond 1 and 31.31 g dry weight/m²/day in pond 2.

The second method used to calculate production was based on the relationship of chlorophyll to hourly production rate. Strickland (1960) reported an average figure of 4 mg of carbon synthesized per hour per mg of chlorophyll at optimum light (ca. 20°C). Manning and Juday (in Ryther, 1956) reported that 1 mg of chlorophyll corresponded to a mean gross production of 6.7 mg O₂ per hour at the depth of maximum photosynthesis. This is equivalent to 2.09 mgC/hour/mg chlorophyll (assuming a photosynthetic quotient of 1.2; that is, $lgO_2 \times 0.312 = lgC$; Westlake, 1974b). A rate of 3mgC/hour/mg chlorophyll was chosen for the following calculations. This represented production under optimal light conditions. Although diurnal variation in photosynthetic rate may be unimportant for the calculation of integral daily production in lakes (Fee, 1975), allowance must be made for the increased influence of diurnal changes in physico-chemical conditions upon photosynthesis in shallow ponds (Stengel and Soeder, 1975; Anderson, 1974). Light period was probably about 14 hours during the growing season at Gumeracha. A 9 hour period has been chosen to compute daily production to allow for sub-optimal conditions and surface inhibition at high light intensities. This gave a correction factor of 0.64 times optimal daily rate which corresponded with the ratio of mean photosynthesis in the euphotic zone to rate under optimum light conditions of 0.65 reported by Verduin (1956). Gross production was converted to net production as above.

Chlorophyll a concentrations (mg/m³) in both ponds were converted to mg per square metre of pond surface and daily net production rates (g dry weight/m²/day) calculated for each sampling date. Results

are presented in Table 3.1. Average daily production rates were 1.904 g dry weight/m²/day ($\pm$ standard error equal to 37.1% of the mean) in pond 1 and 11.589 g dry weight/m²/day ($\pm$ 26.3%) in pond 2. Daily production rates were plotted against time for each pond and the area under the curves (total net production or total yield) determined using an Ott compensating polar planimeter, type 30 115. Total annual production was 288 g dry weight/m²/year in pond 1 and 2,513 g dry weight/m²/year in pond 2 during an equivalent growth period.

Maximum daily yields of outdoor mass cultures of *Scenedesmus* may exceed 30 g dry weight/m²/day for short periods (less than 30 days) during summer (Goldman, 1979a, b). Average long term yields (60-90 days) range from 10-25 g dry weight/m²/day (Goldman, 1979a; Becker, 1978; Heussler et al., 1978; Payer et al., 1978; Shelef et al., 1978; Stengel and Soeder, 1975). These culture systems generally employ artificial nutrient media, mechanical mixing, and the addition of CO₂. Yield is considerably reduced in cultures without CO₂ enrichment (Becker, 1978; De Pauw et al., 1978). The average daily yield from pond 2 calculated using the first method (31.31 g dry weight/m²/day) appeared much too high for a pond lacking CO₂ enrichment. Heussler et al. (1978) reported average summer yields of 25 g dry weight/m²/day at chlorophyll concentrations of 400-700 mg/m². The second method of production calculation afforded more realistic results for a pond dependent upon natural CO₂ replenishment. Daily rates were similar to those reported from a WSP with similar organic loading under operational conditions (Bartsch and Allum, 1957).

The nitrogen content of *Scenedesmus* grown in sewage ranges from 7.7-9.0% dry weight (Becker, 1978; Payer et al., 1978; Shelef et al., 1978) and the phosphorus content from 2-3.1% dry weight (Becker, 1978; Shelef et al., 1978). Strickland (1960) reported a phosphorus content of 1.0-2.7% dry weight for natural populations. In the following

TABLE 3.1

Chlorophyll a concentration (mg/m^2) and calculated
daily net production rate ($\text{g dry weight}/\text{m}^2/\text{day}$)
in ponds 1 and 2 at Gumeracha.

Date	Pond 1		Date	Pond 2	
	Chlorophyll a (mg/m^2)	Net Prod ⁿ (g dry wt/ m^2/day)		Chlorophyll a (mg/m^2)	Net Prod ⁿ (g dry wt/ m^2/day)
5.1.77	0	0	4.1.78	239.4	7.025
19.1.77	36.0	1.057	18.1.78	440.0	12.913
2.2.77	29.4	0.863	1.2.78	506.0	14.850
16.2.77	68.3	2.004	22.2.78	913.4	26.807
2.3.77	0	0	15.3.78	1304.0	38.271
			29.3.78	610.9	17.930
			13.4.78	381.8	11.205
21.9.77	0	0	27.4.78	114.5	3.360
5.10.77	11.2	0.329	10.5.78	5.8	0.171
26.10.77	5.8	0.170			
8.11.77	14.7	0.431	8.11.77	6.5	0.196
23.11.77	98.3	2.885	23.11.77	162.5	4.768
7.12.77	154.0	4.520	7.12.77	276.1	8.103
22.12.77	231.0	6.779	22.12.77	172.3	5.055
$\bar{x}$		1.904			11.589
Standard Error as % $\bar{x}$		$\pm 37.1\%$			± 26.3

calculations the nitrogen content of *Scenedesmus* has been taken as 8.0% and phosphorus as 2.0% dry weight.

Total annual phytoplankton net production (yield), calculated using the second method above, was 41.472 kg in pond 1 and 3,128.062 kg in pond 2 during 1977. In pond 1 during 1977 total phytoplankton production represented a nutrient store equivalent to 0.63% of TKN retained in the pond annually, 0.38% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained annually, and 1.69% of total $\text{PO}_4\text{-P}$ retained annually. In pond 2 total phytoplankton production represented a nutrient store equivalent to 540.8% of total nitrogen retained in the pond during 1977, and 119.6% of total $\text{PO}_4\text{-P}$ retained annually.

It must be stressed that the above phytoplankton production estimates are highly speculative; conclusions based upon them must be guarded. Calculated production rates are likely to be overestimates as the relationship between chlorophyll concentration and production was assumed to be linear. This will not hold at very high phytoplankton densities where self-shading reduces net production (Jewson and Taylor, 1978; Bindloss, 1976; Talling et al., 1973). Temperature variation during the growing season ($17\text{-}25^\circ\text{C}$) has not been taken into account.

In view of the assumptions involved in the method it was felt that this The accumulated errors in the methods used above could be large. would be false accuracy. It may be concluded that harvest of total net phytoplankton production in pond 1 during 1977 would probably have removed less than 2% of total nitrogen and $\text{PO}_4\text{-P}$ retained in the pond.

In pond 2 during 1977, harvest of total net phytoplankton production could, perhaps, have removed a significant percentage of total nitrogen and $\text{PO}_4\text{-P}$ (possibly 50-100%) retained in the pond.

3.3.5 Dynamics and Production of *Cladophora*. Seasonal fluctuation in percentage surface coverage of ponds 1 and 2 by floating *Cladophora* mats is shown in Figure 3.6. *Cladophora* was present in large amounts on the bottom of pond 1 from July to October 1976. Surface coverage

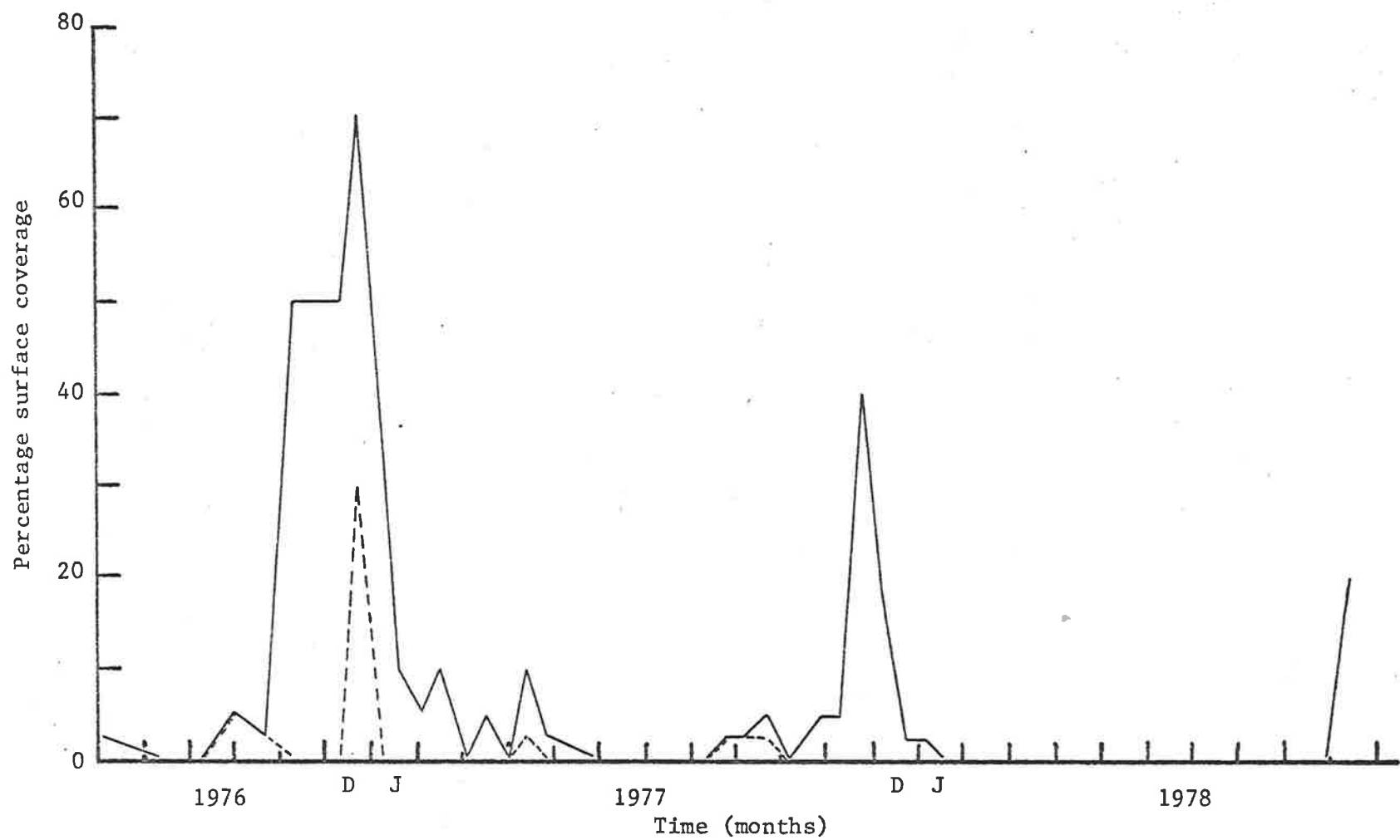


FIGURE 3.6 Percentage pond surface coverage by *Cladophora* mats. Pond 1 (—), pond 2 (----).

was less than 10% during this period. Coverage increased rapidly in November and reached 70% by 22 December. Mats were discoloured at this time. Coverage declined to 10% on 19 January 1977, and although *Cladophora* was fairly dense on the bottom of pond 1 until May, surface coverage was less than 10%. *Cladophora* disappeared from pond 1 during June and July 1977. A small amount reappeared in August 1977, but surface coverage was less than 10%. Abundance increased during November 1977; coverage reached 40% on 23 November, but declined to less than 5% in late December 1977. *Cladophora* was absent from pond 1 by mid-January 1978 and did not reappear until October 1978.

Cladophora was less abundant in pond 2 than in pond 1 from July to November 1976 and coverage reached 30% briefly during late December 1976. *Cladophora* was absent from pond 2 by 5 January 1977, and reappeared in small amounts in April 1977. Coverage was less than 5% during April and from August to late September 1977. *Cladophora* was absent from pond 2 in early October 1977, and did not reappear in that pond during the remainder of the present study.

In summary, high surface coverage occurred in pond 1 from November 1976 to January 1977 and a phytoplankton bloom was not observed in that pond. Moderate coverage occurred only briefly in pond 2 during December and a dense phytoplankton bloom developed in that pond. Moderate coverage occurred only briefly in pond 1 in late November 1977 and a phytoplankton bloom developed in that pond. No floating mats occurred in pond 2 during late 1977 and a phytoplankton bloom developed.

The biomass of *Cladophora* at Gumeracha was not sampled directly. Tentative estimates of mean biomass during 1977 were calculated from the relationship of mean annual total inorganic phosphorus concentration (mg/l) and mean annual dry weight (g/m^2) of *Cladophora* presented by Pitcairn and Hawkes (1973). This relationship is based upon stream samples taken above and below points of sewage input. Mean annual total

$\text{PO}_4\text{-P}$ concentration during 1977 was 7.99 mg/l ($\pm$ standard error equal to 13.1% of mean) in pond 1, and 4.78 mg/l ($\pm$ 10.9%) in pond 2. Mean annual biomass was calculated as 362.5 g dry weight/m² in pond 1 and 202.0 g dry weight/m² in pond 2. Estimated biomass values fell within the range recorded from fast flowing streams of lower nutrient status (Whitton, 1970).

The ratio of production to biomass (P/B) is a measure of the extent to which production exceeds biomass or standing crop. P/B ratios for *Cladophora* during the vegetation period vary from 15-16.5/1 (Bohr and Luścińska, 1975; Gak et al., 1972). Total production of *Cladophora* for the year occurs during the growing season and may be approximated by multiplying mean annual biomass by P/B. Annual net production of *Cladophora* was calculated as 5.709 kg dry weight/m²/year in pond 1 and 3.182 kg dry weight/m²/year in pond 2, using a P/B ratio of 15.75/1.

Maximum growth of *Cladophora* in temperate localities occurs during two short periods in late spring and autumn (May-June and September-October in the northern hemisphere) (Mantai, 1978; Wong et al., 1978; Wong and Clark, 1976; Whitton, 1970; Herbst, 1969; Bellis and McLarty, 1967). Crops usually decrease during midsummer and growth rate is highest at intermediate temperatures (approximately 18-20°C) (Wong et al., 1978; Mantai, 1974; Whitton, 1970; Herbst, 1969; Mason, 1965). Maximum growth at Gumeracha during 1977 would thus have occurred during March and October-November (Figure 2.4). This coincided with northern hemisphere periodicities.

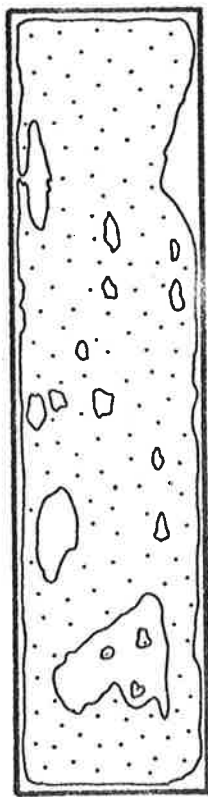
Floating mats of *Cladophora* during summer are the result of thalli deteriorating and breaking loose from the substrate (Mantai, 1978). Trapped oxygen bubbles then lift mats to the surface (Whitton, 1970). The extent of floating mats present during a given summer will therefore reflect bottom coverage during the two prior growth periods as mats overwinter (between growth periods) on the bottom (Mason, 1965). Total

annual net production is equivalent to maximum area of surface coverage (m^2) multiplied by areal net production ($\text{kg}/\text{m}^2/\text{year}$). Surface coverage in pond 1 was 40% during late November 1977. Coverage in pond 2 was less than 5% during September 1977 (*Cladophora* was absent after that time). Total net production during 1977 was calculated as 3,288.600 kg dry weight/year in pond 1 and 198.048 kg dry weight/year in pond 2.

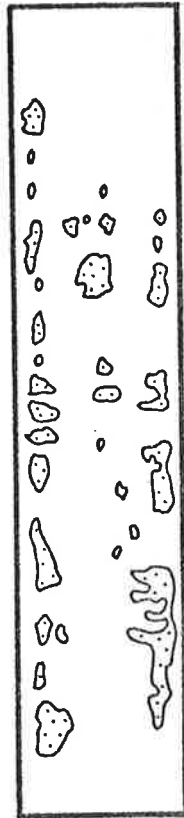
Mean phosphorus content of *Cladophora* tissue is 0.7% of dry weight (Kwei Lin, 1977; Whitton, 1970). During the course of the growing season tissue nitrogen content may vary from approximately 1.4 to 5.7% of dry weight with a mean value of 3.2% (c.f. Mantai, 1978). Total estimated annual net production of *Cladophora* in pond 1 during 1977 represented a nutrient store equivalent to 47.1% of total $\text{PO}_4\text{-P}$ retained in the pond annually, 20.1% of TKN retained, and 12.0% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained. Total estimated annual net production in pond 2 represented a nutrient store equivalent to 1.3% of total $\text{PO}_4\text{-P}$ retained in the pond annually and 6.9% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained.

The above calculations are speculative and, like those for the estimation of phytoplankton production, involve many assumptions. The results must, therefore, be interpreted with caution. It appeared that total annual net production of *Cladophora* in pond 2 during 1977 represented a minor nutrient store (probably less than 2% of total $\text{PO}_4\text{-P}$ and less than 7% of total nitrogen retained annually) and that harvest of *Cladophora* from that pond would not have provided a significant pathway for nutrient removal. Harvest of total annual net production of *Cladophora* from pond 1 during 1977 could, perhaps, have removed a significant percentage of the nutrients retained (possibly 40% of total $\text{PO}_4\text{-P}$ and 10% of total nitrogen) in that pond.

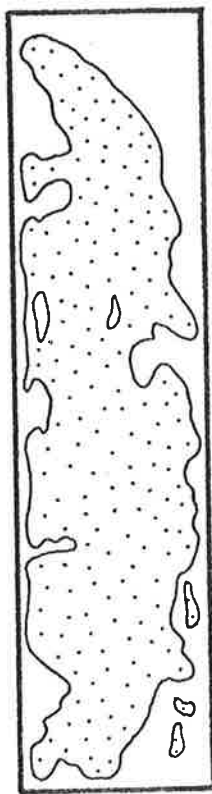
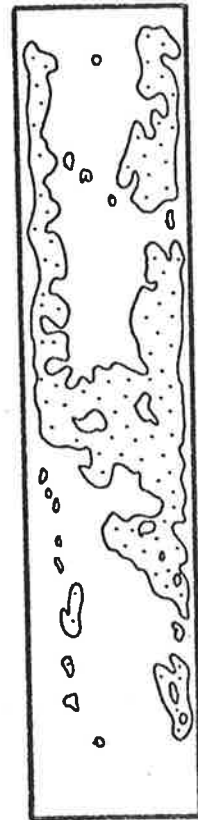
3.3.6 Dynamics and Production of *Potamogeton ochreatus*. Maps of *P. ochreatus* beds in the Gumeracha ponds on 15 June, 10 October, and 13 December 1977, and 30 August 1978 are shown in Figure 3.7, A-D. Area



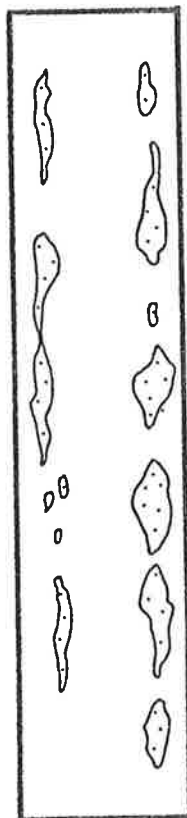
A



B

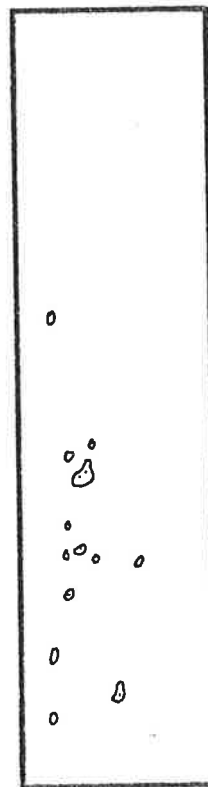


Pond 1



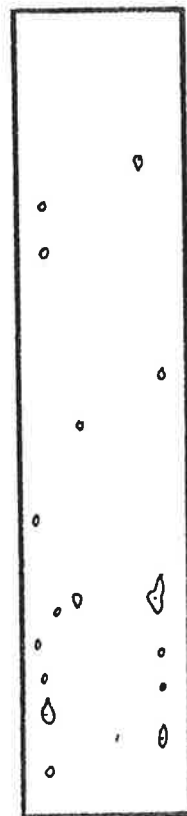
C

Pond 2



Pond 1

D



Pond 2

FIGURE 3.7 Bottom coverage () by *Potamogeton ochreatus* in the Gumeracha ponds on A: 15.6.77, B: 26.10.77, C: 13.12.77, and D: 30.8.78.

of coverage by *P. ochreatus* (m^2 and as percentage of bottom area) on these dates is presented in Table 3.2. *P. ochreatus* was abundant in both ponds from July to late September 1976. In pond 2 plants lost colouration and became overgrown by *Cladophora* during October and November. *P. ochreatus* was not present in pond 2 by December and did not reappear in that pond until May 1977. *P. ochreatus* remained in pond 1 throughout late 1976 and early 1977 and although shoots were overgrown by *Cladophora*, bottom coverage was high. Shoot height and bottom coverage in pond 1 increased from March until June 1977. Growth from the previous season disappeared during this period. Bottom coverage reached a maximum in June (87.7%) (Fig. 3.7, A) and remained fairly constant until flowering occurred in late October (inflorescence spikes on peduncles reached the surface). In pond 2 shoot height increased during May 1977; bottom coverage reached a maximum during October (36.8%) (Fig. 3.7, A and B). Flowering occurred during early October in pond 2. *P. ochreatus* may flower from August to March although this generally occurs in November and December (Jessop, 1978; Aston, 1973). *P. ochreatus* beds in both ponds were overgrown by *Cladophora* during November and December 1977. Plants collapsed and lost their colouration (assuming a brownish appearance), and bottom coverage decreased (Fig. 3.7, C). A rapid decline in bottom coverage occurred in both ponds during late December and *P. ochreatus* was absent from both ponds by 4 January 1978. *P. ochreatus* did not reappear in either pond until August 1978 when very small stands, consisting of only a few plants, became established (Fig. 3.7, D).

P. ochreatus thus behaved as a perennial in pond 1 from July 1976 until October 1977; in pond 2, *P. ochreatus* behaved as an annual with regrowth from May to November 1977. In pond 1 plants from the 1976 season had disappeared by the time the 1977 crop had reached maximum biomass. Bottom coverage in pond 1 during late 1976 and early

Table 3.2

Area (m^2) and percentage of bottom covered by
P. ochreatus in the Gumeracha ponds,

Pond 1 (Bottom area = 1117 m^2)			Pond 2 (Bottom area = 1006 m^2)	
Date	Area (m^2)	% bottom coverage	Area (m^2)	% bottom coverage
15.6.77	978.9	87.7	100.0	9.9
26.10.77	-	-	370.2	36.8
13.12.77	804.2	72.0	109.7	10.9
30.8.78	6.7	0.6	8.0	0.8

1977 was high (although plants were not growing actively) and a phytoplankton bloom did not develop in that pond. *P. ochreatus* was about from pond 2 during the same period and a dense phytoplankton bloom developed. *P. ochreatus* was absent from both ponds during late 1977 and early 1978 and phytoplankton blooms were observed in each.

Mean wet and dry biomass (g/quadrat) ($\pm$ standard error expressed as percentage of the mean) and biomass per unit area (g/m^2) of *P. ochreatus* in ponds 1 and 2 on 15 June 1977 are presented in Table 3.3. Biomass was sampled during maximum bottom coverage in pond 1 but prior to maximum coverage in pond 2. The determinants of areal biomass (shoot density and height) appeared not to change after June 1977 in pond 2, although in the absence of regular biomass samples this observation is subjective. The similarity of dry areal biomass in both ponds during June suggested that maximum areal biomass was achieved at the same time in both ponds. A standard error equivalent to 10% of the mean is acceptable in this type of study (Davies, 1970) and biomass samples from pond 2 met this requirement despite the approximate nature of the sampling method. The variability of biomass samples in pond 1, therefore, appeared to reflect inherent variation in the distribution of biomass within that pond.

Dry weight of *P. ochreatus* was equivalent to 7.9% of wet weight ($\pm$ standard error equal to 2.8% of the mean). No encrustations of Ca CO_3 occurred on the stems of *P. ochreatus* plants from the Gumeracha ponds. Plant weight was not, therefore, subject to over-estimation from this source. Organic compounds in sewage apparently prevent the formation of marl encrustations even at high pH (Sculthorpe, 1967).

Net production of a true annual macrophyte is defined as the amount of material produced over a year and is equivalent to maximum biomass if losses, other than respiration, are small. Losses at Gumeracha, prior to maximum biomass, were not obvious (see above) but

Table 3.3

Mean biomass of *P. ochreatus* per quadrat (g), $\pm$ standard error expressed as percentage of the mean, and biomass per unit area (g/m^2) in the Gumeracha ponds on 15 June 1977.

	Pond 1		Pond 2	
	Wet	Dry	Wet	Dry
Biomass (g/quadrat)	115.9($\pm 32.7\%$)	9.6($\pm 33.9\%$)	128.9($\pm 10.9\%$)	9.6($\pm 10.8\%$)
Areal biomass (g/m^2)	609.9	50.4	677.9	50.5

are likely to have occurred to some extent. Losses that are not obvious may also occur. These include leaf fall, stem damage, and invertebrate grazing (Westlake, 1975, 1965). In addition, positive net photosynthesis may occur after maximum biomass has been reached (Dawson, 1976). Production estimates must be corrected for these losses. This can be done using the ratio of production to maximum biomass (P/B). This ratio is a measure of the amount by which annual production exceeds maximum biomass.

Westlake (1975) has estimated the production of aquatic vascular plants with pronounced seasonal growth (annuals or perennials in which loss of the previous year's growth occurs before maximum biomass is reached) by adding 20-25% to the seasonal maximum biomass (giving, in effect, P/B ratios of 1.2-1.25/1). P/B ratios for submerged macrophytes, including *Potamogeton*, range from 1.1-1.5/1 (Howard-Williams, 1978; Kvet and Husák, 1978; Dawson, 1976; Gak et al. 1972). Ratios of 1.5/1, or higher, occur only in populations with long growing seasons and in which mortality of the current year's crop is high prior to maximum biomass (Kvet and Husák, 1978; Adams and McCracken, 1974; Matthews and Westlake, 1969). A P/B ratio of 1.2/1 was used in this study.

Annual production (net) is equivalent to the biomass increase (regardless of the length of the growing season) multiplied by the P/B ratio. Daily production must, of course, be related to the actual period of growth. Annual areal production ($\text{g dry weight/m}^2/\text{year}$) ($\pm$ standard error as percentage of the mean) and total annual production per pond ($\text{kg dry weight/year}$) of *P. ochreatus* in the Gumeracha ponds during 1977 are presented in Table 3.4. Annual areal production of *P. ochreatus* was similar in both ponds during 1977. Total annual production in pond 1 was 2.64 times that in pond 2 due to higher bottom coverage and larger bottom area in pond 1.

Table 3.4

Annual areal production (g dry weight/m²/year), $\pm$ standard error expressed as percentage of the mean, and total annual production per pond (kg dry weight/year) of *P. ochreatus* at Gumeracha during 1977.

	Pond 1	Pond 2
Annual areal prod ⁿ (g/m ² /year)	60.5 ($\pm$ 33.9%)	60.6 ($\pm$ 10.8%)
Total annual prod ⁿ (kg/year)	59.240	22.423

Mean kjeldahl nitrogen content of *P. ochreatus* tissue at maximum biomass in the Gumeracha ponds was equivalent to 1.92% of dry weight ($\pm$ standard error equal to 20.1% of the mean). A tissue nitrogen content of 1.8-2.5% of dry weight has been reported for *P. ochreatus* from fertile New Zealand lakes (Rawlence and Whitton, 1977). Although tissue nitrogen and phosphorus content of submerged macrophytes varies seasonally (Carpenter and Adams, 1975; Wile, 1975; Adams and McCracken, 1974; Cowgill, 1974; Boyd, 1970; Gerloff and Krombholz, 1966) content at the time of harvest (maximum biomass) is of most importance for nutrient removal. The total annual production of *P. ochreatus* in pond 1 during 1977 represented a nitrogen store equivalent to 0.22% of TKN retained in the pond annually and 0.13% of the total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained. In pond 2 total annual production represented a nitrogen store equivalent to 0.91% of the total nitrogen retained annually.

The nutrient content of submerged macrophytes at maximum biomass in natural lakes generally lies in the middle of the annual range (Carpenter and Adams, 1977; Nichols and Keeney, 1976; Wile, 1975; Adams and McCracken, 1974). A reasonable value for tissue phosphorus content in *P. ochreatus* would appear to be about 0.25% of dry weight (Rawlence and Whitton, 1977). However, intra-specific variation of nitrogen and phosphorus content in submerged macrophytes is apparently correlated with habitat nutrient status (Ho, 1979; Rawlence and Whitton, 1977; Hutchinson, 1975; Boyd, 1970). The only study reporting nutrient content of *Potamogeton* from the hypereutrophic conditions of aerobic WSPs is that by McNabb (1976). McNabb reported a significant linear relationship between plant tissue phosphorus content and ambient soluble phosphorus. This relationship yielded tissue phosphorus values of 2.11% of dry weight for *P. ochreatus* in pond 1 and 1.44% of dry weight for *P. ochreatus* in pond 2. These appear extremely

high compared to literature values for *Potamogeton* species (including *P. ochreatus*) from natural lakes (Rawlence and Whitton, 1977; Wile, 1975; Cowgill, 1974; Boyd, 1970; Gerloff and Krombholz, 1966). However, *Spirodella oligorhiza* may have a tissue phosphorus content equivalent to 2.84% of dry weight when cultured in swine waste (Culley and Epps, 1973).

In lake water, nitrogen and phosphorus concentrations are generally highest prior to the period of plant growth and decline as plant growth becomes heavier (Gerloff and Krombholz, 1966). This may explain why tissue nitrogen and phosphorus of submerged macrophytes from lakes is lower at maximum biomass than early in the season. In WSPs, nutrient input is continual and plants have access to water of high nutrient concentration while growing most vigorously. This could explain why McNabb (1976) found highest tissue nutrient content at maximum biomass and an extremely high phosphorus content.

Using tissue phosphorus content calculated from McNabb (1976), total annual net production of *P. ochreatus* in pond 1 at Gumeracha during 1977 would have represented a phosphorus store equivalent to 2.56% of the total $\text{PO}_4\text{-P}$ retained in the pond. In pond 2, the phosphorus store represented by total annual net production of *P. ochreatus* would have been equivalent to 0.62% of the total $\text{PO}_4\text{-P}$ retained in the pond. Total annual production of *P. ochreatus* was higher in pond 1 than in pond 2 but represented a higher percentage of total nitrogen retained in pond 2 due to a negative TKN retention. As total $\text{PO}_4\text{-P}$ retention was similar in both ponds the higher production of *P. ochreatus* in pond 1 represented a higher percentage of total $\text{PO}_4\text{-P}$ retained.

The use of a harvesting strategy which removed half the standing crop at certain critical times during the period of maximum biomass could, theoretically, increase total yield by 180% (McNabb, 1976). Even if this could be accomplished at Gumeracha when bottom coverage was

100%, theoretical upper limits to nutrient removal by *P. ochreatus* harvest would be less than 5% of total nitrogen and total $\text{PO}_4\text{-P}$ retained annually in the ponds. That these yields could be achieved in reality is extremely doubtful. Production of *P. ochreatus* did not represent a significant nutrient store in the Gumeracha ponds and harvest of this macrophyte would not have provided a useful pathway for nutrient removal.

Primary Production - Summary. Total annual net production (kg/year) of *P. ochreatus*, *Cladophora*, and phytoplankton in ponds 1 and 2 during 1977, together with the percentage of total primary production represented by each group is presented in Table 3.5. Despite the approximate nature of the methods used to estimate the production of *Cladophora* and phytoplankton, total net primary production in both ponds showed a close correspondence. Production of *P. ochreatus* represented a minor proportion of total primary production in both ponds. *Cladophora* was the major primary producer in pond 1 during 1977 and phytoplankton the major contributor to primary production in pond 2.

3.4 Discussion

The algae that occur in WSPs must obviously be capable of adaptation to high concentrations of organic compounds. Although 4 phyla are represented in the flora of WSPs (the Chlorophyta, Euglenophyta, Chrysophyta, and Cyanophyta), relatively few genera have been recorded irrespective of geographical location, climate, sewage composition, or degree and type of pretreatment (Ward and King, 1976; Fitzgerald and Rohlich, 1964, 1958). The most common genera are *Anabaena*, *Anacystis*, *Ankistrodesmus*, *Chlamydomonas*, *Chlorella*, *Euglena*, and *Scenedesmus*. This holds for northern and southern North America (Goulden, 1976; Palmer, 1974, 1969; Gloyna, 1968; De Noyelles, 1967), Central America and the West Indies (Palmer, 1974), Europe (Melchow-Møller et al., 1955), the United Kingdom (White, 1975), India (Patil et al., 1975; Ahmed,

Table 3.5

Total annual net production (kg/year) of
P. ochreatus, *Cladophora*, and phytoplankton
 in the Gumeracha ponds during 1977.

	Pond 1		Pond 2	
	Total net prod ⁿ (kg/year)	%	Total net prod ⁿ (kg/year)	%
<i>P. ochreatus</i>	59	1.7	22	0.7
<i>Cladophora</i>	3288	97.0	198	5.9
phytoplankton	41	1.3	3128	93.4
Σ	3388	100	3348	100

1974; Singh and Saxena, 1969), New Zealand (Haughey, 1969, 1965), and Australia (this study; Hussainy, 1978). No local or regional floras develop and attempts to influence species composition via inoculations are ineffective (Goldman, 1979b; Fitzgerald and Rohlich, 1964; Bartsch, 1961).

Apart from cursory references to the periods of peak algal abundance (e.g. De Noyelles, 1967; Neel and Hopkins, 1956), little attempt has been made to describe the seasonal dynamics of algal populations in WSPs. In the Gumeracha ponds a single, annual algal population increase occurred from November to March (summer). Maximum chlorophyll concentrations occurred from mid to late March. This type of algal cycle has been described in maturation ponds in the United Kingdom (Potten, 1972) and is similar to seasonal events in highly eutrophic, temperate lakes where the spring and autumn phytoplankton maxima are obliterated by an extended mid-summer peak (Mathieson, 1971; Round, 1971). A fundamentally different situation has been reported for maturation ponds in southern Africa (Shillinglaw and Pieterse, 1977). Although organic loads and chlorophyll a maxima in the African ponds were similar to those at Gumeracha, higher ambient temperatures resulted in the occurrence of dense phytoplankton populations during all seasons. The algae underwent a series of rapid, although short-lived (less than one month), population increases throughout the year.

Light and temperature influence the seasonal occurrence of algae (Jones, 1977; Lund, 1965) and population growth rates (Stengel and Soeder, 1975; Moss, 1973b). No data were collected on the seasonal variation of incident light intensity or the underwater light climate at Gumeracha and it is, therefore, difficult to separate the effects of temperature and photoperiod. It has been shown that although the onset of phytoplankton blooms apparently occurred when temperatures exceeded 17-18°C, temperature variation accounted for only 42% of the

variance of chlorophyll a concentration. Furthermore, chlorophyll a concentration was maximal in pond 1 at 16.6°C. That is, temperature appeared to be important for triggering the onset of phytoplankton blooms but was not a major factor terminating blooms.

Self-shading at high algal densities can reduce net productivity by decreasing the depth of the euphotic zone (making the lake "optically deep" by reducing the relative fraction of water volume within the euphotic zone) and increasing respiration relative to photosynthesis (Jewson and Taylor, 1978; Bindloss, 1976; Talling, 1971). Talling *et al.* (1973) reported severe self-shading by phytoplankton in African lakes with chlorophyll a concentrations of 900-2000 mg/m³ and euphotic zones less than 30 cm deep. At maximum chlorophyll a concentrations in the Gumeracha ponds (March 1978) the depth of the euphotic zone would have been less than 50 cm in pond 1 and less than 25 cm in pond 2 (c.f. Wetzel, 1975, p. 337). Light inhibition at the pond surface may have further restricted the optimal zone for photosynthesis. Self-shading may have reduced net phytoplankton production in the Gumeracha ponds.

The importance of nitrogen and phosphorus for algal growth has been repeatedly demonstrated and, generally, phosphorus is dominant as the nutrient most frequently controlling production (Welch *et al.*, 1978; Schindler and Fee, 1974; Schindler *et al.*, 1971; Fogg, 1973; Jordan and Bender, 1973). NO₃⁻ and soluble PO₄-P concentrations in both ponds at Gumeracha exceeded limiting values (300 µg/l and 25 µg/l respectively : Hart, 1974; Stewart and Rohlich, 1967) throughout the study. Carbon may become limiting in WSPs (King, 1976, 1972) although this is rare in natural lakes unless nutrient inputs are extremely high (Steeman-Neilsen, 1955). Carbon limitation may occur diurnally in facultative ponds due to the rapid depletion of CO₂ accumulated during the night (Bartsch, 1961). Talling *et al.* (1973) reported algal crops

of over 2000 mg/m³ chlorophyll a in the Bishfotu soda lakes. These authors pointed out that while the soda lakes were similar to sewage lagoons in that they exhibited high phytoplankton concentrations and high rates of oxygen production, they differed fundamentally in their CO₂ reserves and pH buffering capacity. It was calculated from Prosser et al. (1968) that the total alkalinity (HCO₃⁻ + CO₃⁼) in the soda lakes at the time of Talling's study would have been 2866-3062 mg/l of which 2282-2605 mg/l was in the form of HCO₃⁻. That is, the carbon supply for species able to use HCO₃⁻ would have been adequate even at high cell densities. The TIC concentration in the Gumeracha ponds during the latter stages of phytoplankton blooms (March 1977 and 1978) was less than 5 mg/l. At the pH values attained during these times (10.5-10.8) no free CO₂ would have been present and inorganic carbon would have been present as HCO₃⁻ : CO₃⁼ = 1:1 (c.f. Wetzel, 1975, p. 168). That is, the concentration of HCO₃⁻ was probably less than 2 mg/l. Talling et al. (1973) stated that in waters within the normal alkalinity range (0.1-5 meq/l or 6-305 mg/l if present as HCO₃⁻) population densities such as occurred in the Bishfotu lakes (900-2000 mg/m³ chlorophyll a) would soon exhaust all available carbon. The equilibrium levels of inorganic carbon in the Gumeracha ponds were below even normal alkalinity levels during March 1977 and 1978. However, WSPs differ fundamentally from the Bishfotu lakes in that the ponds receive continuous inputs of decomposable organic matter. Thus, equilibrium concentrations are not a true indication of carbon availability. Controlled carbon enrichment experiments would be required to determine the extent of carbon limitation.

NH₃ concentrations greater than 2 mM (34 mg/l) at pH above 8.0 inhibit photosynthesis and growth of *Scenedesmus obliquus* in high rate oxidation ponds (Abeliovich and Azov, 1976). NH₃ concentrations in both ponds at Gumeracha were substantially lower than this critical

concentration throughout the study; NH_3 toxicity was not involved in phytoplankton decline at Gumeracha.

Active chlorophyll a concentrations in the Gumeracha ponds from May to November were low, generally less than 5 mg/m^3 . Algal cells in the water column during winter are probably stirred up from the sediments by wind mixing. A high proportion of phaeophytin might, therefore, be expected. However, phaeophytin contributed less than 50% of total chlorophyll a during this period in 1977; most chlorophyll a was in an active state. During winter a thin, bright green layer of algal cells, mainly *Scenedesmus* and diatoms, was found on the sediment surface. The presence of this type of winter algal benthos dominated by *Scenedesmus* has been reported in other WSPs (Benson-Evans and Williams, 1975; Bartsch, 1961). While this benthos may be formed by dormant cells which have sedimented out of the water column, epipellic strains of *Scenedesmus quadricauda* exhibiting growth at low temperatures do exist (Moss, 1973b). Epipellic communities in the Gumeracha ponds might be expected to become more active during the periods when phytoplankton density was low and light penetration high (i.e. autumn-late spring). The higher percentage of phaeophytin from May to October 1978 suggested that the algal benthos was less well developed.

The algae of facultative WSPs undergo a characteristic succession of dominance during warmer months when standing crops are high. Usually, an initial mixed population of flagellated greens is followed by *Euglena*, then *Scenedesmus*, *Chlorella*, and finally mixed blue-greens (Patil et al., 1975; King, 1972; Haughey, 1965; Singh and Saxena, 1969; De Noyelles, 1967; Fitzgerald, 1964; Neel et al., 1961). Succession was less obvious in the Gumeracha ponds, although during early 1978 the small, unicellular green was replaced by *Scenedesmus*. Cell count data was limited but indicated a shift in *Scenedesmus* species composition culminating in the dominance of *S. quadricauda*. Little ecological information is available for species of *Scenedesmus* although *S. quadricauda* has been

rated the most pollution tolerant member of the genus (Palmer, 1969). Succession in WSPs generally favours species less tolerant of high organic concentrations (King, 1972). BOD and TOC increased in the Gumeracha ponds as algal blooms progressed. The liberation of organic acids, polysaccharides, and nitrogenous compounds during photosynthesis and cell decomposition (Hobbie, 1976; Ward and King, 1976) may mean that algae themselves appreciably increase the organic content of their medium. Succession also generally favours species able to use low concentrations of free CO_2 (King, 1972). TIC concentrations were low during March 1978 (Fig. 2.18) when *S. quadricauda* was dominant and this species is able to use HCO_3^- directly as a carbon source (Moss, 1973a; Osterlind, 1949).

It has been shown that a phytoplankton bloom did not develop in pond 1 when it was dominated by a *Potamogeton* - *Cladophora* association. A bloom did develop when *P. ochreatus* was absent and surface coverage by *Cladophora* was brief. As in natural ponds and lakes, the presence of submerged macrophytes and/or filamentous algae can apparently inhibit phytoplankton development in WSPs. This is reflected in the similarity of net production of *Cladophora* in pond 1 (3288 kg) and phytoplankton in pond 2 (3128 kg) during 1977.

It has been suggested that macrophytes and filamentous algae compete directly with phytoplankton for phosphorus and nitrogen (McCord and Loyacano, 1978; Fitzgerald, 1969; Hutchinson and Bowen, 1941). It is extremely doubtful that nitrogen and phosphorus ever constituted a limited resource in the Gumeracha ponds. Neither *P. ochreatus* nor *Cladophora* were in an active growth phase in pond 1 during early 1977. That is, nutrient uptake by these species would have ceased. In fact, it is likely that both were undergoing bacterial decomposition and that nutrients were released during the period favourable for phytoplankton growth. It is unlikely, therefore, that the *Potamogeton* - *Cladophora*

association at Gumeracha competed with phytoplankton for nitrogen and phosphorus.

A more likely explanation for the effect upon phytoplankton is that the *Potamogeton* - *Cladophora* association restricted light penetration into the water column thereby inhibiting photosynthesis. Floating algal mats can reduce illumination drastically (Goulder, 1969) and phytoplankton productivity beneath mats may be reduced (Boyd, 1973) or suppressed entirely (Goulder, 1969). Light penetration and phytoplankton productivity are both higher amongst submerged macrophytes than beneath algal mats (Boyd, 1973; Goulder, 1969). Shoot density of *P. ochreatus* at Gumeracha was low (c.f. Howard-Williams, 1978) and light penetration would have been greater than beneath algal mats. It is unlikely that *P. ochreatus* stands at Gumeracha would have reduced phytoplankton productivity completely. It appears that phytoplankton development was prevented in pond 1 by the presence of floating *Cladophora* mats. Hartley and Weiss (1970) reported that algae were absent beneath a floating *Oscillatoria* mat but present in the adjacent mat-free portion of a small oxidation pond.

Surface coverage by *Cladophora* in pond 1 during late 1977 and in pond 2 during late 1976 was insufficient to prevent the development of phytoplankton blooms. Apparently, surface coverage must exceed 50% for approximately 2 months during the period of phytoplankton growth onset to inhibit blooms. Surface mats in pond 1 sank to the bottom during late December 1977 and a small increase in chlorophyll a occurred during January and February 1978. However, the presence of *P. ochreatus* was apparently sufficient to prevent the development of high phytoplankton standing crops. It has been postulated that submerged macrophytes may excrete an antibiotic substance which inhibits phytoplankton (e.g. Philips et al., 1978); the existence of such a substance has not, as yet, been experimentally verified.

Pond chemistry and performance at Gumeracha may be interpreted in the light of macrophyte and phytoplankton population cycles.

Dissolved oxygen concentration and percentage saturation were highest in both ponds during phytoplankton blooms but decreased abruptly as blooms declined. Oxygen concentration and saturation in pond 1 were much lower than in pond 2 during the period (from November 1976 to March 1977) that a phytoplankton bloom developed in pond 2 but not in pond 1. Oxygenation of both ponds was greater during the winter of 1977 than the winter of 1978 due to the presence of actively growing *P. ochreatus* stands. Respiration of submerged macrophytes only contributes to deoxygenation when areal biomass is much higher than encountered at Gumeracha (Jorga and Weise, 1977; Buscemi, 1958). Lower oxygen concentrations in pond 1 during the winter of 1977 may have resulted from higher zooplankton respiration (see chapter 4). Oxygen depletion near the bottom of pond 1 during November-December 1977 (Fig. 2.9) may have resulted from bacterial decomposition of senescent *P. ochreatus* and *Cladophora*. This would have been more severe than in pond 2 due to higher standing crops of both. Bacterial decomposition in pond 1 may also have contributed to clinograde oxygen profiles (Fig. 2.10).

The effect of photosynthesis on pH has already been discussed. pH was highest in both ponds during phytoplankton blooms and decreased abruptly as blooms declined. The pH of pond 2 was much higher than pond 1 during the summer of 1977 when a bloom developed in the former but not in the latter. Pond effluent pH exceeded influent during the winter of 1977, probably as a result of photosynthesis of the *P. ochreatus* - *Cladophora* association. The pH of pond 2 effluent fell below influent during May 1977 (Fig. 2.13); this corresponded to the period between the decline of the phytoplankton bloom (April) and the reestablishment of moderate *P. ochreatus* stands.

Effluent BOD and SS exceeded influent values during phytoplankton blooms. That is, the presence of algal cells contributed to the BOD and increased SS. Reduction of BOD and SS was highest in pond 1 from autumn to spring 1977 and was probably effected by actively growing *P. ochreatus* and *Cladophora*. Removal was lower during early 1977 as the *P. ochreatus* population was in a senescent phase. Removal during the winter of 1977 was lower in pond 2 than in pond 1 due to a lower total standing crop of *P. ochreatus* in the former. Mean annual percentage reduction of BOD and SS during 1977 was higher in the macrophyte-dominated pond 1 (Table 2.3). That is, submerged macrophytes and filamentous algae appeared to contribute substantially to BOD and SS reduction. Reduction of BOD and SS during the growing season of *P. ochreatus* and *Cladophora* at Gumeracha approached that recorded in ponds supporting growth of *Eichhornia crassipes* (Dinges, 1978, 1976; Cornwell et al., 1976; Wolverton et al., 1976) and, on some occasions, was equivalent to that effected by the emergents *Scirpus* and *Phragmites* (De Jong, 1976; Seidel, 1976; Spangler et al., 1976).

Effluent TOC also exceeded influent values during phytoplankton blooms. Removal in pond 1 during the winter of 1977 was much higher than in pond 2, as was mean annual removal. Submerged macrophytes apparently contributed to TOC removal although this was substantially lower than BOD and SS removal.

Poor performance of the Gumeracha ponds, individually and overall, with respect to BOD, SS, and TOC reduction occurred during phytoplankton blooms and was the direct result of algae in effluents. Performance overall was highest during periods of macrophyte growth, although other factors (e.g. zooplankton) may have been involved during those times. Even allowing for lower temperatures, oxygen saturation during winter generally exceeded 60%. In fact, severe deoxygenation only occurred during the decline of phytoplankton blooms. It may,

therefore, be asked whether unicellular algae are necessary for oxygenation or the stabilization of organic matter in the Gumeracha ponds. The theory of WSP function based upon the algae-bacteria model appears to be inappropriate for ponds of the Gumeracha type.

NH_3 removal in pond 1 was less than 50% during the summer of 1977, increased as *P. ochreatus* (and *Cladophora*) growth progressed and remained high (> 80%) throughout the rest of 1977 and early 1978. Apparently, *P. ochreatus*, *Cladophora*, and algae (from November 1977) contributed to NH_3 removal. In pond 2, NH_3 reduction was high during the phytoplankton bloom of early 1978 but decreased markedly as the bloom declined. Removal of NH_3 did not improve in pond 2 until peak biomass of *P. ochreatus* was achieved in October. NH_3 may be lost to the atmosphere when pH exceeds 9.0 (King, 1976; Hemens and Stander, 1964). This only occurred in the Gumeracha ponds during phytoplankton blooms and NH_3 reduction during these periods may have resulted from the effects of elevated pH rather than conversion to NO_3^- and biological incorporation.

TKN and organic-N removal in both ponds was highest when *P. ochreatus* and *Cladophora* were well established. Removal in pond 1 was higher than in pond 2 as is consistent with higher standing crops in the former. Effluent TKN exceeded influent values during phytoplankton blooms. NO_3^- reduction, however, was generally highest during phytoplankton blooms, although removal was high in pond 1 during the summer of 1977.

Reduction of total and soluble $\text{PO}_4\text{-P}$ in both ponds was highest during phytoplankton blooms. $\text{PO}_4\text{-P}$ increased in pond 1 during the summer of 1977, probably due to decomposition of senescent *P. ochreatus* and *Cladophora*. This has been observed in maturation ponds elsewhere (Shillinglaw and Pieterse, 1977). $\text{PO}_4\text{-P}$ removal did, however, increase markedly in pond 1 as *P. ochreatus* stands developed during mid 1977.

Removal during periods of macrophyte growth was highest in pond 1; this was consistent with higher standing crops. In pond 2, removal of $\text{PO}_4\text{-P}$ in the absence of phytoplankton only took place in spring 1977 when *P. ochreatus* had achieved maximum biomass. In this pond, phytoplankton rapidly assumed the function of $\text{PO}_4\text{-P}$ removal in late 1977. In pond 1, $\text{PO}_4\text{-P}$ removal decreased completely as *P. ochreatus* and *Cladophora* declined and did not increase again until the phytoplankton standing crop had become well established.

Nutrient removal during periods of *P. ochreatus* - *Cladophora* dominance and during periods of phytoplankton dominance is summarised in Table 3.6. Removal of nitrogenous compounds (except NO_3^-) was highest in pond 1 during periods of *P. ochreatus* - *Cladophora* dominance. NH_3 , TKN, and organic-N generally increased during phytoplankton blooms. However, NO_3^- and $\text{PO}_4\text{-P}$ removal was highest in pond 2 during the summer periods of phytoplankton dominance. In ponds, or lakes, of similar morphometry and flushing rate, nutrient retention must be greatly influenced by ecosystem structure. The predominance of phytoplankton in pond 2 and *P. ochreatus* - *Cladophora* in pond 1 during 1977 accounted for the overestimation of the phosphorus retention coefficient in the latter in 1977 (Table 2.6). Nitrogen and phosphorus removal in pond 1 when standing crops of *P. ochreatus* - *Cladophora* were high was equivalent to that reported for *Eichhornia crassipes* cultures (Dinges, 1978, 1976; Cornwell et al., 1976). Nutrient removal during this period was lower than that reported in trials using emergent macrophytes (De Jong, 1976; Spangler et al., 1976). Nutrient removal in the Gumeracha ponds during phytoplankton blooms was equivalent to that for mechanically mixed, shallow, outdoor cultures of *Scenedesmus* in climates of high incident light intensity (De Pauw et al., 1978; Shelef et al., 1978).

Although nitrogen removal during periods of macrophyte dominance was high, influent-effluent comparisons do not give a true

Table 3.6

Percentage nitrogen and phosphorus removal in the Gumeracha ponds during macrophyte dominance in pond 1 and phytoplankton dominance in pond 1 and pond 2.

	Macrophyte	Phytoplankton
NH ₃	80-90%	60, but up to 200% increase
TKN	75-85	30, " " " 40% "
Org-N	75-90	up to 500% increase
NO ₃ ⁻	20-50	60-80
Total PO ₄ -P	20-30	40-70
Soluble PO ₄ -P	20-30	60-90

indication of the nutrient removal capacity of a particular group. This type of experiment fails to take into account nutrient removal by other organisms present in the pond at the same time. The role of a given ecosystem component in nutrient removal can be more accurately determined by comparing the nutrient pool represented by its annual production with total annual pond nutrient retention. It appeared that annual production of *P. ochreatus* during 1977 represented a nutrient store probably equivalent to less than 2.5% of total $\text{PO}_4\text{-P}$ and 2% of total nitrogen retained annually in the Gumeracha ponds. Harvest of this submerged macrophyte would not have provided a useful pathway for nutrient removal. Production estimates for *Cladophora* are approximate but suggested that harvest of the total annual production in pond 1 could possibly have removed up to 40% of total $\text{PO}_4\text{-P}$ and 10% of total nitrogen retained in the pond during 1977. Production of this species represented an insignificant nutrient store in pond 2. *Cladophora* appeared to be responsible for a major part of the nutrient removal observed during the period of macrophyte dominance and contrary to the figures in Table 3.5 was more effective in phosphorus removal. Zooplankton may also have contributed to nutrient removal during the period of macrophyte dominance. Comparison of influent and effluent concentrations can present a misleading picture of nutrient removal pathways. The tendency is to ascribe the effects observed solely to the organism, or group, of most interest to the researcher.

The phytoplankton production estimates also represent gross approximations but suggested that the incorporation of nitrogen and phosphorus into algal cells was the major removal pathway in pond 2 during 1977. In pond 1 during 1977 phytoplankton production probably represented less than 1% of total $\text{PO}_4\text{-P}$ and total nitrogen retained in the pond. Although net production of *Cladophora* in pond 1 and phytoplankton in pond 2 appeared to be very similar, unicellular algae

have a higher nitrogen and phosphorus content than filamentous algae. The harvest of unicellular algae appeared to be the most effective pathway of nutrient removal at Gumeracha. However, the problems of algal harvest have been discussed. Phytoplankton production in pond 2 appeared to remove a much higher proportion of the total nitrogen retained than of total $\text{PO}_4\text{-P}$. Percentage removal based on influent - effluent comparisons (Table 3.5) suggested that the reverse was the case. As stated above, this type of comparison can be misleading and poor nitrogen removal during phytoplankton blooms reflected the inclusion of algal cells in TKN analyses. That is, the nitrogen in pond 2 effluent would have been bound in algal biomass.

Phytoplankton production in pond 2 may have accounted for more than 100% of the total nitrogen retained during 1977 suggesting that considerable recycling had occurred. A much lower proportion of the annual $\text{PO}_4\text{-P}$ was incorporated into algal cells. This situation might be expected as nitrogen exists in a wider range of chemical forms, is subject to a wider range of biological transformations, and is, therefore, more labile than phosphorus (Walker and Hillman, 1977). A greater proportion of the total phosphorus pool may be bound in the organic state at a given time and, therefore, be unavailable to algae. Nevertheless, phosphorus recycling may have occurred in pond 2 as a considerable amount of influent $\text{PO}_4\text{-P}$ could have been lost via precipitation at pH above 9.0 (Hemens and Stander, 1969; Fitzgerald and Rohlich, 1964). This would have occurred in the Gumeracha ponds during periods of phytoplankton growth but not during macrophyte growth.

Although significant proportions of the nitrogen and phosphorus retained annually in natural lakes may be removed by the harvest of submerged macrophytes (Carpenter and Adams, 1977; Wile, 1975), the production of *P. ochreatus* did not represent a significant nutrient store in the Gumeracha ponds. Production of *P. ochreatus* at Gumeracha

was much lower than has been recorded for other members of the genus from unpolluted sites. For example, Howard-Williams (1978) recorded an annual production of 2506 g dry weight/m²/year for *P. pectinatus* in an African coastal lake. Annual production of submerged macrophytes from fertile, temperate sites is generally in the range 500-800 g dry weight/m²/year (Westlake, 1975; Sculthorpe, 1967). Production of this magnitude at Gumeracha could have accounted for 20-30% of the total nitrogen and PO₄-P retained in the ponds annually. However, maximum biomass of submerged macrophytes at polluted sites is low compared to clean sites; maximum biomass of *P. pectinatus* in a sewage effluent channel has been reported at 120 g/m² (Sculthorpe, 1967). Lower biomass may be due to light limitation resulting from suspended solids (including algae) (McNabb, 1976). The growing season of *P. ochreatus* at Gumeracha extended from autumn until spring. Although water clarity was high during this algal-free period, temperature and incident light intensity were low. Predicted yields of up to 400 g dry weight/m² for submerged macrophytes in WSPs (McNabb, 1976) would appear to be extremely difficult to achieve on a practical basis. Due to their low productivity, the harvest of submerged macrophytes from maturation ponds is of limited value as a nutrient removal pathway.

Incorporation of nitrogen and phosphorus into unicellular algal biomass appeared to be the most effective pathway of nutrient removal at Gumeracha. However, unicellular algae carry their nutrient load (albeit biologically bound) into effluents and must be harvested continuously. The cost of this process offsets the fundamental advantages of WSPs. The turnover time of algae at optimum temperatures is a matter of hours (Stengel and Soeder, 1975) and nutrient recycling is considerable. The production of *Cladophora* appeared to be a major pathway of nutrient removal in pond 1 during 1977. Increased production of this filamentous alga (e.g. to the level in pond 1 during late 1976) could possibly have

removed over 50% of the total nitrogen and $\text{PO}_4\text{-P}$ retained in the pond annually. In submerged vascular plants, individuals are relatively long-lived and store nutrients over a period of time. The accumulated nitrogen and phosphorus can be removed from the pond by a single annual harvest. The turnover time of *Cladophora* ranges from approximately 7-16 days (Bohr and Luscinska, 1975) and for effective nutrient removal from the pond, biomass would have to be harvested every 1-2 weeks. Harvest of *Cladophora* would probably be labour intensive rather than a high technology process. As such it would be cheaper than the harvest of unicellular algae. *Cladophora* harvest could possibly be simplified if the alga could be induced to grow on floating, mesh-covered frames. This was observed to take place on the netting covers of fish enclosures (see chapter 5).

High phytoplankton density was incompatible with other aspects of pond function, particularly BOD, SS, and TOC removal. Although the removal of organic matter and SS is not a primary requirement of maturation ponds, the presence of algae can have a detrimental effect upon effluents previously treated to a reasonable degree of purity. These problems can be overcome by removal of algae from effluents prior to discharge. Although the production of submerged macrophytes did not constitute a significant nutrient removal pathway in the Gumeracha ponds, both submerged vascular plants and filamentous algae may play a role in the control of phytoplankton, the stabilization of organic matter, and the reduction of SS. A system may be envisaged in which the effluent from a phytoplankton culture pond (for nutrient removal) passes through a submerged macrophyte and filamentous alga culture pond. The latter pond would inhibit phytoplankton and theoretically yield an algal-free effluent low in dissolved nitrogen and phosphorus. The inhibition of phytoplankton takes place when filamentous algae from mats which float to the surface. This occurs in natural situations when the

alga is senescent and thalli are deteriorating. A floating culture system, as suggested above, would extend the desired effect over a much longer period. This could reduce light penetration to such an extent as to inhibit the development of rooted macrophytes. However, submerged vascular plants would probably be unnecessary in a system dominated by a high standing crop of *Cladophora*. The proposed system for effluent polishing is simply the reverse of the pond sequence at Gumeracha,; that is, pond 2 should precede pond 1.

The use of phytoplankton, macrophytes, and filamentous algae for effluent polishing suffers a major drawback in temperate localities. The growing seasons of the various groups are restricted and high standing crops are only maintained for part of the year. Periods of maximum growth of phytoplankton (late spring - summer - early autumn) and macrophytes - filamentous algae (autumn - winter - spring) appeared to be out of phase at Gumeracha. Due to the inhibitory effects of macrophytes and filamentous algae on phytoplankton and vice versa (Jupp and Spence, 1977a; Boyd, 1973) this is not surprising. However, it does suggest that a waste treatment system incorporating the three groups would need careful management and could, therefore, be difficult to maintain in an efficient state. The time lag between macrophyte- - filamentous algae harvest and the reestablishment of standing crops sufficient to provide an effluent of acceptable quality could result in operational problems. The amount of *Cladophora* harvested is likely to be critical if over cropping is to be avoided. These types of problems may mean that a system, such as that suggested above, is not workable on a practical basis.

Alternative methods of phytoplankton control and pathways for nutrient removal require attention. Herbivorous zooplankton incorporate the nitrogen and phosphorus bound into the algal cells upon which they graze. Zooplankton grazing pressure may reduce the phytoplankton

standing crop completely, or could, conceivably, maintain the phytoplankton population in an active growth phase resulting in high productivity from a low standing crop. The population dynamics of the dominant species of zooplankton and their influence upon phytoplankton abundance and effluent quality in the Gumeracha ponds are examined in the following chapter.

Chapter 4. Zooplankton

4.1 Introduction

The algae-bacteria model of WSP function (Fig. 1.1) minimizes the importance of organisms from higher trophic levels, and has promoted the assumption that such organisms cannot contribute to the overall treatment process. A more realistic trophic model (Fig. 1.2) suggests that organisms of higher trophic status may prove useful for pond management. The detrimental effects of algae upon maturation pond effluent quality emphasize the need for research into methods of algal control. However, the harvest of unicellular algae is a major pathway for nutrient removal from maturation ponds. Therefore, if algae are excluded from ponds (as opposed to harvest from effluents), an alternative nutrient removal pathway must be provided. Filamentous algae and submerged macrophytes reduced organic matter and inhibited phytoplankton development in the Gumeracha ponds. While the role of submerged macrophytes in nutrient removal from the Gumeracha ponds was limited, harvest of filamentous algae may have removed a reasonable proportion of annual nutrient retention. However, problems associated with the use of filamentous algae for pond management require that alternative biological methods of algal control be investigated. This chapter examines the role of planktonic microcrustacea in algal control and nutrient removal to assess the usefulness of the group as a tool for managing maturation ponds.

Learner (1975) reported that crustaceans were found only occasionally in sewage works and concluded that the group was unlikely to prove important in the purification process. In fact, a variety of entomostraca, often in large numbers, has been recorded from WSPs over a wide geographic range (Table 4.1). The entomostracan fauna of WSPs includes littoral and limnetic species but is generally dominated by *Daphnia* and cyclopoid copepods. Calanoid copepods appear to be poorly

Table 4.1

Species of entomostraca recorded from waste
stabilization ponds.

Species	Recorded from				
	North America	England	Europe	South Africa	Australia
Cladocera					
Daphniidae					
<i>Daphnia magna</i>	x	x	x	x	
<i>D. pulex</i>	x	x	x		
<i>D. similis</i>	x				
<i>D. catawba</i>	x				
<i>D. longispina</i>		x			
<i>D. carinata</i>					x
<i>Ceriodaphnia rigaudi</i>				x	
<i>C. quadrangula</i>					x
<i>Simocephalus exspinosus</i>				x	
Macrothricidae					
<i>Macrothrix spinosa</i>					x
Bosminidae					
<i>Bosmina longirostris</i>	x	x			
Sididae					
<i>Diaphanosoma</i> sp.	x				
Moinidae					
<i>Moina dubia</i>	x		x	x	
<i>M. macropa</i>	x				
<i>M. brachiata</i>	x				
<i>M. micrura</i>	x				
<i>M. rectirostris</i>			x		x
<i>M. tenuicornis</i>					x
<i>Moina</i> sp.				x	

Species	Recorded from				
	North America	England	Europe	South Africa	Australia
Chydoridae					
<i>Chydorus sphaericus</i>	x	x			x
<i>Alona diaphona</i>				x	
<i>Pleuroxus inermis</i>					x
Ostracoda					
Cyprididae					
<i>Candonocypris assimilis</i>					x
<i>Cypridopsis</i> sp.					x
Copepoda					
Cyclopoida					
Cyclopidae					
<i>Mesocyclops leuckarti</i>					x
<i>Microcyclops minutus</i>			x		
<i>Acanthocyclops gigas</i>			x		
<i>Cyclops vernalis</i>	x	x			
<i>C. vicinus</i>		x			
<i>Eucyclops speratus</i>	x				
Calanoida					
Temoridae					
<i>Eurytemora affinis</i>	x				
Diaptomidae					
<i>Diaptomus gracilis</i>		x			
Centropagidae					
<i>Boeckella</i> sp.					x

Compiled from Hussainy (1978), Shillinglaw and Pieterse (1977), Goulden (1976), White (1975), Teoh (1974), Dinges (1973), Kryutchkova (1968) De Noyelles (1967), Jolly and Chapman (1966), Loedolff (1965) and Elster (1965).

represented. More intensive study may reveal that benthic ostracods are abundant in WSPs.

Due to the varying functional requirements of different pond types (primary, secondary, and tertiary) the presence of zooplankton in ponds, particularly *Daphnia*, has been variously regarded as both beneficial and detrimental. Much of the early study of WSPs dealt with primary and secondary ponds in which oxygenation, and therefore a high algal standing crop, was desirable. The frequent observation that a decline in algal standing crop was often accompanied by an increase in the abundance of *Daphnia* (and a reduction of dissolved oxygen concentration) resulted in the view that zooplankton were detrimental to pond function (see review by Dinges, 1973). Daborn et al. (1978) have suggested that the abundance of *Daphnia* in aerated WSPs can exert a major influence upon the efficiency of the stabilization process and the rate at which oxygen must be supplied. The development of ponds for tertiary treatment and the appreciation of the major operating problem of maturation ponds (algae in effluents) has brought about a reevaluation of the role of zooplankton in pond function. The effects of zooplankton grazing upon algal populations in natural lakes and ponds can be profound (e.g. Porter, 1977). Zooplankton may crop over 100% of the daily net phytoplankton production (Haney, 1973) and rapidly eliminate the entire algal standing crop (Pennington, 1941). The apparent ability of filter-feeding cladocerans to produce a "klarewasserstadium" in WSPs (Dinges, 1973; Uhlmann, 1971, 1967) is now regarded as one potential solution to the problem of algal removal from maturation pond effluents (e.g. Dinges, 1973; McKinney et al., 1971; Ehrlich, 1966). This approach offers a relatively inexpensive alternative to chemical and mechanical methods of algal harvest.

The role of zooplankton in WSPs may not be restricted solely to algal control. Significant BOD and SS reduction can occur in ponds

during cladoceran blooms (Dinges, 1973; McKinney et al., 1971; Loedolff, 1965; Elster, 1965). That is, pond purification capacity does not diminish during a "klarewasserstadium" even though algae are excluded. It has been suggested that BOD and SS reduction by zooplankton is effected via filtration and flocculation of organic and inorganic suspended material (Uhlmann, 1967; Loedolff, 1965). However, few of the above studies have monitored zooplankton standing crop quantitatively or correlated seasonal fluctuations in zooplankton population density with effluent quality and algal standing crop. In some cases (e.g. Dinges, 1973), observed fluctuations in effluent quality could not definitely be ascribed to the effects of zooplankton.

A primary mechanism of wastewater purification may be the incorporation of unstable organic material into living tissue. Thus, zooplankton production and metabolism (assimilation) can be considered as a means of waste stabilization (Andronikova, 1978; Kryutchkova, 1968). The major operating problem of maturation ponds arises because a significant proportion of the influent organic material is converted into algal biomass (Goulden, 1976; Bartsch, 1961). The current inability to remove this biomass from effluents economically means that organic matter, albeit in a changed form, is exported from ponds into receiving water bodies. The possibility of converting algal biomass into a trophically higher, more easily harvestable form (i.e. zooplankton) there^{fore} warrants investigation. The efficiency of assimilation by zooplankton varies with temperature, food type and density, body size, and reproductive condition (Schindler, 1971b, 1968; Richman, 1958). For populations of *Daphnia* in natural waters, assimilation is generally about 40% of gross annual phytoplankton production (Gulati, 1975; Gak et al., 1972; Korinek, 1972; Wright, 1965). Kryutchkova (1968) has shown that daily production and respiration of cladocerans (including *Daphnia*) in WSPs may be energetically equivalent to almost 100% of the daily influent organic

load. Such a value suggests that the zooplankton were feeding directly upon suspended organic material rather than on phytoplankton. In any event, it is likely that a significant proportion of the influent organic load could be converted into zooplankton biomass in WSPs, whether algae were present or not.

At the same time, the stabilization of organic material is not the only requirement of tertiary treatment; nutrient removal is also important. The function of zooplankton in the assimilation of organic material, and hence in energy transfer, need not reflect the relative importance of this group as a nutrient store. Although the study of nutrient cycling within aquatic ecosystems is as yet incomplete (e.g. Schindler *et al.*, 1975; Keeney, 1973), it is apparent that nitrogen and phosphorus are both continuously and rapidly utilized and regenerated by the plankton (Keeney, 1973; Rigler, 1973, 1964, 1956). Uptake of inorganic phosphorus by microcrustacea may be rapid (Rigler, 1961; Whittaker, 1961) but, due to high rates of food consumption and metabolism, zooplankton consume and release back into the water an amount of nutrients many times greater than their body content. Recent research upon aquatic nutrient cycles has focussed upon the rates of transfer between ecosystem compartments. However, in the context of nutrient removal from WSPs, nutrient partitioning between compartments at the time of harvest is of more interest than rates of transfer. Emphasis is placed upon the nutrient store represented by the annual production of a species (or trophic group) rather than its role in nutrient regeneration. This is not a return to a static model of nutrient cycling but, instead, focusses upon a dynamic system at one point in time.

Although 60-80% of the total phosphorus present in natural waters may be bound in the seston at any given time (Rigler, 1964), nutrient partitioning between sestonic compartments has been little studied. Kitchell *et al.* (1979) calculated that 36-68% of the total

phosphorus pool (dissolved + algal-P + zooplankton-P) may be bound into zooplankton biomass. In the present study, the nutrient store represented by the annual production of the dominant herbivorous zooplankton in the Gumeracha ponds was measured to determine the usefulness of zooplankton harvest for nutrient removal. In a sense this is an artificial situation as it assumes that 100% of annual production can be removed from ponds. For organisms such as zooplankton, with high turnover rates, removal would require periodic cropping rather than a single annual harvest. Obviously, cropping would substantially alter subsequent production rates.

The concept of utilizing natural phytoplankton grazers to clarify WSP effluents has helped promote the trophic model of pond function. This has prompted the design of wastewater treatment schemes incorporating unicellular algae (for nutrient removal) and organisms from successive trophic levels (for algal consumption) (Dinges, 1976; Goldman and Ryther, 1976; Trieff *et al.*, 1976; Ryther *et al.*, 1975, 1972; McShan *et al.*, 1974). Many of these schemes require complex, expensive equipment to maintain constant, artificial culture conditions. Such schemes depart from the fundamental concept of WSPs as a simple wastewater treatment technique. To be successfully and efficiently utilized as a WSP management technique, zooplankton grazing and harvest must be incorporated into existing treatment plants under normal, operational conditions. The basic assumption is that optimal standing crops of a desired species can be maintained throughout the year. It was shown in chapter 3 that the inability to maintain standing crops of submerged macrophytes in temperate maturation ponds represents a major problem in their use for pond management.

Obviously, the dynamics of the zooplankton communities in maturation ponds must be studied intensively before schemes utilizing zooplankton for pond management can be contemplated. In particular,

the factors determining the seasonal abundance of the dominant herbivores must be elucidated. In natural waters, herbivorous zooplankton populations are regulated by food level, predation, and temperature (Golterman, 1975). The relative importance of these factors in maturation ponds requires investigation. Although Daborn et al. (1978) studied the population dynamics of *Daphnia pulex* in aerated oxidation ponds in Canada, this study did not relate population fluctuations to environmental conditions.

Seasonal cycles of the major planktonic entomostracans in the Gumeracha ponds were studied quantitatively and abundance related to various physico-chemical parameters, interspecific interactions, algal standing crop, and effluent quality. Annual net production of the dominant herbivores was measured and the nutrient store represented therein compared with the amount of nitrogen and phosphorus retained in the ponds annually. In this manner, the potential of zooplankton as a management tool for maturation ponds was investigated.

4.2 Seasonality and abundance of zooplankton

4.2.1 Methods

Sampling Zooplankton density (number per litre) was measured fortnightly from July 1976 until October 1978 in pond 1 and from December 1976 until October 1978 in pond 2. Samples were taken (between 1100 and 1300 hours) using a clear perspex tube sampler, 1.4 m long, of 5 cm internal diameter, and graduated in 0.10 litre. The tube was pushed vertically into the pond until it reached the bottom, thereby sampling the entire water column, and a large rubber bung inserted in the top. The tube, plus water contained therein, was then raised and another bung inserted in the bottom of the tube prior to removal from the pond. The sample volume was noted, and a water filter (150 μ m mesh bolting cloth) (Fig. 4.1) inserted in one end of the tube. The sample was filtered and preserved in 4% (v/v) formalin. Mesh size was too large to permit

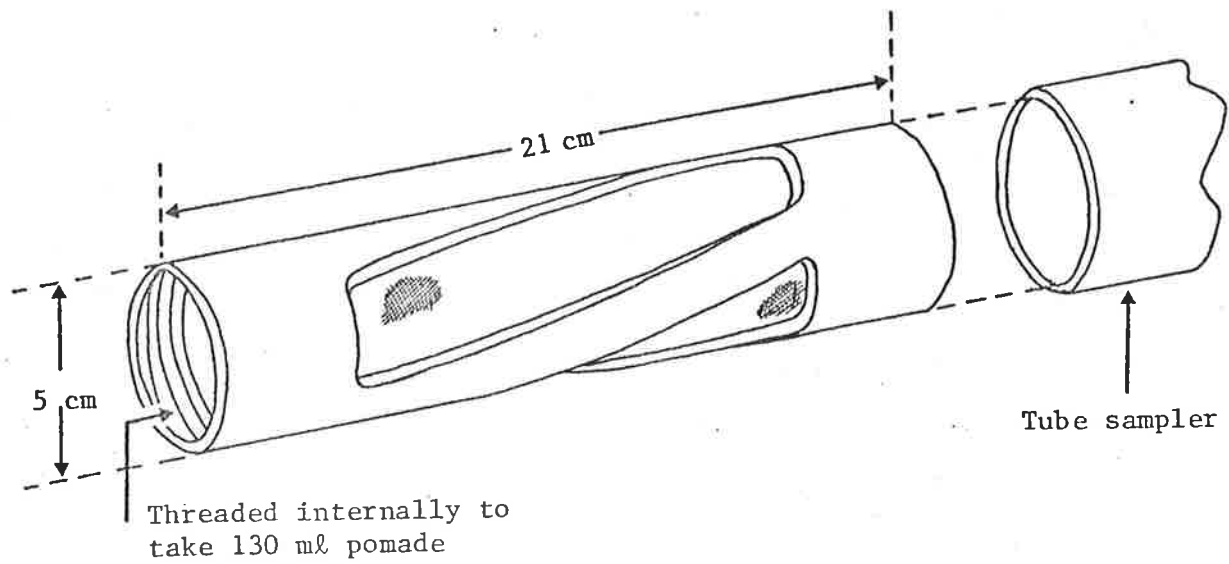


FIGURE 4.1 Zooplankton filter

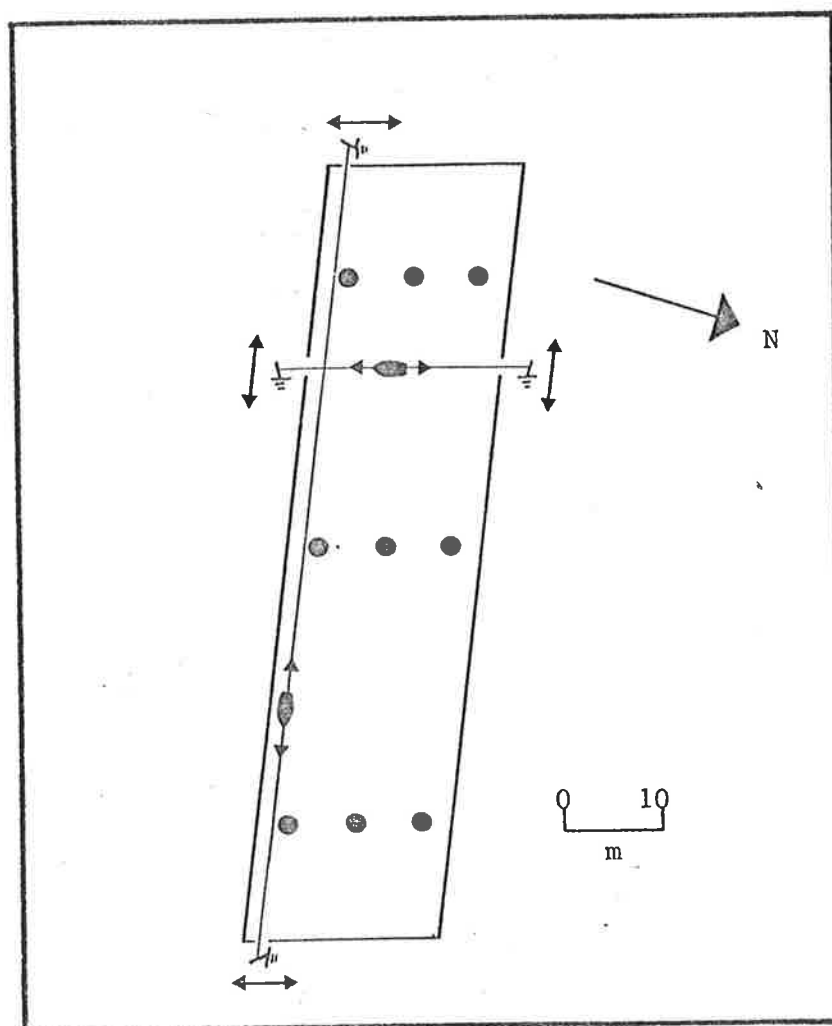


FIGURE 4.2 Sampling stations (●) in both ponds at Gumeracha.

quantitative study of planktonic rotifers.

Prior to field use of the sampler, water loss from the tube due to turbulence and drag during raising was examined using coloured dye. Over the same water depth as encountered in the Gumeracha ponds, dye escaped from the lower 5% of the tube. Loss from this source was not significant in the field as the bottom of the tube was invariably sealed with a "plug" of sediment when lifted to the surface.

During preliminary sampling, the density of *Daphnia carinata* in tube samples was compared with density estimated from samples taken by vertical haul of a zooplankton net at the same sampling station. The net (25 cm mouth diameter, 150 μ m mesh) was allowed to rest upon the bottom for 3-5 minutes and then raised at a rate of approximately 25 cm/second. Volume filtered was taken as cross sectional area of net opening multiplied by distance hauled. Density estimated from net hauls was on average only 13% (range 3-57%) of density in tube samples. Volume samplers characteristically yield higher densities than nets and difference factors of 2.5-8 times have been reported (Bottrell et al.. 1976). Although actively swimming zooplankters may avoid both tube samplers and nets (Prepas and Rigler, 1978; Edmondson and Winberg, 1971) it was concluded that, at least for *D. carinata*, avoidance of the net was greater. An additional disadvantage of net use is that the actual volume of water filtered is not known precisely; calculated volume overestimates filtered volume due to net resistance (Edmondson and Winberg, 1971). It was concluded that for a shallow water body, such as the Gumeracha ponds, in which light penetration was often high, the clear tube sampler was more effective in capturing larger zooplankters than vertical hauls with a zooplankton net.

Submerged stands of *Potamogeton ochreatus* occurred in both ponds at Gumeracha during the study (chapter 3). Pennak (1962) has demonstrated that a tube sampler (6.4 cm diameter) can be used for

effective quantitative sampling of free-swimming zooplankters amongst littoral vegetation.

Samples were taken from a boat at 9 fixed sampling stations in each pond (Fig. 4.2). Steel pegs were driven into the ground on either side of the ponds and a nylon rope drawn taught between them. The boat was attached to this rope and could be pulled across or along the ponds in a straight line; sampling stations were fixed accurately and boat position could be maintained even during windy conditions.

Horizontal and vertical heterogeneity must be accounted for in studies of zooplankton population dynamics and production (Prepas and Rigler, 1978; Bottrell et al., 1976). Vertical heterogeneity was overcome in this study by sampling the entire water column. Preliminary sampling of zooplankton density was conducted at 12 stations in each pond during July and August 1976. The numerically dominant zooplankter at that time, *D. carinata*, was contagiously distributed. It was calculated (after Elliott, 1971, p. 129) that a sample size of 9 would have yielded a standard error equivalent to 40% of mean density at that time. Over 30 samples per pond would have been required to reduce the standard error to 20% of the mean. Fixed, regularly spaced sampling stations were employed during the present study. Samples were thus representative but not independent of position in the pond. This would have been a problem had the population being sampled displayed a consistent horizontal heterogeneous distribution pattern. This was not the case in the Gumeracha ponds. Most statistical methods assume a random distribution of sampling units. However, the data from regular samples may, in practice, be treated as if obtained from the same number of random points provided the spacing of sampling units does not coincide with any repetitive pattern in the population (George, 1974).

Sample treatment. Individual samples taken on each sampling occasion were treated separately. Microcrustacea were identified and

total number per species counted; the number of ovigerous and ehippial females per species was also noted. Mean density values included juvenile and adult cladocerans, and adult copepods plus copepodite stages. Naupliar stages were not included in copepod counts. Samples containing more than about 1000 individuals were subsampled volumetrically. Samples were made up to a known volume, homogenized, and subsampled using a 10 ml bulb pipette (8 mm internal diameter). The error of the subsampling technique in estimating actual sample number averaged from -11.5% to +14.5%. No particular size class appeared to be favoured by the technique.

The arithmetic mean is the best unbiased estimate of a finite population even if the data indicate a contagious distribution (Marchant and Williams, 1977; Elliott, 1971). Zooplankton density has been expressed as the arithmetic mean number of individuals per litre ($n = 9$) on each sampling occasion. The data were converted to logarithms for the calculation of 95% confidence limits as suggested by Elliott (1971) for contagiously distributed populations. The logarithmic confidence limits were converted to the arithmetic scale and combined with the arithmetic mean. Strictly speaking, the log transformation provides confidence limits for the geometric mean. The method employed in this study is thus a compromise (after Marchant and Williams, 1977).

Zooplankton dispersion. The spatial distribution of the major zooplankters in the Gumeracha ponds was investigated using an index of dispersion. Numerous indices of dispersion have been devised (see review by Elliott, 1971) and differ widely in their ability to detect and quantify trends in dispersion (George, 1974). Two types of indices exist: measures of contagion applied to a single sample and measures of dispersion based on a series of samples. The former include chi squared tests of the variance to mean ratio for agreement with a Poisson series (Elliott, 1971), the ratio of "mean crowding" (the mean number per

individual of other individuals in the same quadrat: Lloyd, 1967) to mean density, and Morisita's index of aggregation (Iwao and Kuno, 1971). Indices based on a series of samples include the regression coefficient of the power law relation of mean and variance (Taylor, 1961) and the regression of "mean crowding" on mean density (Iwao and Kuno, 1971).

In a discussion of the spatial distribution of a population, distinction must be drawn between whether the basic component of the distribution is an individual or group of individuals, and how such components are distributed in habitat units. Indices based upon a single sample provide information on the degree of aggregation (departure from randomness) but do not distinguish between the two aspects of spatial distribution (Iwao and Kuno, 1971). These measures are not satisfactory for describing the aggregation patterns of a species, and are, in any event, based upon the variance to mean ratio and therefore essentially identical (Iwao and Kuno, 1971; Stiteler and Patil, 1971; Lloyd, 1967). The variance to mean ratio is largely dependent upon sample size, sample number, and plankton density (Dumont, 1967).

A more comprehensive means of describing the spatial distribution of a population is based on the relationship of Lloyd's (1967) "mean crowding" (x^*) to mean density ($\bar{x}$), where $x^* = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1\right)$. "Mean crowding" is linearly related to mean density over a wide range of density values. That is, $x^* = a + b \cdot \bar{x}$, where a is an index of basic contagion ($a = 0$ when a single individual is the basic component of the distribution; $a > 1$ or $a < 1$ when a positive or negative association of individuals is the basic component of the distribution) and b is the coefficient of density contagiousness ($b = 1$, < 1 or > 1 when the basic components are distributed randomly, uniformly or contagiously) (Iwao and Kuno, 1971). Thus, a linear regression of "mean crowding" on mean density most successfully provides information on both aspects of the spatial distribution of a population; this measure is essentially independent of population density

(George, 1974). When sampling units are widely spaced, the slope coefficient, b , will include an element of variance due to habitat heterogeneity.

4.2.2 Results

4.2.2.1 Composition of the Zooplankton Community. Entomostraca recorded from the Gumeracha ponds during the present study are listed in Table 4.2. The generic composition of the entomostracan fauna of the Gumeracha ponds was similar to WSPs elsewhere (see Table 4.1). The Gumeracha assemblage, typical of natural ponds or the littoral zone of lakes, included the following groups: limnetic, littoral, and benthic cladocerans; limnetic carnivorous and littoral herbivorous cyclopoid copepods; a limnetic herbivorous calanoid copepod; benthic and planktonic ostracods. These groupings were derived from P. De Deckker (Zoology Dept., University of Adelaide, pers. comm., 1979), Sheil (1976), Quade (1969), Fryer (1968, 1957), Geddes (1968), Armitage and Davis (1967), Timms (1967), Elgmork (1966), Byars (1960), and Smyly (1957, 1952). Although macrophytes may control the distribution of littoral crustacea in lakes (Quade, 1969), the distinction between open water and the macrophyte dominated marginal zone in ponds is not necessarily clear cut (Smyly, 1952). For example, *Chydorus sphaericus* is often reported as common in both weed beds and open water (Sheil, 1976; Timms, 1967; Smyly, 1957, 1952) but this species is not adapted for a planktonic mode of existence (Fryer, 1968). Although chydorids occurred frequently in samples from the Gumeracha ponds this group must be regarded as "pseudoplankters" (Pennak, 1962) in that their adaptations are not those of planktonic organisms (Fryer, 1968). The presence of chydorids in the tube sampler probably resulted from their being dislodged from positions of attachment to vegetation. The tube did not sample the microhabitat of this group adequately and chance probably greatly affected their presence in samples.

Table 4.2

Entomostraca recorded from the Gumeracha ponds during
the period July 1976 to October 1978.

Branchiopoda

Cladocera

Daphniidae

Daphnia carinata King

Simocephalus exspinosus Koch

Ceriodaphnia quadrangula Muller

Macrothricidae

Macrothrix hirsuticornis Norman et Brady

Chydoridae

Chydorus sphaericus Muller

Leydigia ciliata Gauthier

L. leydigi Schoedler

Pleuroxus aduncus Jurine

Biapertura affinis Leydig

Alonella sp.

Copepoda

Cyclopoida

Cyclopidae

Mesocyclops leuckarti Claus

Eucyclops agilis Koch

Paracyclops sp.

Calanoida

Centropagidae

Boeckella triarticulata Thomson

Ostracoda

Podacopa

Cyprididae

Candonocypris assimilis Sars

Sarscypridopsis aculeata Costa

Cypridopsis sp.

Although macrothricids are generally bottom dwellers they can swim persistently if necessary; propulsion is by means of the antennae and not, as for the chydorids, by crawling using the trunk limbs or post-abdomen (Fryer, 1974). At times, large numbers of *M. hirsuticornis* were observed near the surface in open water in the Gumeracha ponds. This species may spend considerable time in the water column and the tube samples may be adequate for a quantitative analysis of seasonal population cycles.

Eucyclops agilis and *Paracyclops* sp. were recorded only rarely from the Gumeracha ponds as was *Ceriodaphnia quadrangula*. These species were not an important component of the pond fauna and will not be considered further.

Mesocyclops leuckarti, *Boeckella triarticulata*, and *Daphnia carinata* have been recorded from a wide variety of aquatic habitats in Australia. These species are, however, true free-swimming, limnetic plankters (Timms, 1970; Geddes, 1968; Elgmork, 1966; Jolly, 1963). Although *Simocephalus exspinosus* can attach dorsally to the substrate (Cannon in Horton et al., 1979) this species can probably be considered as a littoral free-swimmer.

The zooplankton of major interest in the present study are, therefore, those species adequately sampled by the tube (including *M. leuckarti* and *M. hirsuticornis*), particularly the larger herbivores *D. carinata*, *B. triarticulata*, and *S. exspinosus*.

The taxonomy of *Daphnia* in south-eastern Australia has been revised by Hebert (1977) who has erected eight new species in the *D. carinata* complex. On the basis of electrophoretic studies Hebert has elevated what were previously thought to be cyclomorphic forms of *D. carinata* (Bayly and Williams, 1973; Jolly, 1967) to species status. However, the assumptions upon which Hebert's electrophoretic interpretations are based may not be valid in all situations (Professor C. Manwell,

Zoology Department, University of Adelaide, pers. comm., 1977).

O'Brien and Vinyard (1978) do not support such an extensive reclassification. Morphologically, many of Hebert's species are difficult to distinguish on the basis of characters other than gross body shape. Many animals were encountered in the Gumeracha collections that could not be satisfactorily identified using Hebert's key. Hebert has stated that individuals can be most readily identified on the basis of species-specific differences in the protein banding patterns of two enzymes. However, his electrophoretic evidence for species recognition remained unpublished at the time of completion of this study. Therefore, even had attempts been made to identify material from Gumeracha electrophoretically (beyond the scope and resources of the present study), in the absence of Hebert's electrophoretic data a particular banding pattern could not have been referred to any of his morphological types. In effect, Hebert's species are unidentifiable.

Hebert (1978b) has gone further and suggested that what was assumed to be cyclomorphosis in *D. carinata* is, in reality, a seasonal change in the relative frequency of several cohabiting species. This phenotypic cycle mimics true cyclomorphosis. The situation is made more complex by the occurrence of true cyclomorphosis in some "species" of the *D. carinata* complex (Hebert, 1978a; Daly, 1974). Seasonal morphological changes (as evidenced by carapace width to body length ratios) in *Daphnia* from the Gumeracha ponds were studied from May 1976 until October 1977 (Mitchell, 1978*). It was concluded that the Gumeracha population of *Daphnia* exhibited both polymorphism and cyclomorphosis. Juvenile and primiparous adult instars maintained constant carapace width to body length ratios throughout the year; carapace expansion occurred only in adults larger than 2 mm in body length.

* This paper is included in Appendix 3.

Juvenile instars were morphologically uniform throughout the year despite changes in adult morphology. Although Hebert (1978b) does not accept the predation hypothesis (e.g. Dodson, 1974) to account for cyclomorphosis, O'Brien and Vinyard (1978) have demonstrated that carapace expansion in *D. carinata* affords protection from notonectid predation.

It appears that some of Hebert's (1977) "species" may be true biological species; introgression does not occur between *D. carinata*, *D. cephalata*, or *D. magniceps* in ponds in which two or more species are present during periods of sexual reproduction (Daly, 1974). The status of the remaining "species" in the *D. carinata* complex awaits verification. *D. cephalata* was not recorded from the Gumeracha ponds, nor was any form that could be confidently identified as *D. magniceps*. Practicality demanded that a conservative approach be adopted during the present study; the population of *Daphnia* at Gumeracha was regarded as consisting of a single species, designated as *D. carinata sensu lato*.

4.2.2.2 Zooplankton Dispersal. "Mean crowding" was calculated on each sampling occasion for the 5 major species of zooplankton. "Mean crowding" was then plotted against mean density for each species in both ponds during 1977 and 1978. These plots are presented in Appendix 1. In each case, except for *B. triarticulata* in pond 1 during 1977, the relation of "mean crowding" on mean density could be fitted to a linear regression accounting for a high proportion of the variance. The regression parameters for each species are summarized in Table 4.3.

The significance of the difference of the intercept a (an indicator of clumping on a scale defined by the limits of the sampling unit) from zero, and the difference of the slope coefficient b (an indicator of clumping in gross environmental terms) from 1, was determined at the 5% level after Bailey (1959). With the exception of *B. triarticulata* in pond 1, b was significantly greater than 1 and a significantly less than zero for all species populations in both the

Table 4.3

Regression coefficients for mean crowding (x^*) on mean density ($\bar{x}$) plus r^2 values (proportion of the variance accounted for by the regression) for major species of zooplankton in the Gumeracha ponds during 1977 and 1978.

	Pond 1			Pond 2		
	1977					
Species	b	a	r ²	b	a	r ²
<i>Daphnia carinata</i>	1.77	-22.82	0.95	5.13	-239.25	0.73
<i>Simocephalus exspinosus</i>	6.26	-131.63	0.96	1.77	2.81	0.89
<i>Mesocyclops leuckarti</i>	2.72	-30.10	0.91	1.63	7.47	0.66
<i>Boeckella triarticulata</i>	1.24	2.70	0.30	2.28	-3.80	0.91
<i>Macrothrix hirsuticornis</i>	6.08	-67.12	0.90	1.99	5.64	0.78
	1978					
<i>D. carinata</i>	1.66	-63.04	0.90	1.12	4.33	1.00
<i>S. exspinosus</i>	3.67	-1.69	0.97	-	-	-
<i>M. leuckarti</i>	1.11	3.76	1.00	1.05	0.75	1.00
<i>B. triarticulata</i>	-	-	-	-	-	-
<i>M. hirsuticornis</i>	-	-	-	-	-	-

Gumeracha ponds during 1977. For *B. triarticulata* in pond 1 during 1977, b was not significantly different from 1 and a was significantly greater than zero. In pond 2 during 1977, a was significantly less than zero for *D. carinata* and *B. triarticulata* but significantly greater than zero for *S. exspinosus*, *M. leuckarti*, and *M. hirsuticornis*.

In pond 1 during 1978, b was significantly greater than 1 and a was significantly less than zero for *D. carinata* and *S. exspinosus*. b was not significantly different from 1 and a was significantly greater than zero for *M. leuckarti* in both ponds and *D. carinata* in pond 2 during 1978. a and b for a given species thus varied between ponds and over time within a pond.

The dispersion patterns for each species, in terms of the relative magnitude of a and b , could be described as follows:

D. carinata. In pond 1 during 1977 and 1978 and pond 2 during 1977 this species was contagiously distributed on a gross scale (over the pond) but negative a intercepts suggested repulsive interactions between individuals. In pond 2 during 1978 this species was contagiously distributed on a small scale, or formed clumps, and the clumps were randomly distributed over the pond.

S. exspinosus. In pond 1 during 1977 and 1978 this species was contagiously distributed over the pond and negative a intercepts suggested repulsive interactions between individuals. In pond 2 during 1977 this species exhibited small scale and gross aggregation. That is, animals formed clumps which were contagiously distributed over the pond.

M. leuckarti. In pond 1 during 1977 this species was contagiously distributed over the pond and a negative a intercept suggested repulsive interaction between individuals. In pond 1 during 1978 and pond 2 during 1977 this species formed clumps which were contagiously distributed. In pond 2 during 1978 this species formed clumps which were distributed randomly.

B. triarticulata. In pond 1 during 1977 this species formed clumps which were distributed randomly. In pond 2 during 1977 this species was contagiously distributed over the pond and a negative a intercept suggested a repulsive interaction between individuals.

M. hirsuticornis. In pond 1 during 1977 this species was contagiously distributed over the pond and a negative a intercept suggested a repulsive interaction between individuals. In pond 2 during 1977 this species formed clumps which were contagiously distributed.

That is, species were generally contagiously distributed on a gross scale; a random distribution over the pond was rare. Individuals were never randomly distributed on a small scale (i.e. $a = 0$) for any species.

On 21 October 1976, during very calm conditions, dense aggregations of *D. carinata* were observed in clear water between stands of *P. ochreatus* in pond 1. These clumps, roughly cylindrical in shape, were approximately 0.5-0.75 m in diameter and extended from the surface to the pond bottom. The clumps were discrete with well-defined limits, although the outer boundaries were continually changing shape. Animals were relatively rare in the water between clumps.

Species differences in overall patchiness were summarized by a comparison of the slope coefficient b for each species in both the Gumeracha ponds during 1977 and 1978 (Fig. 4.3). Overall patchiness was generally more pronounced in pond 1 than in pond 2 during 1977. In pond 1 during 1977 the littoral cladocerans *S. exspinosus* and *M. hirsuticornis* exhibited the highest level of overall patchiness (Fig. 4.3,A). The true limnetic species *D. carinata* and *B. triarticulata* exhibited the lowest level of overall patchiness in pond 1 during 1977. In pond 1 during 1978 *S. exspinosus* exhibited the highest level of overall patchiness while *D. carinata* exhibited a low level similar to that for 1977. *M. leuckarti* exhibited a lower level of overall patchiness in

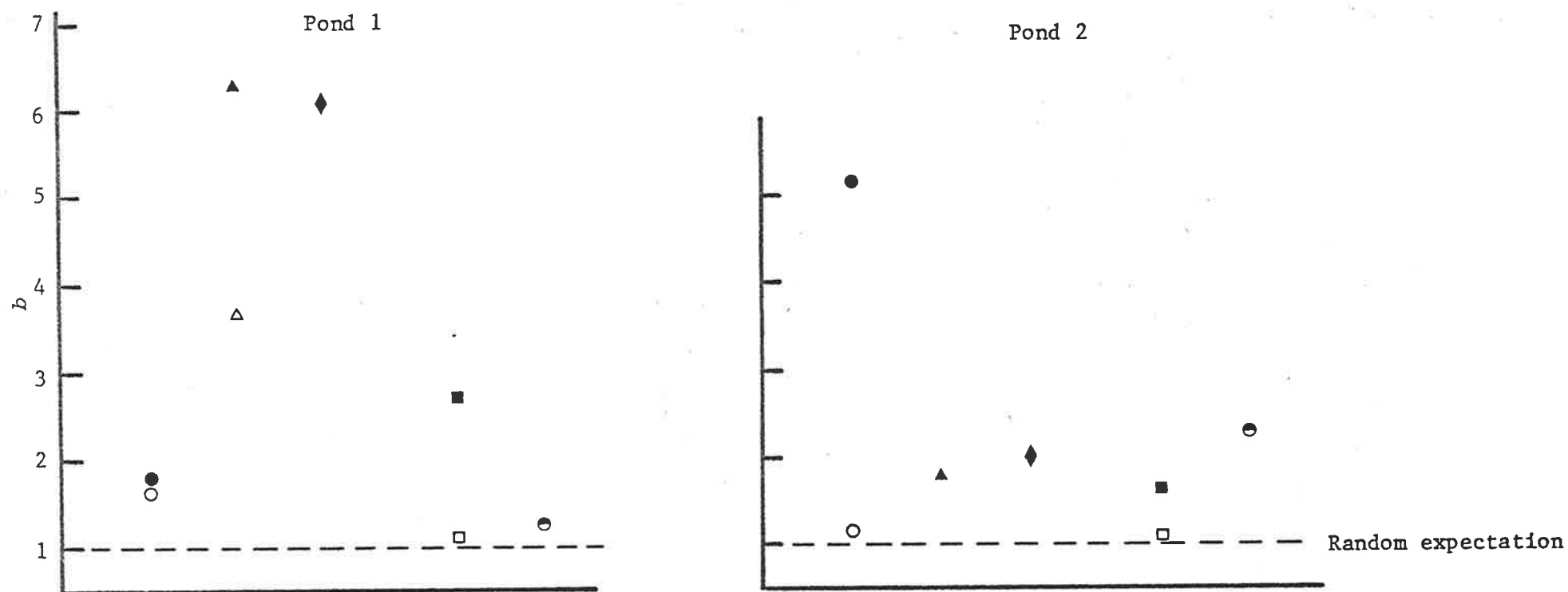


FIGURE 4.3 Comparison of the slope coefficient b (overall patchiness) for major zooplankters in the Gumeracha ponds.

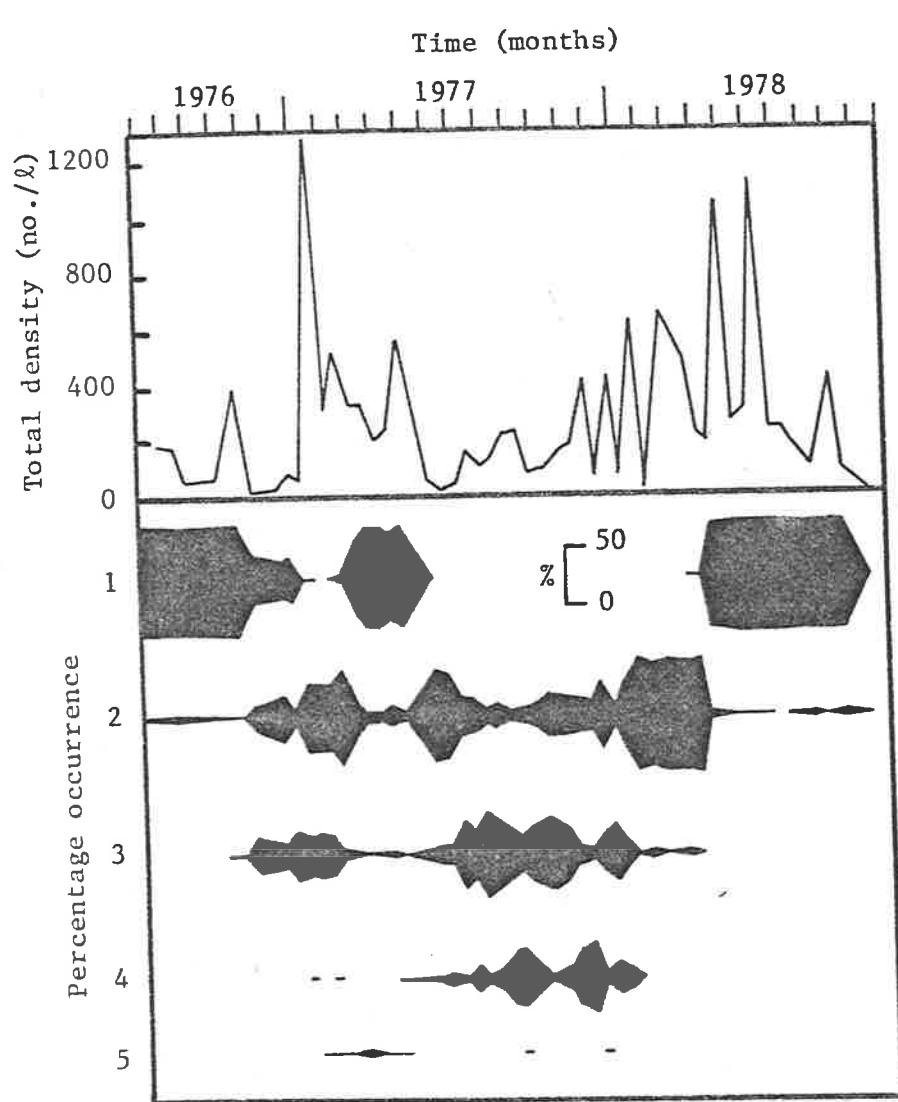
Daphnia carinata 1977 ●, 1978 ○ *Mesocyclops leuckarti* 1977 ■, 1978 □
Simocephalus exspinosus 1977 ▲, 1978 △ *Boeckella triarticulata* 1977 ⊖
Macrothrix hirsuticornis 1977 ◆

pond 1 during 1978 than during 1977. In pond 2 during 1977 *D. carinata* exhibited the highest level of overall patchiness while all other species exhibited similar, low levels (Fig. 4.3,B). In pond 2 during 1978 *D. carinata* and *M. leuckarti* both exhibited similar, very low levels of overall patchiness.

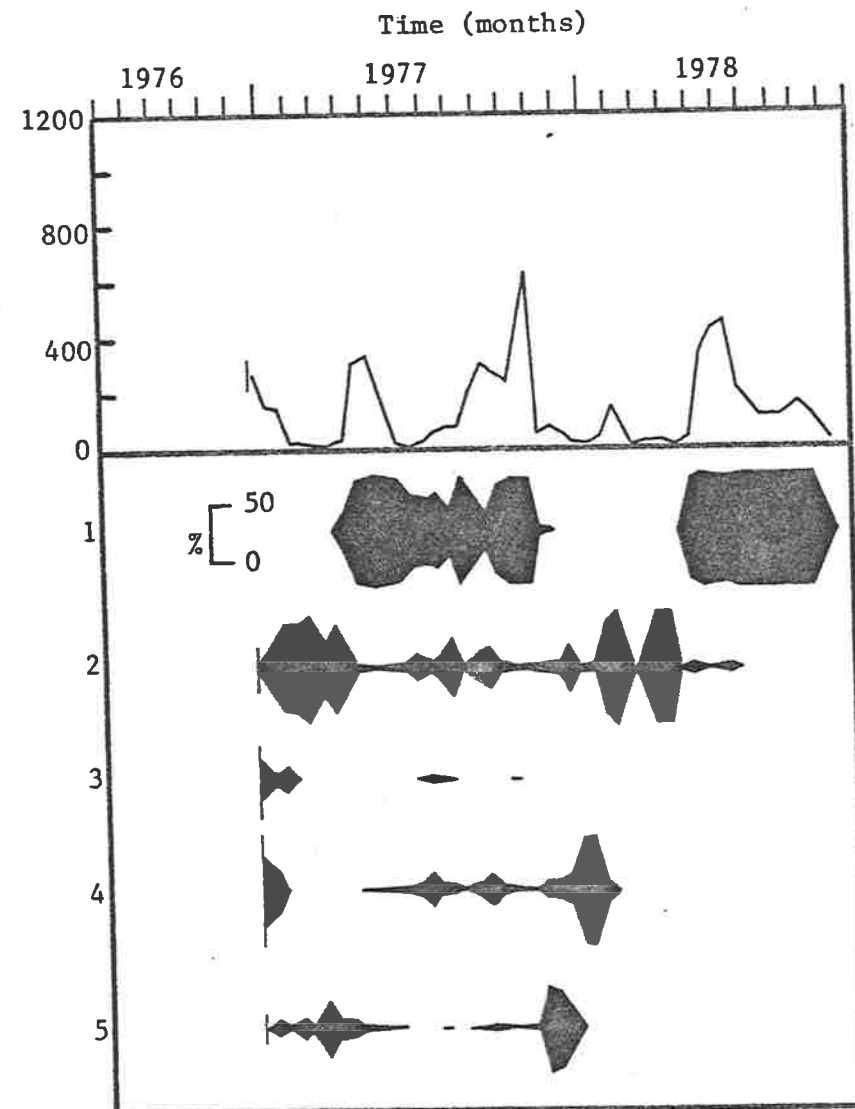
D. carinata exhibited another type of distributional heterogeneity in the Gumeracha ponds. On most sampling occasions this species was observed to be aggregated in the lower 10-20 cm of the sampling tube. This was not invariably true; on some occasions aggregation was observed in samples from one pond while animals were distributed throughout the tube in samples from the other pond.

4.2.2.3 Seasonal Abundance. Seasonal variation in total zooplankton standing crop and percentage occurrence of the major zooplankters in pond 1 are shown in Figure 4.4,A. Zooplankton blooms (>200 individuals/litre) occurred during October 1976, from mid January until late April 1977, and from November 1977 until early September 1978. Large fluctuations in total zooplankton density occurred during the latter period. A succession of species was apparent during blooms. Initially (mid-summer) blooms consisted of *M. leuckarti* and *S. exspinosus*, although the former was dominant. *D. carinata* replaced *M. leuckarti* as the dominant during autumn or autumn-winter. This species dominated the zooplankton during the latter part of 1976 and 1978. Although *M. leuckarti* exhibited a secondary increase in dominance during June 1977 total zooplankton density was very low. During the latter half of 1977, *D. carinata* was absent from pond 1 and the zooplankton was dominated fairly equally by *M. leuckarti*, *S. exspinosus*, and *M. hirsuticornis*. *B. triarticulata* was a minor component of the pond 1 zooplankton community.

Seasonal variation in total zooplankton standing crop and percentage occurrence of the major zooplankters in pond 2 are shown in Figure 4.4,B. Zooplankton blooms (>200 individuals/litre) occurred



A



B

FIGURE 4.4 Total zooplankton density and percentage occurrence of major species in pond 1 (A) and pond 2 (B)

D. carinata, 1
M. leuckarti, 2

S. exspinosus, 3
M. hirsuticornis, 4

B. triarticulata, 5

during April 1977, from August until the end of October 1977, and during May 1978. Fluctuations in zooplankton standing crop in pond 2 were less erratic than in pond 1. In contrast to pond 1, *D. carinata* was dominant throughout zooplankton blooms in pond 2 (except for a brief period in early September 1977). Although *M. leuckarti* was dominant during mid-summer total zooplankton standing crop was very low. As in pond 1 *D. carinata* was dominant during autumn-winter. In contrast to pond 1 *D. carinata* was present in pond 2 throughout the latter half of 1977. Accordingly, *M. leuckarti* and *M. hirsuticornis* did not contribute greatly to the zooplankton standing crop during that period. *S. exspinosus* was a minor component of the pond 2 zooplankton community. *B. triarticulata* contributed a higher percentage of the total zooplankton standing crop in pond 2 than in pond 1 but during periods when total numbers were low.

Average zooplankton standing crops were fairly similar in each pond during 1977 and 1978. However, maximum standing crops were much higher in pond 1 than in pond 2. The major difference between the zooplankton cycles of the Gumeracha ponds was the absence of a marked midsummer bloom in pond 2. Although *M. leuckarti* was dominant in both ponds at these times total zooplankton numbers were much lower in pond 2. Interpond differences in the relative importance of the major zooplankton species suggested that species populations in each pond were, to some extent, independent.

Seasonal variation in mean population density (plus 95% confidence limits) of *D. carinata* in the Gumeracha ponds is shown in Figures 4.5 and 4.6. *D. carinata* was present in pond 1 from the commencement of sampling (Fig. 4.5) and although mean density peaked at 380/l in late October 1976 confidence limits overlapped. A significant decrease in mean density occurred in early November 1976 followed by a small, secondary peak in late December 1976. *D. carinata* was not recorded in

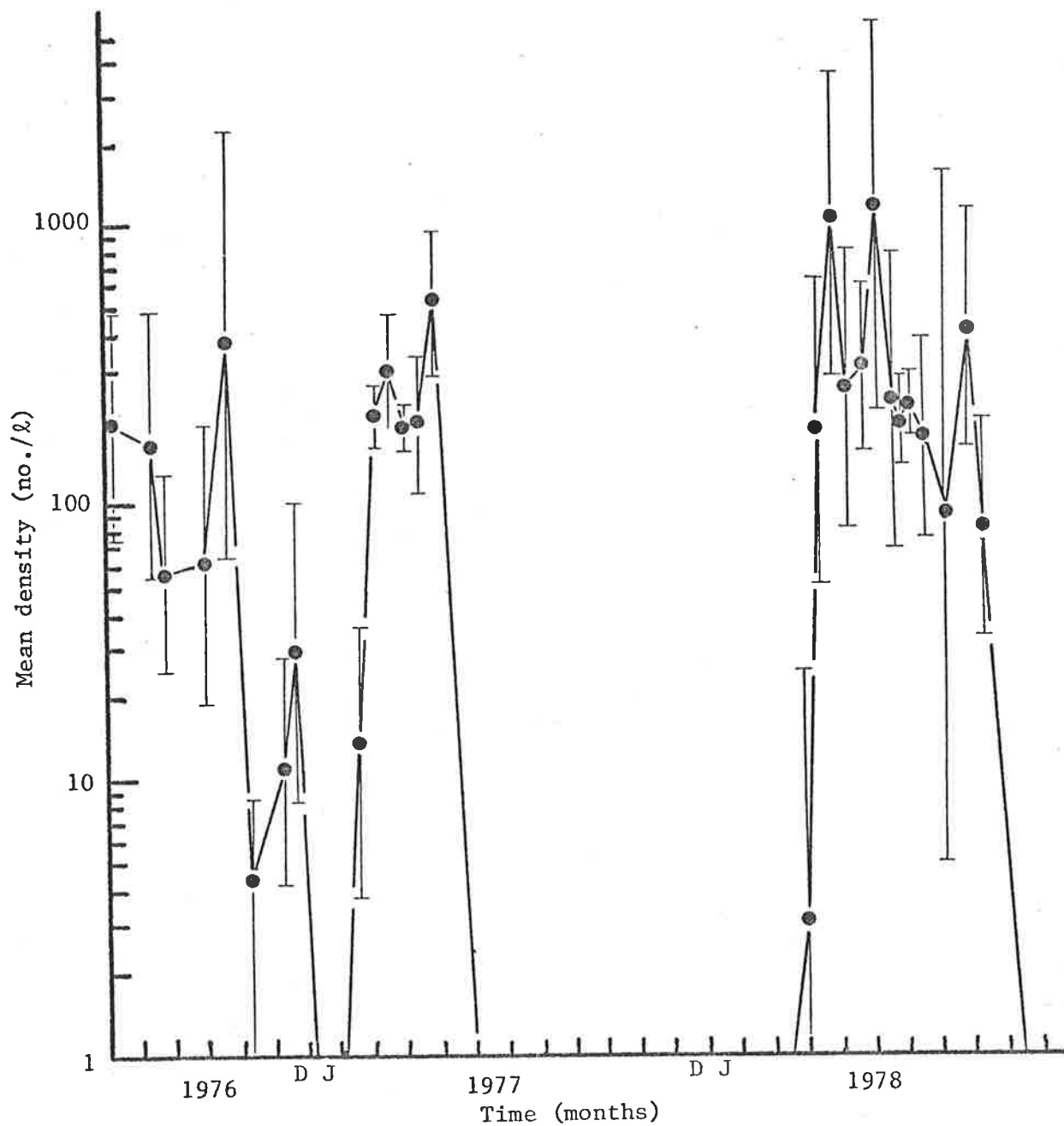


FIGURE 4.5 Mean population density of *D. carinata* (plus 95% confidence limits) in pond 1.

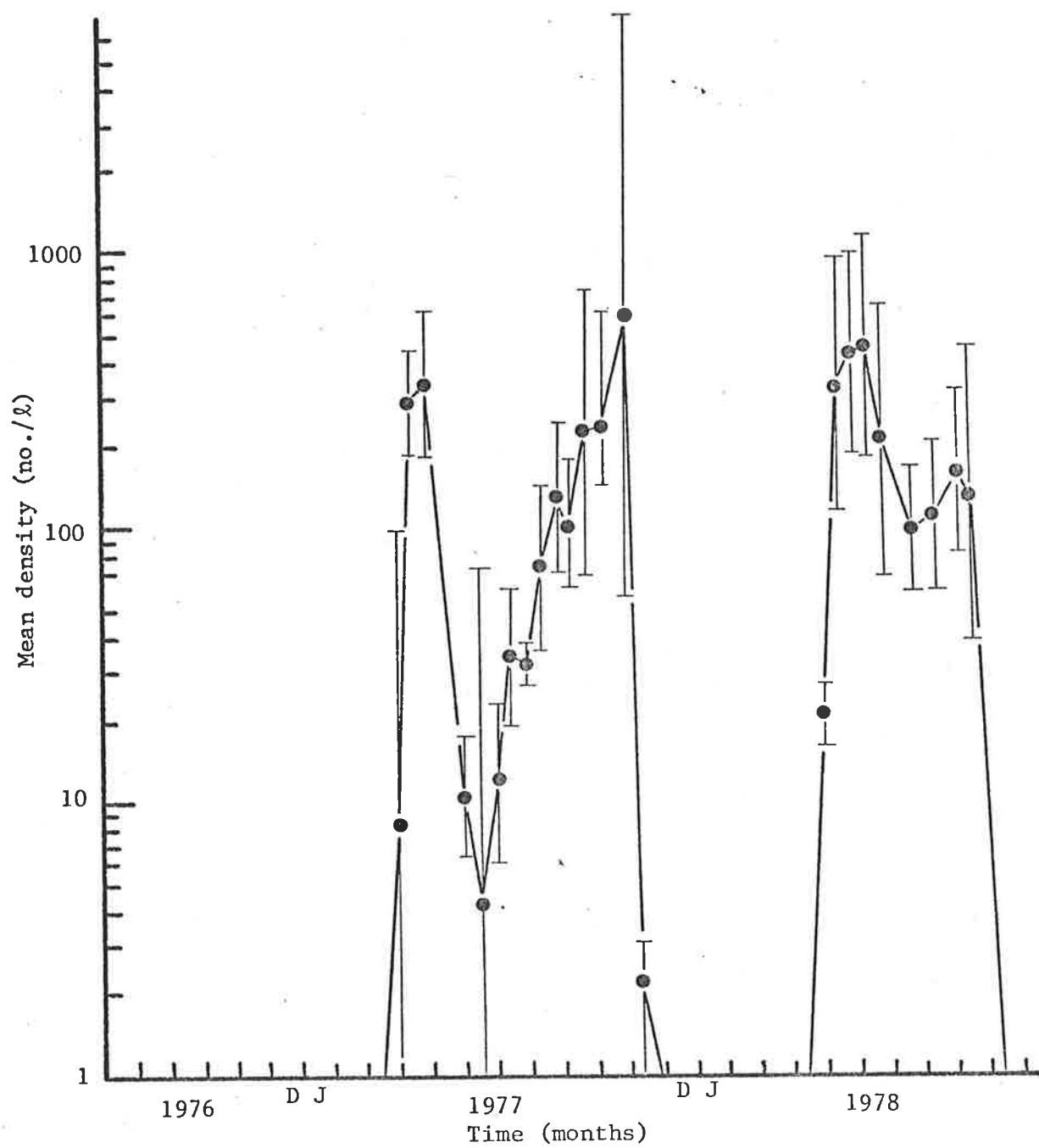


FIGURE 4.6 Mean population density of *D. carinata* (plus 95% confidence limits) in pond 2.

samples from mid-January to mid-February 1977. A rapid increase in mean density occurred during late February and early March 1977; population peaks ($>1000/1$) occurred in mid-March and again in late April 1977. Mean population density declined rapidly during May 1977. *D. carinata* was not recorded from June 1977 until late March 1978. Mean population density increased during early April 1978 and peaked in late April and again in early June 1978. Although mean density declined from June to August confidence limits were wide and overlapped. A secondary peak in mean density occurred in late August 1978; this was followed by a rapid decline and *D. carinata* was not recorded in mid October.

D. carinata was not recorded in pond 2 until May 1977 (Fig. 4.6). Mean density increased rapidly during April 1977, and peaked briefly ($333/1$) in late April. A significant decline occurred during May and June 1977. Thereafter mean density gradually increased, reaching a second peak ($590/1$) in late October 1977. Mean density declined rapidly during November. *D. carinata* was not recorded from early December 1977, until late April 1978. Mean density increased rapidly during April and May 1978 and peaked ($447/1$) in early June. Mean density declined during July and although a secondary, smaller peak occurred in late August confidence limits overlapped. Mean density declined rapidly thereafter and *D. carinata* was not recorded in mid October. Although population cycles were similar in both ponds during 1978, events differed during 1977. Onset of the 1977 *D. carinata* bloom occurred in pond 1 earlier than in pond 2 but the species was present for several months longer in pond 2. Maximum densities were higher in pond 1 than in pond 2. Highest mean densities occurred in both ponds in autumn and early spring and *D. carinata* was generally present throughout the winter.

Seasonal variation in mean population density (plus 95%

confidence limits) of *S. exspinosus* in the Gumeracha ponds is shown in Figures 4.7 and 4.8. *S. exspinosus* was first recorded in pond 1 in late August 1976 (Fig. 4.7). Mean density increased steadily during November and December 1976 and peaked (521/l) in mid-January 1977. A significant decline occurred during early March 1977 and mean density remained low (<10/l) until late June. A second population increase occurred during June and July 1977; although mean density was highest in late December 1977, confidence limits were wide and overlapped from July. Mean density declined during January 1978; density increased briefly during March but *S. exspinosus* was not recorded thereafter. Thus, *S. exspinosus* was present in pond 1 throughout 1977, but highest mean densities occurred during mid-summer. Although *S. exspinosus* was present in pond 2 (Fig. 4.8) at the commencement of sampling mean density declined during December 1976 and January 1977. *S. exspinosus* was not recorded in pond 2 after February 1977 apart from a small number of animals taken on 27 July 1977. Thus, in contrast to pond 1, *S. exspinosus* was rare in pond 2 and constituted a minor component of the zooplankton community in that pond.

Seasonal variation in mean population density (plus 95% confidence limits) of *M. hirsuticornis* in the Gumeracha ponds is shown in Figures 4.9 and 4.10. *M. hirsuticornis* was recorded only rarely in pond 1 (Fig. 4.9) until July 1977. From July until December 1977 this species underwent a series of marked density fluctuations with maxima in September, November, and December 1977. Confidence limits were extremely wide but significant decreases occurred in early October and early December 1977. Mean density declined during January 1978 and *M. hirsuticornis* was not recorded in pond 1 after that time.

M. hirsuticornis was present in pond 2 at the commencement of sampling (Fig. 4.10) but mean density declined during January 1977. The species was not recorded in pond 2 from February to May 1977. Mean

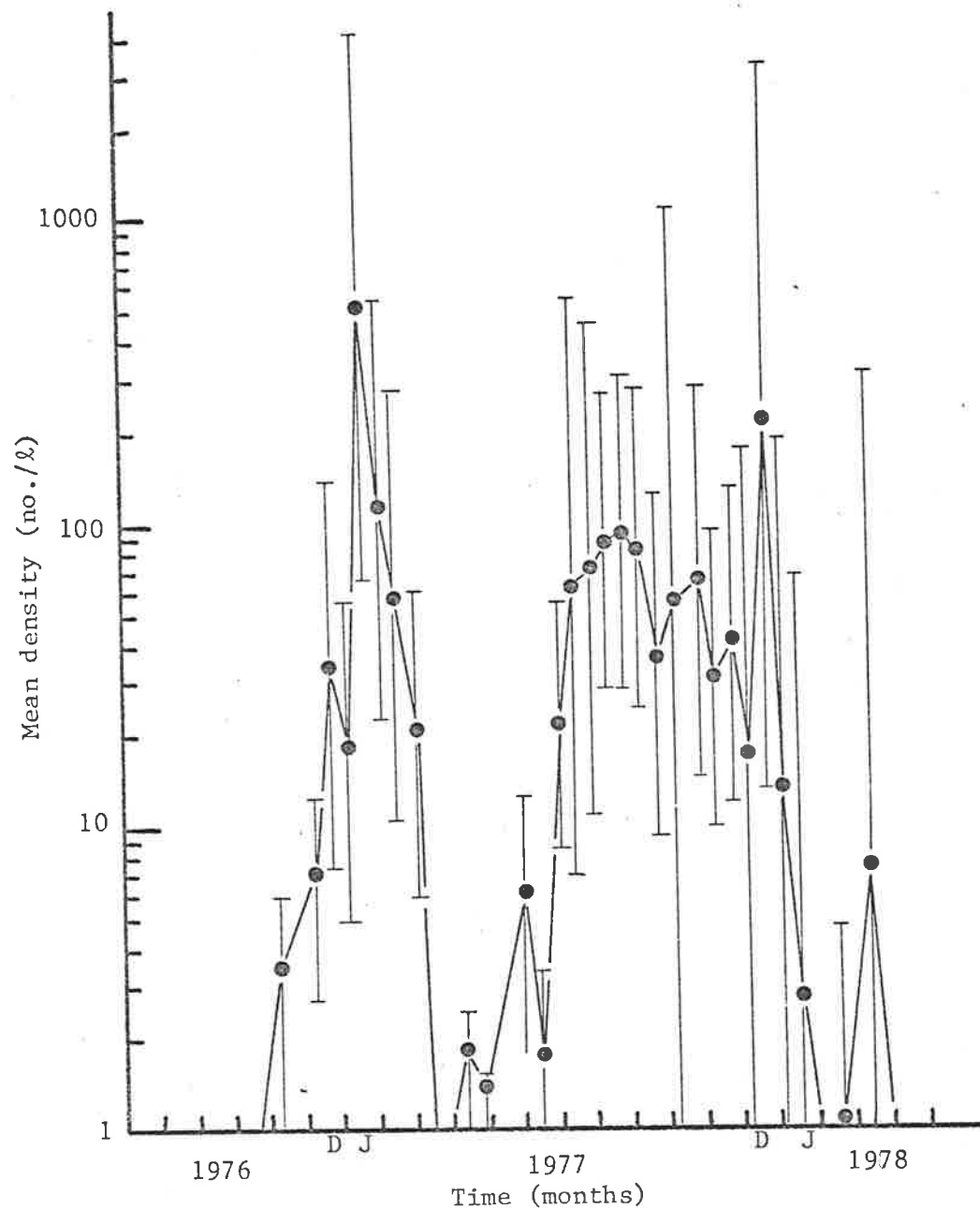


FIGURE 4.7 Mean population density of *S. exspinosus* (plus 95% confidence limits) in pond 1.

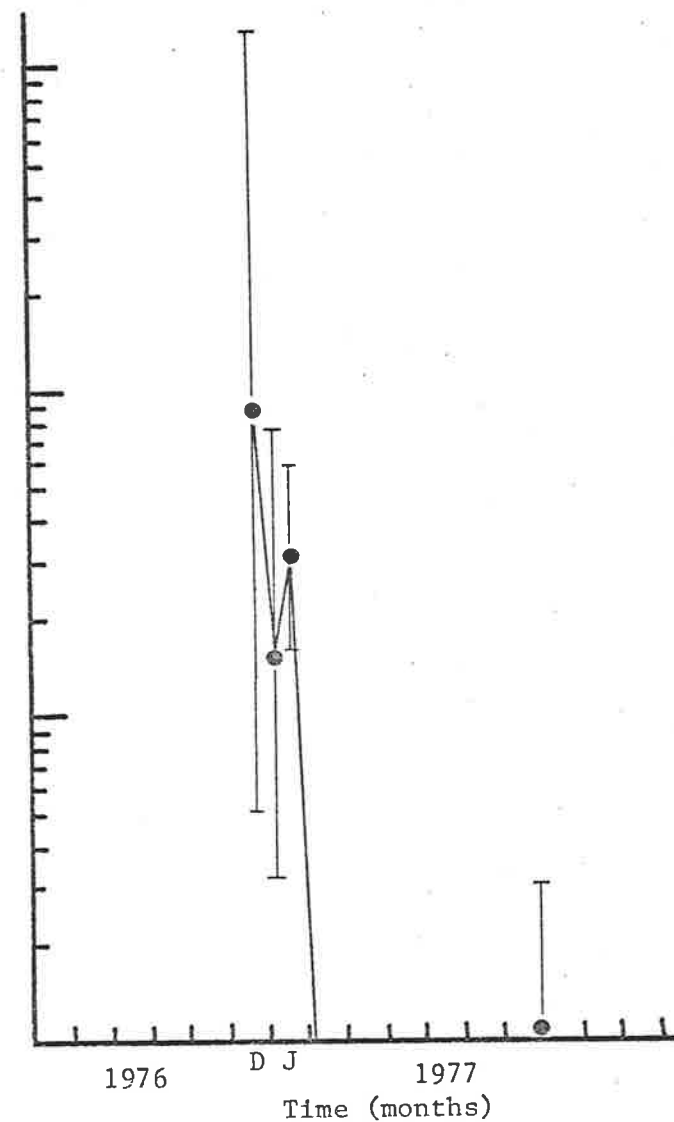


FIGURE 4.8 Mean population density of *S. exspinosus* (plus 95% confidence limits) in pond 2.

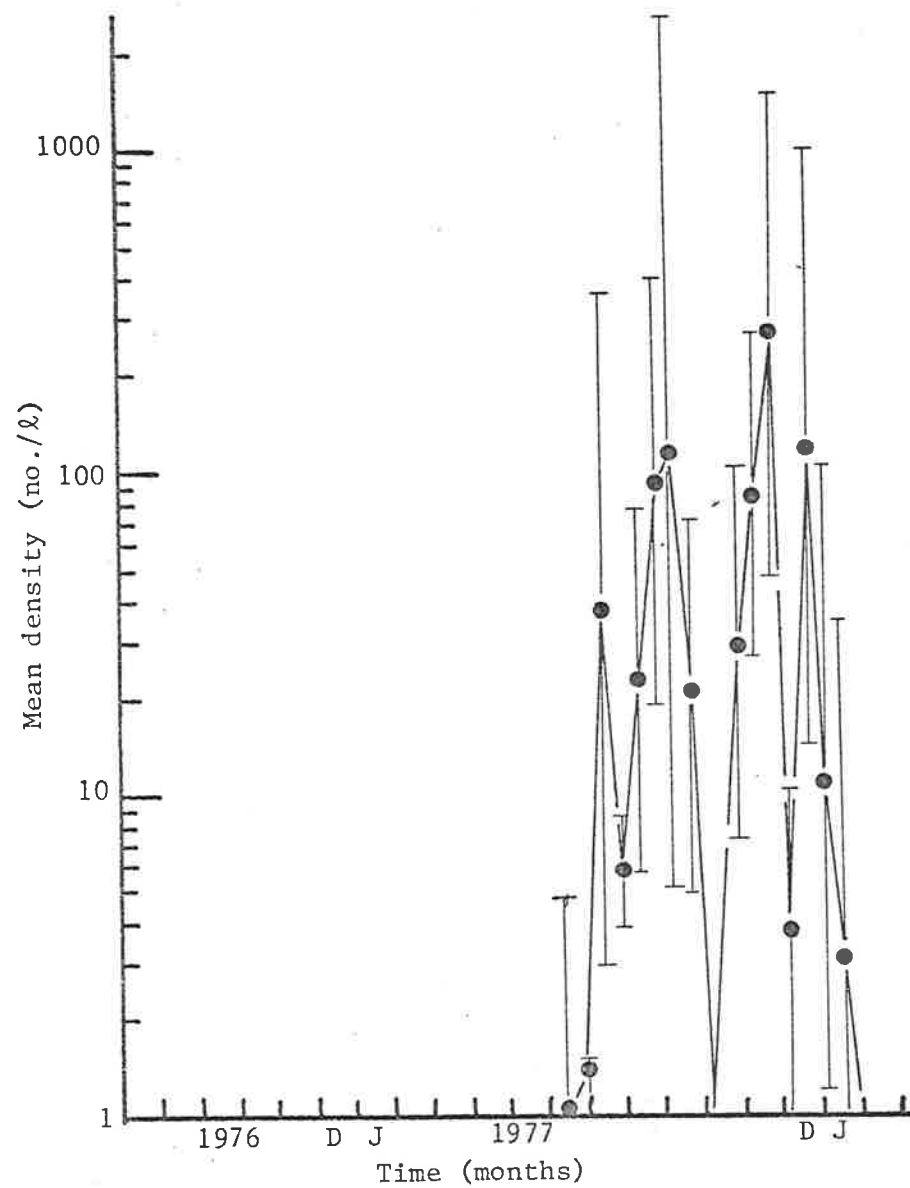


FIGURE 4.9 Mean population density of *M. hirsuticornis* (plus 95% confidence limits) in pond 1.

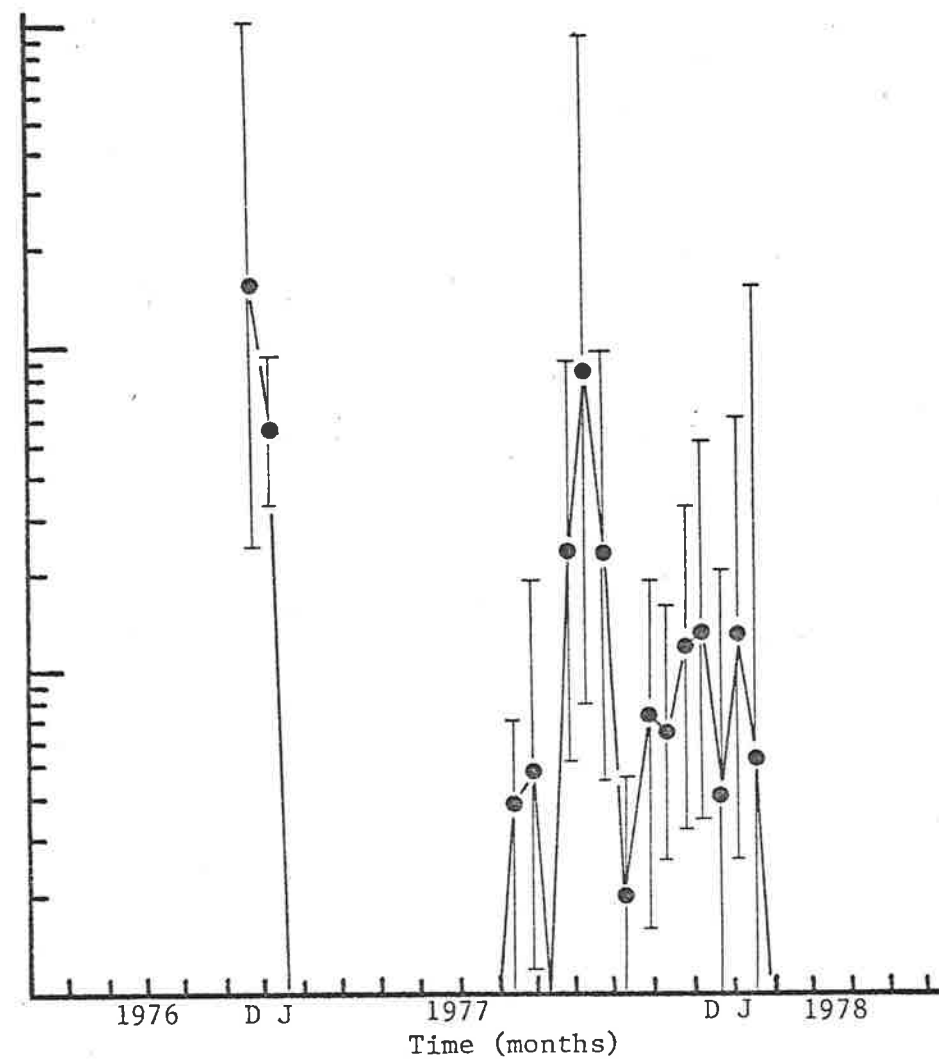


FIGURE 4.10 Mean population density of *M. hirsuticornis* (plus 95% confidence limits) in pond 2.

density increased during July and August 1977 and reached a peak (85/1) in early September 1977. A significant decrease in mean density occurred in early October and although mean density increased through November and December 1977 confidence limits were very wide and overlapped. Mean density declined during January 1978 and *M. hirsuticornis* was not recorded in pond 2 after that time. Mean density was generally higher in pond 1 than in pond 2; population cycles in both ponds during the latter half of 1977 appeared to be synchronized. Wide confidence limits for all mean density values may indicate that the tube sampler was not adequate for a quantitative study of this species.

Variation in the percentage of ovigerous and ehippial females in samples of *M. hirsuticornis* from the Gumerachaponds is shown in Figure 4.11. The percentage of ovigerous females fluctuated widely (5-80%) in both ponds. An inverse relationship appeared to exist between population density and the percentage of ovigerous females in both ponds; percentage of ovigerous females was highest when population density was low and declined as density increased. Thus peaks in percentage of ovigerous females occurred prior to population increases. Ehippial females were rare in both ponds; in pond 1 the percentage of ehippial females reached a maximum of 10% just prior to the decline of the population.

Seasonal variation in mean population density (plus 95% confidence limits) of *M. leuckarti* in the Gumeracha ponds is shown in Figure 4.12 and 4.13. *M. leuckarti* was present in pond 1 throughout the study (Fig. 4.12). Mean population density increased from November 1976 until January 1977 and peaked from January until February 1977. Confidence limits overlapped during the latter period. A significant decline in mean density occurred during March 1977. Although mean density increased gradually from March until December 1977 confidence limits overlapped during that period. Mean density reached a peak

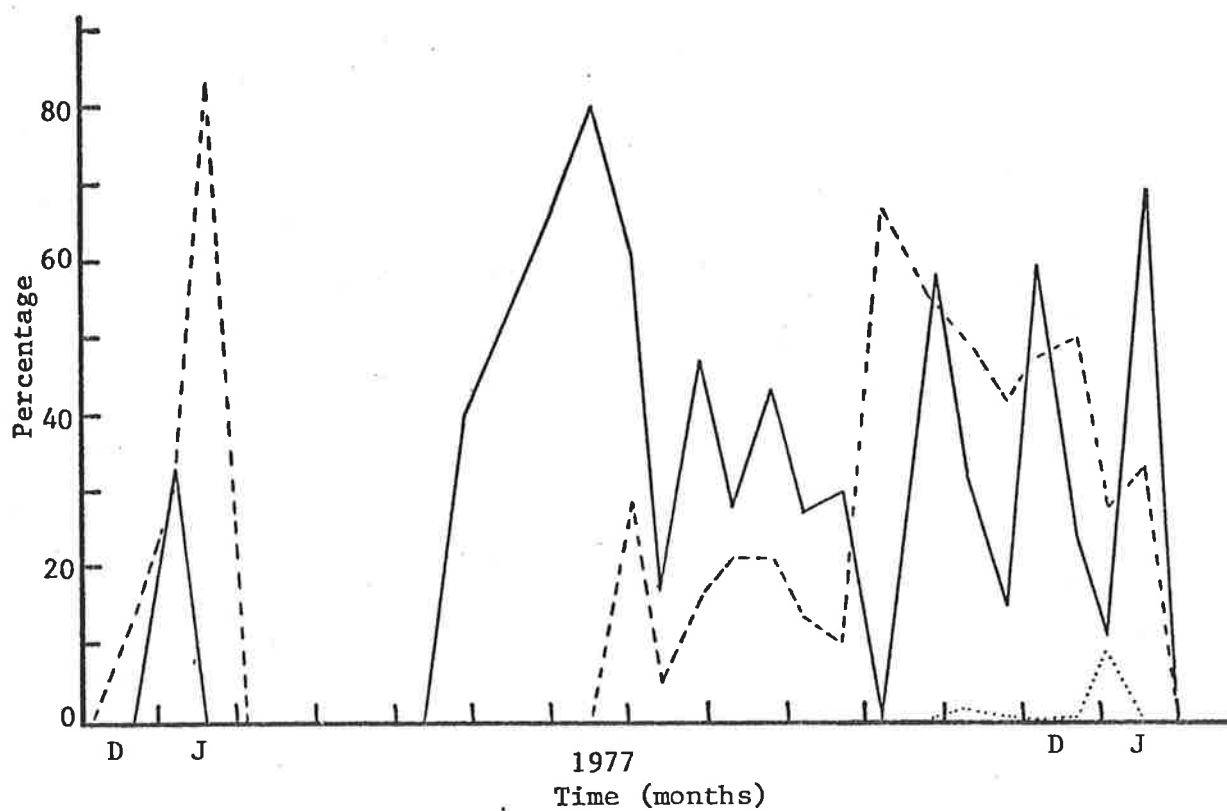


FIGURE 4.11 Percentage of the total number of female *M. hirsuticornis* carrying eggs in pond 1 (—) and pond 2 (---), and carrying ephippia in pond 1 (.....).

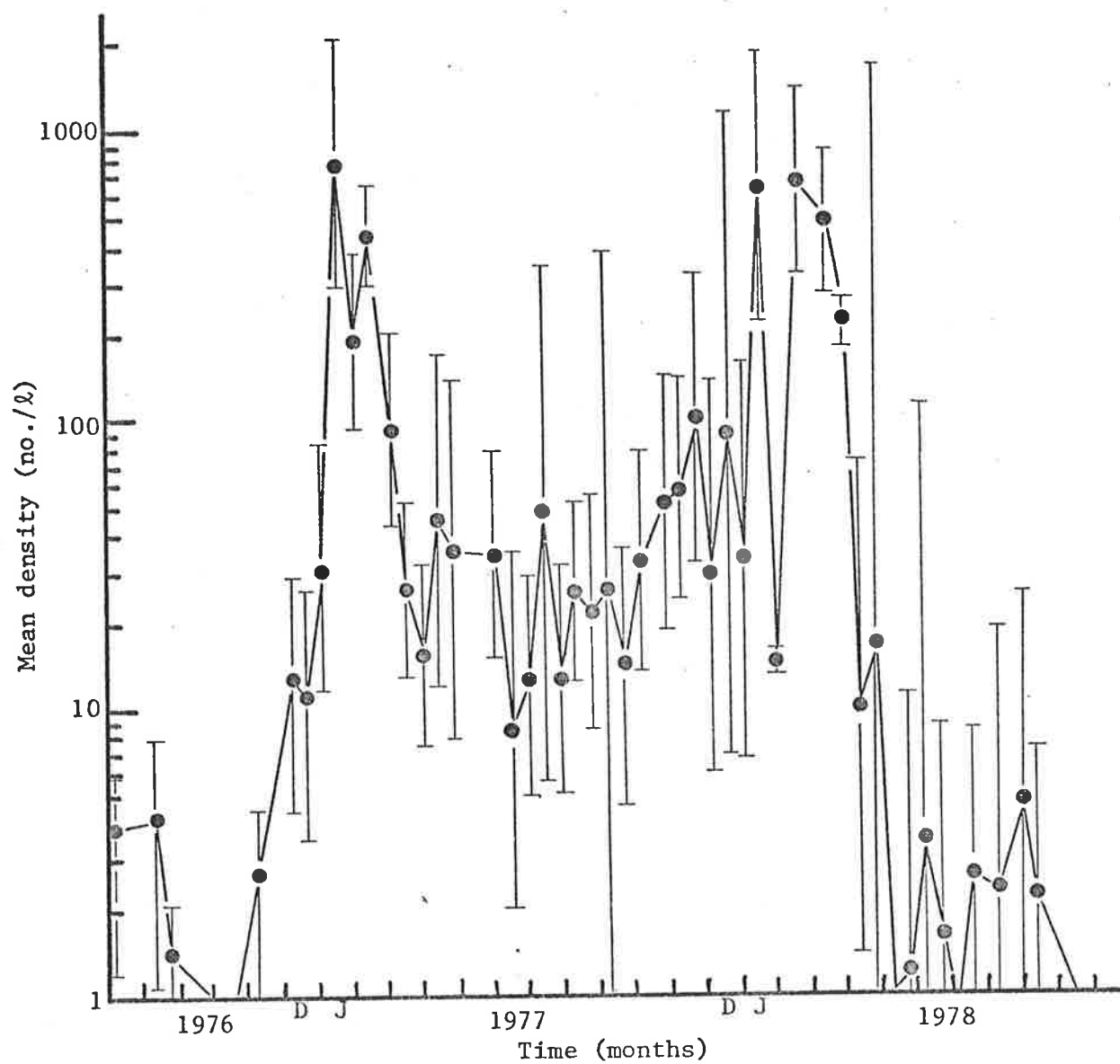


FIGURE 4.12 Mean population density of *M. leuckarti* (plus 95% confidence limits) in pond 1.

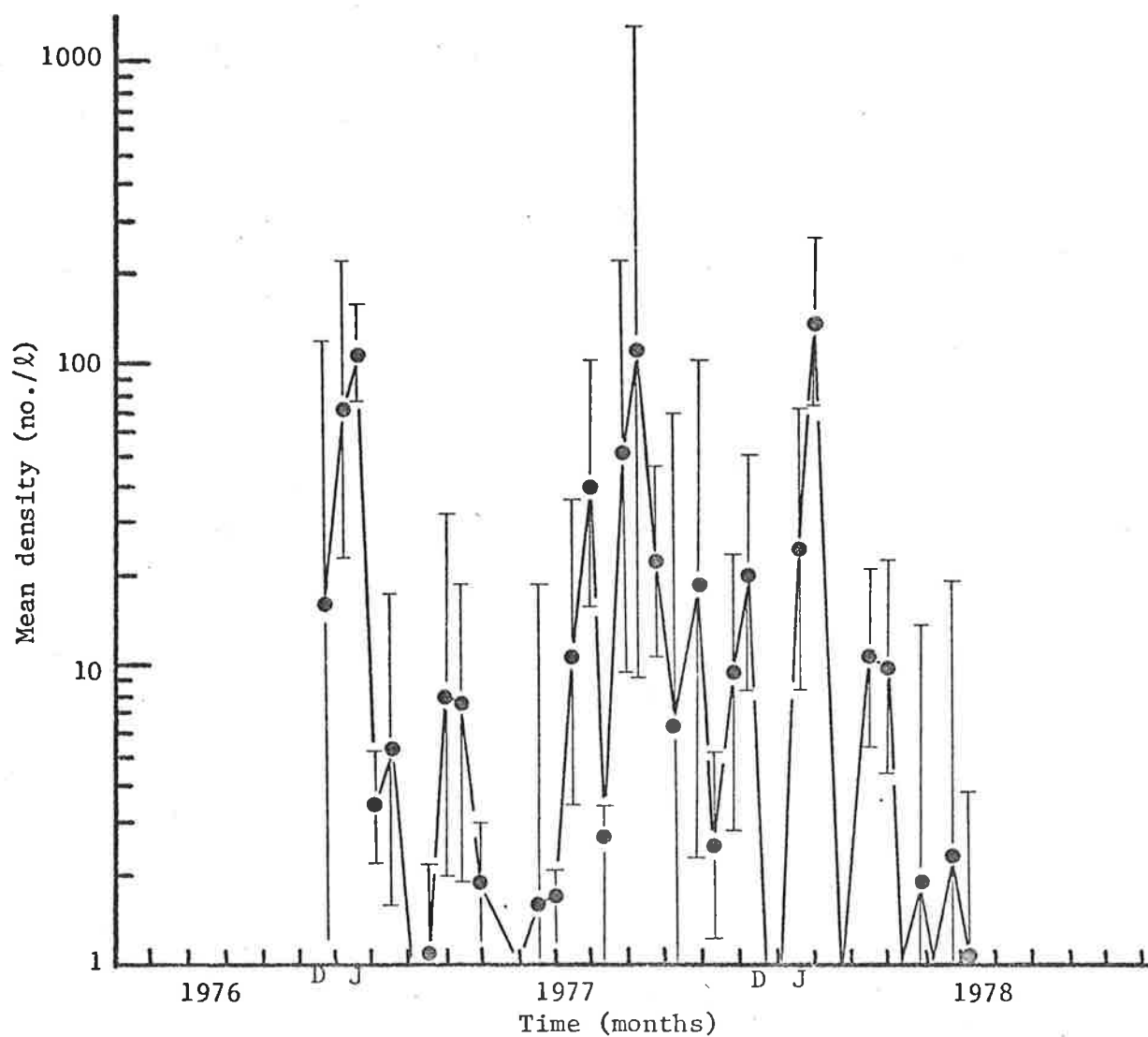


FIGURE 4.13 Mean population density of *M. leuckarti* (plus 95% confidence limits) in pond 2.

during mid-January 1978 (616/1) but this was followed by a rapid, significant decline at the end of that month. A significant increase occurred again during mid-February 1978 (653/1). Thereafter, mean density declined during March and April 1978. Despite considerable fluctuation mean density remained low ($<10/1$) until September 1978. *M. leuckarti* was not recorded in samples from pond 1 on the final sampling date in October 1978. Although *M. leuckarti* was present in pond 1 throughout the year density maxima occurred during summer and mean density was probably fairly constant (20-40/1) during the winter.

Mean density of *M. leuckarti* fluctuated widely and somewhat erratically in pond 2 (Fig. 4.13). As in pond 1 a peak in mean density (109/1) occurred during January 1977. This was followed by a significant decline in February and early March. A small increase in mean density occurred in late March-April 1977. Mean density again declined during late May. Thereafter, significant increases in mean density occurred during late July, early September (peak at 112/1), and early December 1977. A peak in mean density occurred in late January 1978 (137/1). This was followed by a significant decline in late February and a significant, but small, increase in March 1978. Mean density fluctuated at very low levels ($<10/1$) until early June 1978. *M. leuckarti* was not recorded in pond 2 after that time. Density of *M. leuckarti* was lower in pond 2 than in pond 1; although peaks occurred during summer in pond 2 a late winter peak also occurred in that pond.

Variation in the percentage of ovigerous females in samples of *M. leuckarti* from the Gumeracha ponds is shown in Figure 4.14. Ovigerous females were present in pond 1 from December 1976 until the end of January 1978. Four peaks occurred in the percentage of ovigerous females during that period: late December 1976 (38%), early June 1977 (39%), mid July (46%), and mid-December (23%). The peaks in December 1976 and 1977 preceded a population increase by about one month. The mid-year peaks

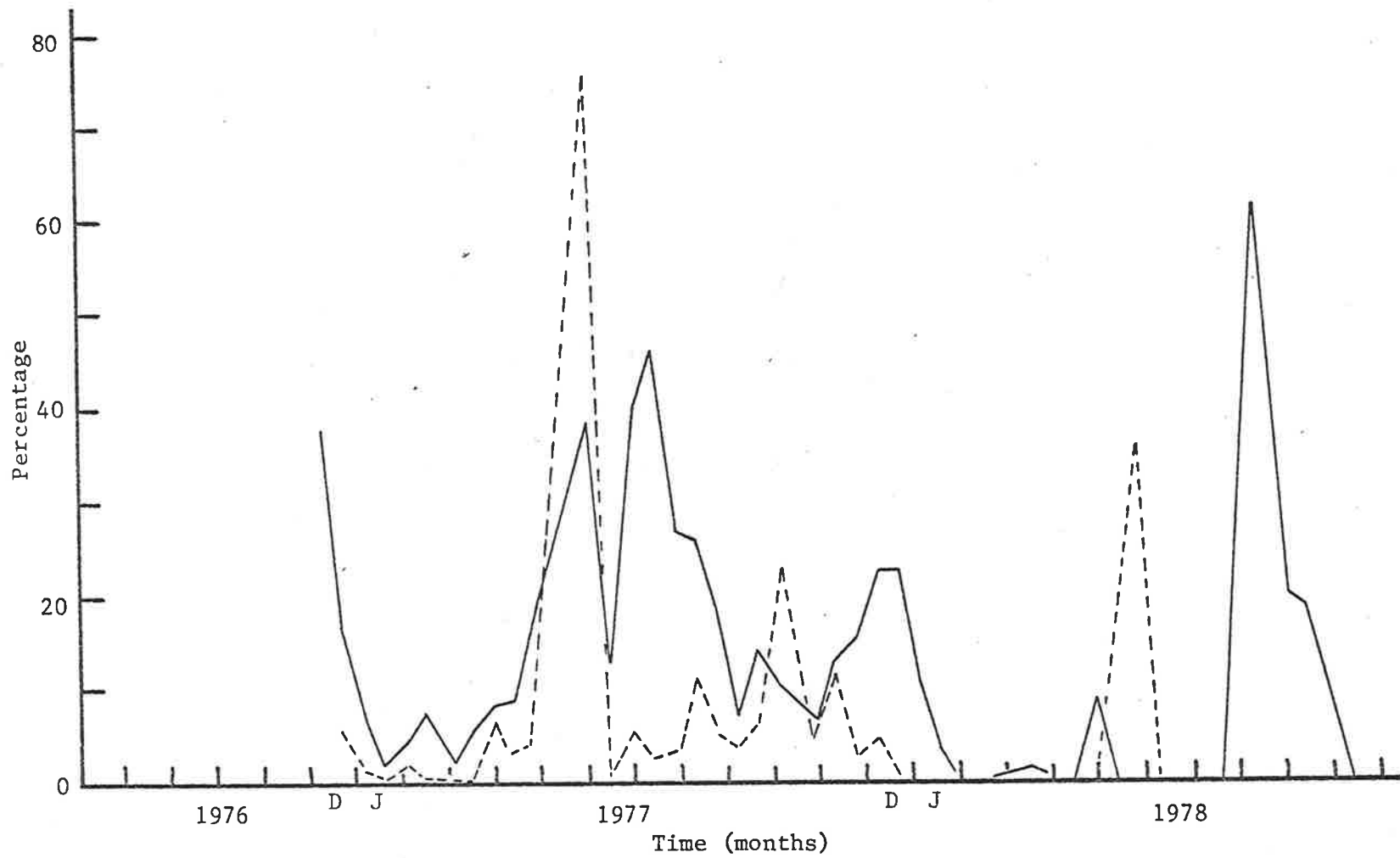


FIGURE 4.14 Percentage of the total number of *M. leuckarti* carrying eggs in pond 1 (—) and pond 2 (---).

in 1977 were not followed by an increase in mean density. Ovigerous females appeared briefly in March and late April 1978. The peak in early August 1978 (62%) may be an artifact as mean density was very low. A minor increase in mean density, probably not significant, followed the August peak. A series of peaks in the percentage of ovigerous females occurred in pond 2 during 1977. Peaks in late May (75%), early August (11%), early October (23%), and early November (12%) were followed by increases in mean density. The peak in late May 1978 (35%) was probably an artifact resulting from very low sample numbers.

Seasonal variation in mean population density (plus 95% confidence limits of *B. triarticulata* in the Gumeracha ponds is shown in Figure 4.15 and 4.16. *B. triarticulata* occurred in pond 1 from January until the end of March 1977 and then briefly in September 1977 (Fig. 4.15). Mean density was very low (maximum of 5/1) and *B. triarticulata* was a minor component of the pond 1 zooplankton community. *B. triarticulata* was present in pond 2 throughout 1977 except for June of that year (Fig. 4.16). Peaks in mean density occurred in April (7.6/1) and November (50/1) 1977. Mean density declined rapidly during December 1977 and *B. triarticulata* was not recorded from pond 2 after that time. Mean density of *B. triarticulata* in pond 2 was similar to pond 1 except for the peak in November 1977.

Variation in the percentage of ovigerous females in samples of *B. triarticulata* from the Gumeracha ponds is shown in Figure 4.17. In both ponds peaks in the percentage of ovigerous females coincided with peaks in mean density. Only in pond 2 during late October 1977 was an increase in percentage of ovigerous females followed by an increase in mean density.

In summary, *D. carinata* attained the highest mean population densities in the Gumeracha ponds, although *M. leuckarti* was present for longer periods of time. *D. carinata* and *S. exspinosus* were the dominant

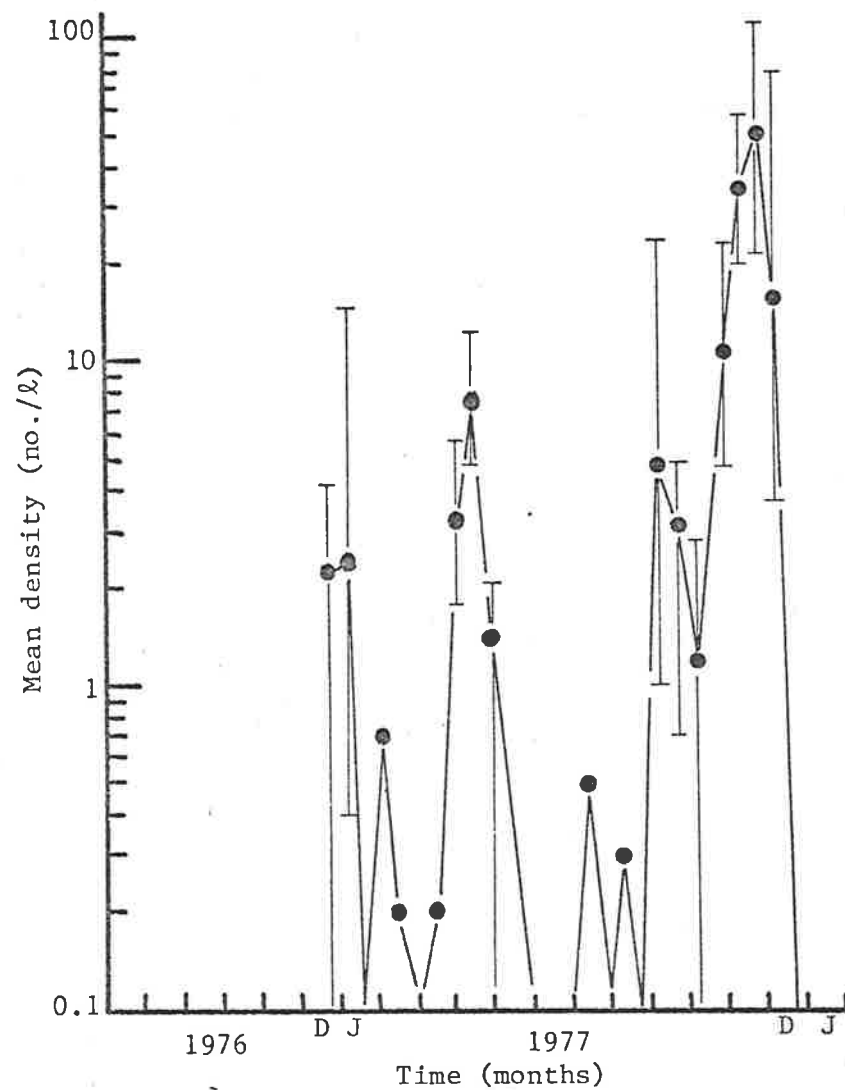


FIGURE 4.15 Mean population density of *B. triarticulata* (plus 95% confidence limits) in pond 2.

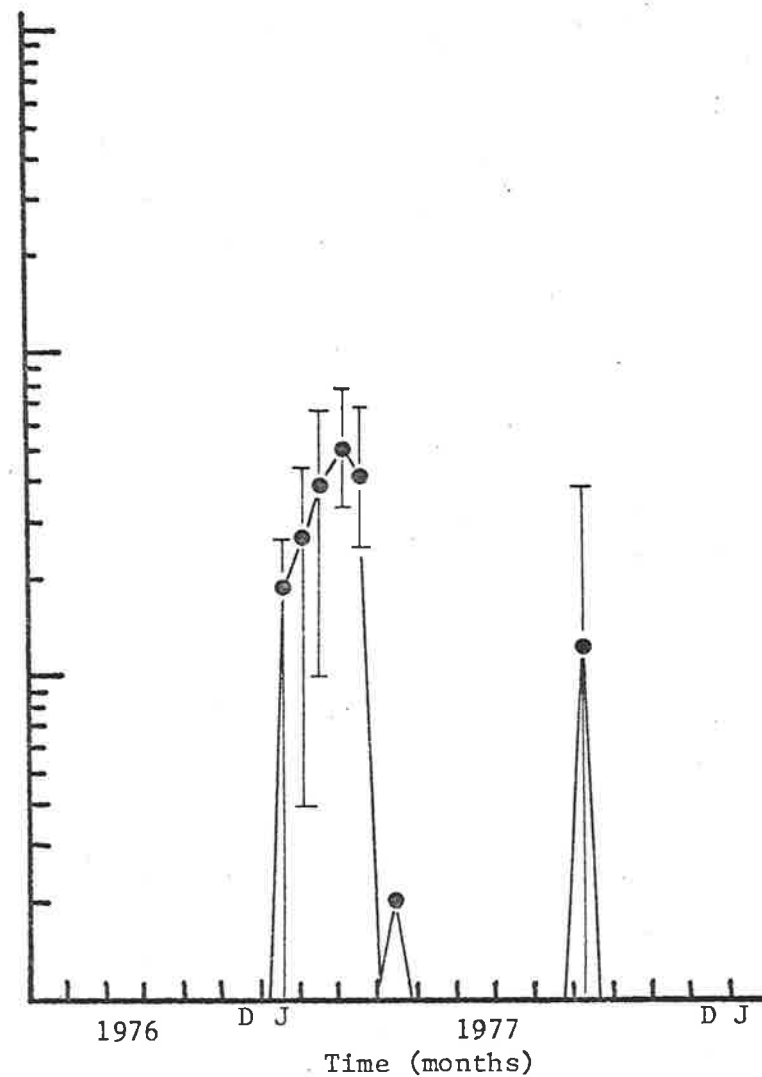


FIGURE 4.16 Mean population density of *B. triarticulata* (plus 95% confidence limits) in pond 1.

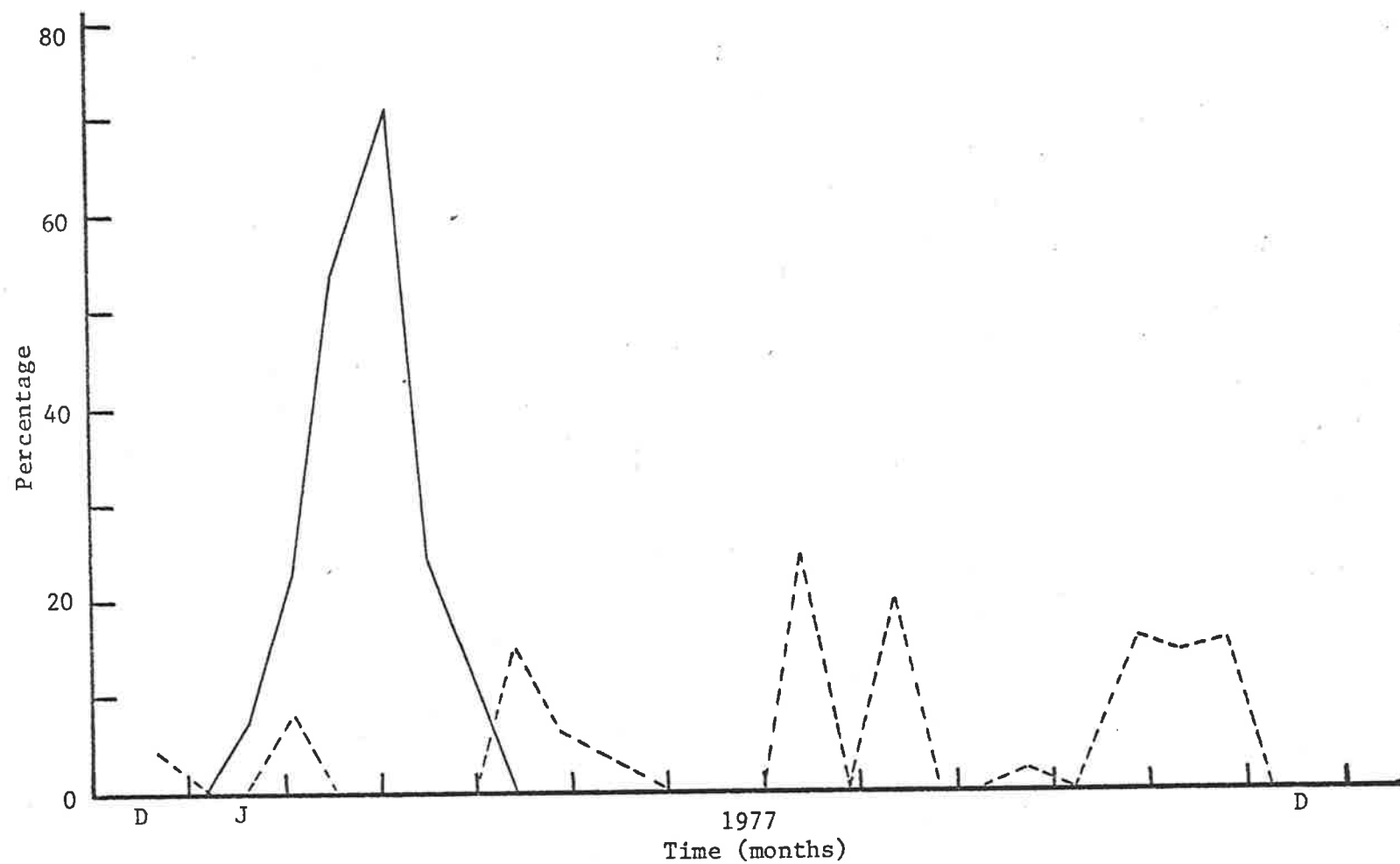


FIGURE 4.17 Percentage of the total number of *B. triarticulata* carrying eggs in pond 1 (—) and pond 2 (---).

herbivores in pond 1 and *D. carinata* and *B. triarticulata* were the dominant herbivores in pond 2. In the latter case, mean density of *B. triarticulata* was very low. Population cycles of a particular species were not necessarily synchronous in both ponds. Although pond 2 received the effluent from pond 1, zooplankton populations in each pond were independent to some measure. In fact, observations made during a bloom of *D. carinata* in pond 1 suggested that animals avoided the area immediately surrounding the outflow pipe.

Environmental factors. The entomostracans that occur in WSPs are obviously capable of adaptation to extremely high nutrient and organic levels. It seemed unlikely, therefore, that seasonal abundance would be affected by influent nitrogen, phosphorus, or BOD levels. Physico-chemical parameters that underwent the most pronounced seasonal variations in the Gumeracha ponds, and which might be expected to affect zooplankton populations, were water temperature, dissolved oxygen concentration, and pH. The influence of variation in these parameters upon the zooplankton cycles observed in the Gumeracha ponds was investigated via individual linear regressions of log mean zooplankton density on each parameter. Semilog plots of mean density on water temperature, dissolved oxygen, and pH for the major zooplankters in the Gumeracha ponds during 1977 and 1978 are presented in Appendix 2. Regression lines accounting for over 40% of the variance in mean density are also included. The regression coefficients for each of these plots are summarized in Table 4.4.

The relative importance of variation in water temperature, dissolved oxygen concentration, and pH in accounting for variation in mean density of the major zooplankters was as follows:

D. carinata. Best fit for the regression of log mean density on water temperature for this species was obtained if the points above and below 12°C in pond 1 and 13°C in pond 2 were treated independently. r^2 values for the pooled data were 0.14 in pond 1, 1978 (all 1977 values were above 12°C), 0.00 in pond 2, 1977, and 0.01 in pond 2, 1978. Highest mean

Table 4.4

Regression of log population density (no./l) of major zooplankton species in the Gumeracha ponds during 1977 and 1978 on water temperature ($^{\circ}\text{C}$)*; dissolved oxygen concentration (mg/l)* and pH**. a, intercept; b, slope of regression line; r^2 , goodness of fit (or amount of variance accounted for by variation in temperature, dissolved oxygen, and pH). (n.p. = not present).

	Pond 1						Pond 2					
	a	1977 b	r^2	a	1978 b	r^2	a	1977 b	r^2	a	1978 b	r^2
Temperature:	($<12^{\circ}\text{C}$)						($<13^{\circ}\text{C}$)					
<i>Daphnia carinata</i>	-	-	-	0.91	0.15	0.30	-2.08	0.35	0.95	0.93	0.13	0.65
" "	($>12^{\circ}\text{C}$)						($>13^{\circ}\text{C}$)					
	6.98	-0.27	0.66	8.37	-0.45	0.76	8.89	-0.42	0.42	-	-	-
<i>Simocephalus exspinosus</i>	1.04	0.02	0.01	-3.47	0.20	0.23	-1.67	0.13	0.83	n.p.		
<i>Mesocyclops leuckarti</i>	0.43	0.08	0.50	-1.29	0.17	0.64	0.73	0.01	0.00	-0.46	0.07	0.17
<i>Boeckella triarticulata</i>	-1.46	0.08	0.20	n.p.			-0.50	0.04	0.04	n.p.		
<i>Macrothrix hirsuticornis</i>	0.88	-0.01	0.00	n.p.			-0.68	0.09	0.26	n.p.		
Dissolved Oxygen:												
<i>D. carinata</i>	1.10	0.11	0.27	3.16	-0.15	0.70	4.02	-0.22	0.28	2.93	-0.11	0.82
<i>S. exspinosus</i>	1.76	-0.05	0.02	2.14	-0.12	0.49	3.38	-0.33	0.66	n.p.		
<i>M. leuckarti</i>	1.61	-0.01	0.00	0.02	0.15	0.46	1.14	-0.04	0.02	0.96	-0.02	0.02
<i>B. triarticulata</i>	1.60	-0.19	0.44	n.p.			-0.44	0.05	0.02	n.p.		
<i>M. hirsuticornis</i>	0.70	0.02	0.00	n.p.			-2.06	0.22	0.29	n.p.		
pH:												
<i>D. carinata</i>	2.80	-0.05	0.12	6.45	-0.56	0.70	1.68	0.01	0.00	-5.79	1.06	0.57
<i>S. exspinosus</i>	4.43	-0.41	0.30	-	-	-	-4.65	0.55	0.74	n.p.		
<i>M. leuckarti</i>	1.30	0.03	0.01	-4.17	0.67	0.70	1.33	-0.06	0.01	1.01	-0.04	0.01
<i>B. triarticulata</i>	6.01	0.73	0.66	n.p.			-0.30	0.05	0.00	n.p.		
<i>M. hirsuticornis</i>	3.70	-0.37	0.14	n.p.			-2.02	0.28	0.12	n.p.		

* Averaged over depth

** pH of pond taken as equivalent to pH of effluent.

densities occurred in the range 11-15°C. A positive relationship between log mean density and water temperature was found below 12-13°C while a negative relationship was found above 12-13°C. Temperature variation accounted for the highest amount of variance in log mean density in both ponds during 1977. In both ponds during 1978, variation in temperature, dissolved oxygen concentration, and pH all accounted for high amounts of variance in log mean density. Negative relationships were found between log mean density and both dissolved oxygen concentration and pH. Although *D. carinata* was recorded up to pH 10.5 at Gumeracha, only one record occurred above pH 9.5. Significant positive correlations occurred between water temperature and dissolved oxygen concentration in pond 1 ($\rho = 0.68$, $p < .01$) and pond 2 ($\rho = 0.50$, $p < .05$) and between water temperature and pH in pond 1 ($\rho = 0.83$, $p < .05$) and pond 2 ($\rho = 0.85$, $p < .01$) during 1978. These correlations explained the importance of dissolved oxygen and pH during 1978. Temperature appeared to be the most important parameter affecting *D. carinata*; this species generally occurred at lower temperatures, dissolved oxygen concentration, and pH.

S. exspinosus. Variation in temperature and dissolved oxygen concentration were unimportant in accounting for variance in log mean density of this species in pond 1 during 1977. Variation in pH accounted for a low amount of the variance in log mean density in pond 1 during 1977. Variation in dissolved oxygen concentration accounted for the highest amount of variance in log mean density in pond 1 during 1978. However, the number of data points was low (3) and they fell over a restricted range of dissolved oxygen concentrations. Variation in temperature, dissolved oxygen concentration and pH all accounted for high amounts of variance in log mean density in pond 2 during 1977. Temperature and pH were significantly correlated ($\rho = 0.59$, $p < .01$) in pond 2 during 1977. Although *S. exspinosus* occurred over a wide

temperature range, highest densities occurred in summer around temperatures of 22°C.

M. hirsuticornis. Variation in temperature and dissolved oxygen concentration accounted for none of the variance in log mean density in pond 1 during 1977. Variation in pH accounted for a very low amount of the variance in log mean density. *M. hirsuticornis* was recorded up to pH 11.2 at Gumeracha, with several records above pH 9.5. Variation in temperature and dissolved oxygen accounted for similar, low amounts of variance in log mean density in pond 2 during 1977. Weak positive relationships were found between log mean density and both temperature and dissolved oxygen concentration. *M. hirsuticornis* occurred over a wide temperature, oxygen, and pH range.

M. leuckarti. Variation in temperature accounted for the highest amount of the variance in log mean density in pond 1 during 1977. A positive relationship was found between temperature and log mean density. Highest mean densities occurred over the range 18-24°C, although *M. leuckarti* was present throughout the year. Variation in temperature, dissolved oxygen and pH all accounted for high amounts of the variance in log mean density in pond 1 during 1978. It has been shown above that dissolved oxygen and pH were significantly correlated with temperature during 1978. *M. leuckarti* occurred up to pH 11.1 at Gumeracha with several records above pH 9.5. Temperature, dissolved oxygen, and pH were all unimportant in accounting for the variance in log mean density in pond 2 during 1977. Variation in temperature accounted for the highest amount of variance in log mean density in pond 2 during 1978. *M. leuckarti* occurred over a wide temperature, dissolved oxygen, and pH range although blooms occurred in summer.

B. triarticulata. Variation in pH accounted for the highest amount of variance in log mean density in pond 1 during 1977. A negative relationship was found between pH and log mean density. Although

B. triarticulata was recorded up to pH 11.1 at Gumeracha, few records occurred above pH 9.5. Temperature, dissolved oxygen concentration, and pH were all unimportant in accounting for variance in log mean density in pond 2 during 1977. *B. triarticulata* occurred over a wide temperature range but appeared to occur at lower pH.

Other factors which may be important in regulating zooplankton populations are food level and interactions with other organisms (predation and competition). *S. exspinosus*, although a littoral dweller, is not a sediment feeder but typically attaches dorsally to the substrate and filters suspended material from the water (Cannon in Horton et al., 1979). It is highly probable that *M. hirsuticornis* is detritivorous (c.f. Fryer, 1974). No data are available on the diet of *B. triarticulata* but it is likely that this calanoid copepod is an obligate filter feeder (c.f. McNaught, 1975). While the nauplii and early copepodite stages of *M. leuckarti* are herbivorous (Gophen, 1977), late copepodids and adults are carnivorous and include cladocerans, rotifers, and the young of other copepods in their diet (Gophen, 1977; McQueen, 1969; Fryer, 1957). The diet of *D. carinata* in the Gumeracha ponds was investigated during this study.

D. carinata was collected from the ponds and individuals washed with distilled water. The distal half of the intestine (plus postabdomen) was dissected out and gut contents ejected onto a microscope slide. Animals were collected from pond 1 on 30 March 1977 (chlorophyll a concentration 10 mg/m^3) and pond 2 on 10 August 1977 (chlorophyll a concentration 24 mg/m^3). On both occasions gut contents included *Scenedesmus* cell fragments, diatoms, and large amounts of detritus. Gut contents of animals collected from pond 2 on 29 March 1978 (chlorophyll a concentration 555 mg/m^3) included mainly fragments of *S. opoliensis*, although some cells were still intact, but very low proportions of diatoms (*Navicula* and *Nitzschia*) and detritus. It thus appeared that *D. carinata*

was a filter feeder during phytoplankton blooms but ingested sediment when phytoplankton were not abundant.

Live animals plus water from pond 2 collected on 29 March 1978 were placed in a laboratory tank. On 26 April 1978 water in the tank was observed to be quite clear. Microscopic examination of water samples from the tank revealed the presence of a small number of ciliate and flagellated protozoa but no *Scenedesmus*. Surface sediment from the tank bottom consisted of both intact and fragmented *Scenedesmus* cells, diatoms, and detritus. Gut contents of *D. carinata* in the tank at that time (the second generation that had developed since the tank had been set up) consisted of sedimented material as present on the tank bottom. Animals in the tank were observed to periodically sink to the bottom, roll over until horizontal, and then place their ventral carapace margin onto the sediment surface. Animals either remained in the one position (with trunk appendages beating) for up to 2 seconds or moved horizontally across the sediment surface. This behaviour was consistent with gut contents of animals collected from the field during periods of low phytoplankton abundance. *D. carinata* thus appeared to be a "facultative browser" (Horton et al., 1979). That is, *D. carinata* is capable of switching from suspension feeding to foraging on the bottom and ingesting the sediments when the suspended food concentration is low.

Based upon dietary considerations, the following interspecific interactions may have occurred in the Gumeracha ponds. *D. carinata*, *S. exspinosus*, and *B. triarticulata* may have competed for food during periods of phytoplankton presence. After the decline of phytoplankton blooms, *D. carinata* (a facultative browser) might have been expected to be at a competitive advantage over the obligate filter feeders *S. exspinosus* and *B. triarticulata*. In this context, *D. carinata*, *S. exspinosus* and *B. triarticulata* could be expected to exert considerable grazing pressure upon phytoplankton populations at Gumeracha. It was also thought that

M. leuckarti could have preyed upon the juvenile instars of *D. carinata* and *S. exspinosus*.

The nature of interspecific interactions and the effect of zooplankton upon phytoplankton abundance in the Gumeracha ponds was investigated via determination of the correlation between species densities, and between species density and chlorophyll a concentration. Regression analysis was not applicable in studying these relationships as it could not be assumed that the independent variable (mean density) was normally distributed; measurement of mean density also involved a considerable error component. The non-parametric Spearman's rho (ρ) rank correlation coefficient was used. In some cases mean density data included a large number of zero values (that is, a particular organism was absent). These values were retained and treated as tied values. Due to the large number of tied zero values ρ was calculated by applying the formula for Pearson's product moment correlation coefficient to ranked data after Conover (1971).

Chlorophyll a concentration versus zooplankton density. Values of ρ , plus significance level, between chlorophyll a concentration (mg/m^3) and mean population density (number/litre) of the major herbivores in the Gumeracha ponds are presented in Table 4.5.

Significant negative correlations were found between mean density of *D. carinata* and chlorophyll a in both ponds during 1977 and 1978. Chlorophyll a concentration declined in pond 1 during March-April 1978, and in pond 2 during March-April 1977 and April-May 1978 as mean density of *D. carinata* increased. During early 1978 *D. carinata* appeared in pond 2 approximately one month after it was first recorded in pond 1. Chlorophyll a concentration in pond 2 remained higher than in pond 1 during that period. That is, temperature did not appear to be the major factor terminating phytoplankton blooms in the Gumeracha ponds. Phytoplankton blooms developed in both ponds during November 1977 and

Table 4.5

Spearman's ρ (plus level of significance) between chlorophyll a concentration and population density of herbivorous zooplankton and between percentage phaeopigments and density of *D. carinata* in the Gumeracha ponds during 1977 and 1978.

	Pond 1				Pond 2			
	1977		1978		1977		1978	
	ρ	sig. level	ρ	sig. level	ρ	sig. level	ρ	sig. level
chlor. &								
<i>D. carinata</i>	-0.50	5%>p>1%	-0.57	1%>p>.1%	-0.75	p<.1%	-0.82	p<.1%
<i>S. exspinosus</i>	0.42	p>5%	0.33	p>5%	-0.41	p>5%	-	-
<i>B. triarticulata</i>	-0.04	p>5%	-	-	0.07	p>5%	-	-
% phaeo. &								
<i>D. carinata</i>	0.59	1%>p>.1%	0.70	1%>p>.1%	0.36	p>5%	0.88	p<.1%

October 1978 after *D. carinata* standing crops had declined. However, if the absence of grazing pressure had been the major factor triggering phytoplankton blooms the onset of the bloom in pond 1 in late 1977 would have occurred earlier than in pond 2. This was not the case. It has been shown (Chapter 3) that phytoplankton blooms developed above temperatures of 18°C. Although temperature effects may have explained the negative correlation between *D. carinata* density and chlorophyll *a*, high chlorophyll *a* values did occur at temperatures below 18°C and *D. carinata* was present at temperatures above 18°C.

No significant correlation was found between chlorophyll *a* concentration and the mean density of *S. exspinosus* or *B. triarticulata* in pond 1 during 1977 and 1978 or in pond 2 during 1977. Although *B. triarticulata* was present during periods of phytoplankton abundance mean density was very low. The negative ρ for *S. exspinosus* in pond 2 was probably an artifact due to a low number of data values. This species declined soon after sampling commenced and was rare in pond 2 thereafter. The non-significant positive ρ values for *S. exspinosus* in pond 1 may have resulted from temperature effects. Although *S. exspinosus* and *B. triarticulata* would have consumed *Scenedesmus* during phytoplankton blooms, neither species appeared to be very important in reducing phytoplankton standing crop.

The digestion of algal cells by zooplankton results in the formation of phaeopigments. The correlation between mean density of *D. carinata* and the percentage of phaeopigments in the total chlorophyll *a* pool in the Gumeracha ponds has also been presented in Table 4.5. Significant positive correlations were found between mean density of *D. carinata* and the percentage of phaeopigments in pond 1 during 1977 and 1978 and in pond 2 during 1978.

A non-significant positive correlation was

found in pond 2 during 1977. However, chlorophyll degradation is influenced by temperature; phaeopigments are most abundant when water temperature is highest (Glooschenka et al, 1972). The importance of temperature in the Gumeracha ponds was investigated via a linear regression of the percentage of phaeopigments in the total chlorophyll a pool on average water temperature. Variation of water temperature accounted for none of the variance in the percentage of phaeopigments in both ponds during 1977. Variation in water temperature accounted for 78% of the variance in the percentage of phaeopigments in pond 1 during 1978 and 52% of the variance in pond 2 during 1978. However, in both ponds during 1978 a negative relationship between temperature and percentage phaeopigments was found (Fig. 4.18, A and B).

Although this may have resulted from resuspension of senescent cells from the sediments, it has been shown that *D. carinata* was a predominantly cold water form and highest mean densities occurred at lower water temperature.

D. carinata appeared to be the major herbivore in the Gumeracha ponds. Grazing by *D. carinata* reduced phytoplankton standing crops during early autumn, thereby terminating phytoplankton blooms. However, temperature, and not the release from grazing pressure, was the major factor triggering the onset of phytoplankton blooms during late spring. *D. carinata* was a cold water species and, therefore, prevented from limiting phytoplankton on an annual basis by high temperatures.

Interspecific interactions. Values of ρ , plus significance level, between mean density of *D. carinata* and mean density of *S. exspinosus*, *B. triarticulata*, and *M. leuckarti*, and between mean density of *S. exspinosus* and mean density of *M. leuckarti* in the Gumeracha ponds are presented in Table 4.6.

A significant negative correlation was found between mean density of *D. carinata* and mean density of *S. exspinosus* in pond 1

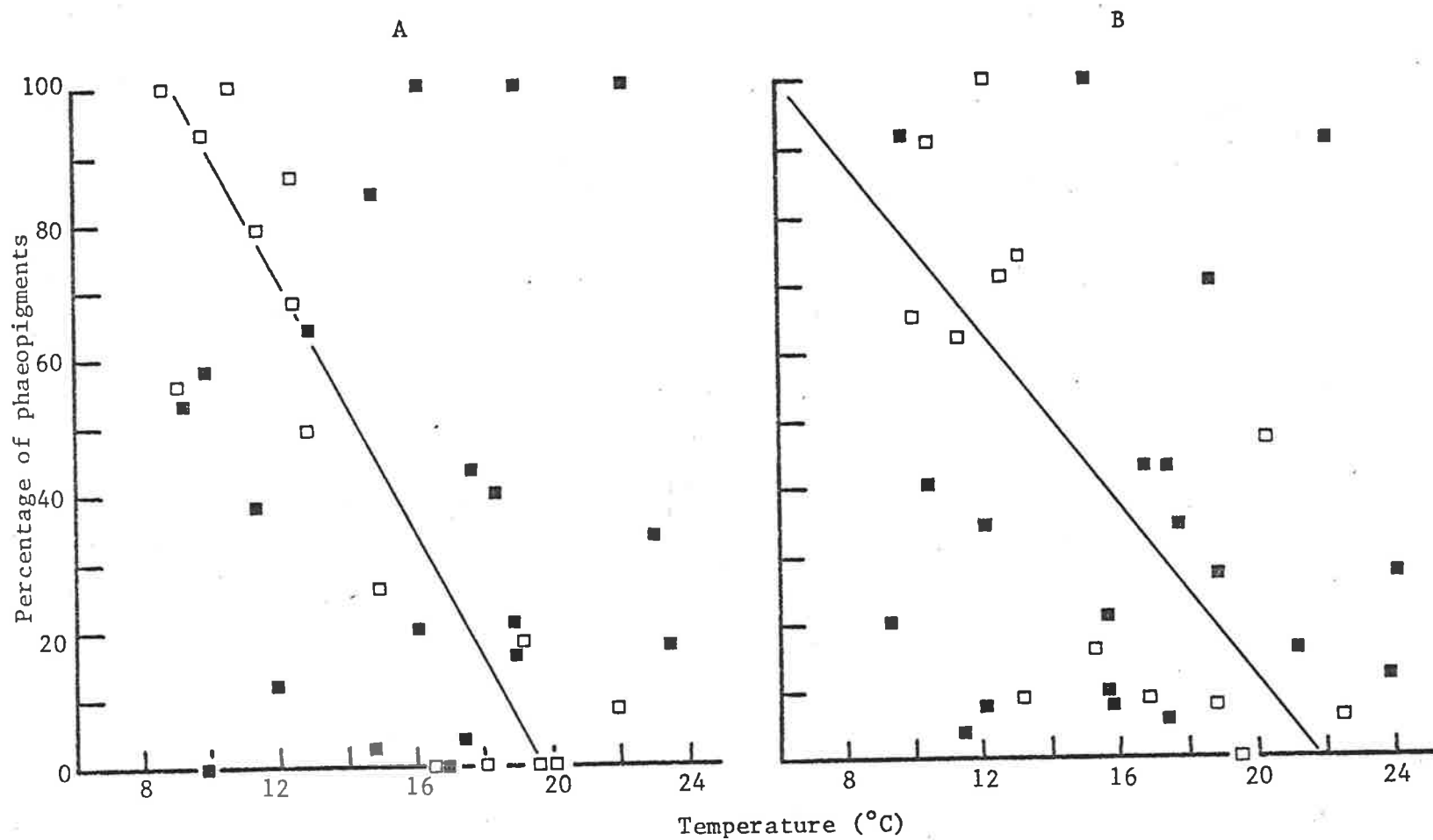


FIGURE 4.18 Phaeopigments, expressed as percentage of total chlorophyll a, versus depth-averaged water temperature in pond 1 (A) and pond 2 (B) during 1977 (■) and 1978 (□), plus regression lines.

Table 4.6

Spearman's ρ (plus level of significance) between population density of *D. carinata* and major zooplankters and between density of *S. exspinosus* and *M. leuckarti* in the Gumeracha ponds during 1977 and 1978.

	POND 1				POND 2			
	1977		1978		1977		1978	
	ρ	sig. level	ρ	sig. level	ρ	sig. level	ρ	sig. level
<i>D. carinata</i> & <i>S. exspinosus</i>	-0.79	p<.1%	-0.68	1%>p>.1%	0.34	p>5%	-	-
<i>D. carinata</i> & <i>B. triarticulata</i>	0.09	p>5%	-	-	0.13	p>5%	-	-
<i>D. carinata</i> & <i>M. leuckarti</i>	0.01	p>5%	-0.57	5%>p>1%	0.06	p>5%	-0.57	p>5%
<i>S. exspinosus</i> & <i>M. leuckarti</i>	0.33	p>5%	0.54	5%>p>1%	0.39	5%>p>1%	-	-

during 1977 and 1978. During February-March 1977 mean density of *S. exspinosus* decreased as mean density of *D. carinata* increased; a secondary increase in mean density of *S. exspinosus* occurred in pond 1 during June 1977 after the decline of *D. carinata*. Mean density of *S. exspinosus* decreased in late March 1978 as mean density of *D. carinata* increased. Although highest mean densities of *S. exspinosus* occurred during summer the species was present in pond 1 throughout the year. Variation in temperature accounted for a small amount of the variance in mean density of *S. exspinosus*. The non-significant positive correlation between mean density of *D. carinata* and mean density of *S. exspinosus* in pond 2 during 1977 was an artifact due to low number of data points.

Mean density of *D. carinata* and mean density of *B. triarticulata* were not significantly correlated at Gumeracha. Although *B. triarticulata* was present throughout 1977, mean density was apparently too low for serious competitive interactions to occur.

Mean density of *S. exspinosus* and mean density of *M. leuckarti* were not significantly correlated in pond 1 during 1977. Mean density of the two species was positively correlated in pond 1 during 1978 and pond 2 1977. Positive correlation was probably due to temperature effects (both species exhibited highest mean densities in summer) rather than a positive interaction between species.

Mean densities of *D. carinata* and *M. leuckarti* were not significantly correlated in the Gumeracha ponds during 1977. Despite a reduction in mean density, *M. leuckarti* was still present in large numbers during the period of *D. carinata* density increase in pond 1 during February-March 1977. Mean density of both species increased concurrently in pond 2 during late August-early September 1977.

A significant negative correlation was found between mean density of *D. carinata* and mean density of *M. leuckarti* in pond 1 during 1978. Mean density of *D. carinata* increased as mean density of *M.*

leuckarti decreased in March-April 1978. However, temperature accounted for a high amount of the variance in mean density of both species in 1978. The negative correlation may have resulted from temperature effects; *M. leuckarti* bloomed during summer while *D. carinata* was a cold water form. The same negative ρ was found between mean densities of the two species in pond 2 during 1978. A lower sample size made this ρ non-significant. Although temperature accounted for a high amount of the variance in mean density of *D. carinata* in pond 2 during 1978, temperature was not particularly important in accounting for the variance in mean density of *M. leuckarti* during that year. The effects of predation will be discussed further in subsequent sections of this chapter.

In summary, temperature appeared to be the major factor influencing the seasonal occurrence of *D. carinata* in the Gumeracha ponds. This species attained highest mean densities during autumn-winter. The effects of food and predation upon the population dynamics of *D. carinata* are discussed in the subsequent section of this chapter. Temperature also appeared to be a major factor affecting the abundance of *M. leuckarti*. Although present throughout the year, this species attained highest mean densities during summer. Although *S. exspinosus* attained highest mean densities during summer, a competitive interaction with *D. carinata* may have influenced the abundance of this species; the population dynamics of *S. exspinosus* is discussed more fully in section 4.4. *B. triarticulata* and *M. hirsuticornis* both constituted minor components of the zooplankton communities in the Gumeracha ponds.

4.2.3 Discussion.

The zooplankton community of the Gumeracha ponds resembled that of other WSPs in that it was dominated by cladocerans and cyclopoid copepods; calanoid copepods were rare. The composition of WSP zooplankton communities is consistent with the observation made in natural

lakes, that the relative importance of calanoids diminishes as the degree of eutrophication increases (Gannon and Stemberger, 1978; Godenau, 1978; Patalas, 1972). This situation may reflect differing evolutionary responses to variable food conditions. Calanoids appear to be successful in oligotrophic lakes as they are adapted to a dilute food source; calanoids exhibit high ingestion rates at low cell densities and high ingestion efficiency at small cell sizes (McNaught, 1975). Cladocerans tend to be generalist feeders, exhibiting equally high ingestion efficiencies on nanno- and net plankton, and maintaining high filtering rates at high cell densities (Bogdan and McNaught, 1975). Cladocerans are, therefore, adapted to the higher food concentrations of eutrophic waters.

The occurrence of calanoid copepods in WSPs is likely, therefore, to be determined by organic loading. Calanoids have not been found in ponds at Werribee or in other parts of Victoria (Hussainy, 1978). Although influent BOD to the Werribee ponds is much higher than at Gumeracha (initial ponds are anaerobic), several ponds are connected in series and final effluent BOD compares with effluent from pond 2 at Gumeracha. Thus, in some ponds at Werribee, organic loading must be similar to loads at Gumeracha. *B. triarticulata* might be expected to occur in such ponds. Effluent NH_3 concentrations at Werribee are much higher than at Gumeracha and may explain the absence of calanoids (see below). It remains somewhat surprising, however, that calanoids have not been recorded from other Victorian WSPs.

The dominant zooplankters in the Gumeracha ponds were , contagiously distributed on both a small and gross scale. Confidence limits for mean density estimates were often wide. This reflected the extreme nature of contagion. Density varied by up to 3 orders of magnitude between samples on some sampling dates. It might be argued that, due to the small tube diameter, the sampling technique itself

generated contagion. However, the tube sampler was more effective at capturing *D. carinata* than vertical hauls with a zooplankton net of much larger mouth diameter. Due to the vertical distribution of *D. carinata* in the Gumeracha ponds, closure of the bottom door of plankton traps enclosing a large volume of water (e.g. Schindler, 1969) could have excluded animals. The best method of improving the reliability of mean density estimates would have been to increase the number of samples taken. However, over 30 samples per pond would have been required to reduce the standard error to 20% of the mean. Lingeman (1978) reported that 34 samples (12 cm diameter tube sampler) were required from an artificial, rectangular pond 5 x 3 x 1 m deep to provide reliable population estimates for *D. magna*. Time and labour constraints precluded such an intensive sampling programme during the present study.

Overall patchiness of *M. hirsuticornis*, *S. exspinosus*, and *M. leuckarti* was more pronounced in pond 1 than in pond 2 during 1977. This coincided with greater bottom coverage by *P. ochreatus* in pond 1 during that year. Contagious distributions of *Macrothrix spinosa*, *S. exspinosus*, and *M. leuckarti*, apparently related to weedbed variation, have been reported from a billabong with extensive littoral macrophyte development (Sheil, 1976). The limnetic species, *D. carinata* and *B. triarticulata*, displayed low overall patchiness in pond 1 during 1977. Overall patchiness of *D. carinata* and *M. leuckarti* was similar for both ponds during 1978 and lower than during 1977. *P. ochreatus* was absent from both ponds during 1978. Thus, patchiness of littoral microcrustacea in the Gumeracha ponds may have been determined by the degree of macrophyte development. This did not explain the patchiness observed in the distribution of *D. carinata* in pond 2 during 1977.

Stratification in small, shallow water bodies has been discussed in chapter 2. It cannot be assumed that limnetic plankters in such waters are homogeneously distributed by wind action. Planktonic

organisms are generally non-randomly distributed over a wide range of spatial scales and many factors have been implicated in producing patchiness. A dominant factor influencing gross heterogeneity may be the wind-induced circulation pattern (George and Edwards, 1976; Schröder, 1961). This can result in the development of upwind surface aggregations or downwind deeper aggregations of plankters. *D. carinata* did not display aggregations of this type in the Gumeracha ponds. *D. hyalina* has been observed to clump in regions of upwelling midway between foamlines of Langmuir circulations (George and Edwards, 1973). Langmuir foamlines were never observed at Gumeracha during the present study. A minimum fetch (and therefore surface area) is probably required for the development of Langmuir circulations and they may not occur in small water bodies (I. Wallis, Caldwell-Connell Engineers, pers. comm., 1979). Heterogeneity in the distribution of *D. carinata* in the Gumeracha ponds was apparently not due to effects induced by wind.

Patchiness of a planktonic species could also arise due to an inherent aggregation tendency, environmental heterogeneity, or reproductive activity (Tonolli and Tonolli, 1958). That *D. carinata* did not exhibit inherent aggregation behaviour is suggested by the occurrence of negative intercepts in plots of mean crowding on mean density. Although not investigated in the present study, some degree of chemical variation would have been expected from inlet to outlet in the Gumeracha ponds. *D. carinata* did not display any consistent horizontal distribution pattern with respect to this gradient. Aggregations of ehippial females have been observed in *D. carinata* (Santharam et al., 1977), *Daphnia magna* (Young, 1978) and *Ceriodaphnia affinis* (Brandl and Fernando, 1971), and may be caused by sexual activity. The dense clumps of *D. carinata* that occurred in pond 1 on 21 October 1976 were not sampled directly. However, the percentage of adult females carrying ehippia was high on that occasion and sexual activity may have been pronounced. These types of clumps were not

observed often and cannot account for the patchiness observed on a long term basis. It may simply be that, as Roughharden (1977) has suggested, zooplankton patchiness is an inevitable consequence of dispersal in a randomly fluctuating environment. Patchiness can thus be explained without considering the patch structure of the environment, or special behaviour within or between species. Of course, if these phenomena occur they will contribute to patchiness.

The population dynamics of *D. carinata* and *S. exspinosus* at Gumeracha will be discussed more fully in subsequent sections of this chapter. *D. carinata*, although present throughout the winter, generally exhibited a diphasic annual population cycle with peaks in mean density during autumn (March-May) and late winter-early spring (September-October). This agreed with observations on the seasonal distribution of the species in various other water bodies in Australia and New Zealand (Burns, 1979; Timms, 1970; Bayly, 1962; Byars, 1960; Jolly, 1952). In particular, Burns (1979) recorded population peaks of *D. carinata* during February-March and late October in Lake Hayes, New Zealand. Vijayaraghavan (1970) reported a single annual peak of *D. carinata* in a small, shallow pond in India. Maximum population density was similar to peaks in mean density at Gumeracha but occurred at a water temperature of 25°C. Average density throughout the year was much lower (i.e. 10-20/l) than at Gumeracha. Mean density of *S. exspinosus* in the Gumeracha ponds peaked during mid-summer, although the species was present throughout the year. No comparative quantitative data is available on annual population cycles of this species.

In the absence of quantitative data on the abundance of nauplii and copepodite stages little can be concluded concerning population cycles of *M. leuckarti* and *B. triarticulata* in the Gumeracha ponds. *M. leuckarti* was perennial with maximum recruitment during summer. A second period of lower recruitment may have occurred during late winter-spring. Timms

(1970) reported that this species was most abundant from November to March but that peaks at other times were not uncommon. Green (1974) reported that breeding in this species was most intense during spring and summer. Although ovigerous females were not recorded in pond 2 from mid-December 1977 until mid-May 1978, recruitment occurred during January and April 1978. This could have resulted from the hatching of resting eggs (Hutchinson, 1967) or from recruitment of a dormant phase (nauplii or copepodids) (Green, 1974; Hutchinson, 1967).

B. triarticulata exhibited major population peaks in pond 2 during April and November 1977. However, several minor increases in mean density suggested that recruitment was repeated. Geddes (1968) reported that adults, copepodids, and nauplii of this species were present throughout the year in Marshall Reserve pond, Victoria, and that a peak in breeding occurred in August-September.

Temperature has been reported as the most important single factor regulating zooplankton populations in some natural ponds (O'Connell and Andrews, 1977; Byars, 1960). It is, perhaps, unrealistic to attempt to isolate any single factor as most important since the evolution of planktonic populations occurs in response to a suite of factors, including food level and interspecific interactions. Cladoceran mortality at pH in excess of 10.5 has been reported by O'Brien and De Noyelles (1972). *D. carinata* generally occurred below a pH of 9.5 in the Gumeracha ponds, although one collection was made at pH 10.5. The decline of *D. carinata* in pond 2 during late 1977 occurred as pH approached and exceeded 10.5. The onset of *D. carinata* population increases in pond 2 in 1977 and 1978 occurred later than in pond 1. In both years pH exceeded 10.5 in pond 2 and *D. carinata* did not appear until pH fell below 10.5. If pH had been a major factor affecting the occurrence of *D. carinata* at Gumeracha fundamentally different population cycles would have been expected in each pond due to pH differences.

However, population cycles were very similar in both ponds even though the pH of pond 1 never exceeded 10.5. Furthermore, if direct pH mortality had been important a correlation between pH and mean density would not have been expected below the critical pH level. The negative relationship found between pH and mean density of *D. carinata* during 1978 was due to the negative correlation between mean density and temperature rather than pH induced mortality (temperature and pH were positively correlated during 1978). Mortality of *Daphnia* in WSPs may occur due to NH_3 toxicity at pH above 8.0 (Dinges, 1973). However, the critical NH_3 concentration varies between species of *Daphnia* and may be as high as 5 mg/l. It is unlikely that NH_3 concentrations in the Gumeracha ponds were ever high enough to result in direct mortality of *D. carinata*.

D. carinata was a facultative browser in the Gumeracha ponds; after the decline of the phytoplankton standing crop animals ingested sediment. Although the sediments would never have become a limited resource in an absolute sense, population density may have been so great at times that there was simply insufficient bottom area for all animals in the population to obtain adequate nutrition. Maximum mean density of *D. carinata* (approximately 1000/l) corresponded to 100 animals per square centimetre of pond bottom. Animals did not forage on the bottom continuously so the whole population would not be feeding simultaneously. However, at high population densities the probability of being disturbed by another animal while feeding would increase. *D. carinata* may have been limited at high population density by a relative resource shortage (see 4.3.3).

Physico-chemical factors appeared to be unimportant in accounting for the variance in mean density of *S. exspinosus* at Gumeracha. The disappearance of this species from pond 1 in 1978 could have been related to the decline of *P. ochreatus*. The only significant

factor affecting the abundance of this species at Gumeracha appeared to be a negative interaction with *D. carinata*. It is unlikely that the negative correlation between mean densities of the two species was the result of temperature effects. Although maximum mean density of *S. exspinosus* occurred during summer, the species exhibited a second population increase in pond 1 during mid 1977 after the decline of *D. carinata*. It has been demonstrated that *Simocephalus vetulus* is invariably replaced by *Daphnia pulicaria* in mixed laboratory culture (Frank, 1952). Horton et al. (1979) have suggested that Frank's results were due to *S. vetulus*, an obligate suspension feeder, being at a competitive disadvantage in the unstirred medium of the experimental environment. *D. pulicaria*, a facultative browser, was able to utilize sedimented food and therefore maintain itself for longer. Such an explanation could not account for the second population increase of *S. exspinosus* in pond 1 during mid 1977 at a time when suspended food was extremely low. It is tempting to suggest that the decline of *S. exspinosus* (maximum length 3.5 mm) in pond 1 during the increase of *D. carinata* (maximum length 5.6 mm) in February-March 1977 was due to competitive displacement by the larger species in accord with the size-efficiency hypothesis (Brooks and Dodson, 1965). However, the size-efficiency hypothesis has not generally been supported by experimental findings (e.g. Neill, 1975). It now appears that zooplankton competitive ability is a complex interplay between size-selective vertebrate and invertebrate predation (Lynch, 1979; Dodson et al., 1976; Dodson, 1974), reproductive effort (Lynch, 1977), and growth rate (Novakova et al., 1978). The decline of *S. exspinosus* will be discussed further in section 4.4 where birth and death rates are presented. If the decline of this species was due to predation the mortality rate would be expected to increase in the presence of the predator (e.g. Kerfoot, 1977). If the decline was due to competition the birth rate would be expected to

decline as resources became limiting.

Loedolff (1965) concluded that temperature alone was the most important factor controlling the density and appearance of cladocerans in WSPs. It is obvious from the studies at Gumeracha that, while temperature is important, zooplankton communities in WSPs, as in natural waters, may be influenced by other factors. These factors must also be considered when designing effluent polishing schemes utilizing zooplankton communities.

In the absence of experimentally determined filtering rates, the effect of zooplankton grazers upon phytoplankton standing crop in the Gumeracha ponds must be inferred from correlations of population density. *D. carinata* appeared to be the major grazer in the Gumeracha ponds and terminated phytoplankton blooms. The sequence of events during the decline of phytoplankton blooms at Gumeracha was very similar to that described by Pennington (1941). That is, as the density of *D. carinata* increased, phytoplankton standing crop declined, the water turned a dark colour, and dissolved oxygen concentrations fell to very low levels. *D. carinata* collected at that time were bright pink in colour due to the synthesis of haemoglobin in response to lowered ambient oxygen concentrations (Fox, 1948). Although the percentage of phaeopigments in the total chlorophyll *a* pool was significantly correlated with the density of *D. carinata*, such a relationship is not always an accurate indicator of grazing pressure. In shallow ponds, a poor correlation may result from resuspension of sediments (Glooschenka, 1972; Moss, 1970) while a high correlation may result from zooplankton feeding on detrital algal cells already rich in phaeopigments (Glooschenka, 1972). Both processes probably contributed to relatively high percentages of phaeopigments in the Gumeracha ponds during winter (Figure 3.4).

The filtering rate of *Daphnia* (the volume of medium containing the number of cells consumed in a given time: Wetzel, 1975) is influenced by temperature, pH, food concentration, food type, light, oxygen, body length, and reproductive state (Hayward and Gallup, 1976; Kring and O'Brien, 1976a,b; Starksweather, 1975; Kibby, 1961; Ivanova, 1969; Burns, 1969; Burns and Rigler, 1967). Although *D. carinata* is larger than any species of the genus previously studied (maximum length at Gumeracha was 5.65 mm), mean body length of adults ranged from 2.65-3.40 mm during the present study (section 4.3). From Hayward and Gallup (1976) it was estimated that an average adult *D. carinata* would ingest 8-10,000 cells/individual/hour at cell densities (approximately 25,000/ml) and temperatures (approximately 15°C) that were prevalent during periods of population increase. Each animal would thus filter 0.25-0.30 ml/hour or 6-7 ml/day. At mean densities above 150 individuals/litre *D. carinata* could probably have filtered the entire volume of the Gumeracha ponds in one day or less. Outdoor cultures of *Scenedesmus acutus* at optimal areal density (growth rate below maximum) have minimum biomass doubling times of about 3 days (Stengel and Soeder, 1975). *D. carinata* populations appeared to be quite capable of reducing phytoplankton standing crop in the Gumeracha ponds.

While grazing by *D. carinata* terminated phytoplankton blooms in the Gumeracha ponds the onset of blooms was triggered by temperature rather than release from grazing pressure. The dominant zooplankter during summer periods of phytoplankton abundance was *M. leuckarti*, a carnivore. As a result, significant deterioration of effluent quality due to high phytoplankton standing crops occurred during summer. *D. carinata*, the major grazer, was not present during most of the period of phytoplankton growth, and was thus unable to control phytoplankton standing crop on an annual basis. Carbon limitation of the phytoplankton may also have occurred in the Gumeracha ponds during periods of intense

grazing by *D. carinata*. Controlled carbon enrichment experiments would be required to separate the effects of carbon limitation and grazing. Grazing was, therefore, one of a suite of factors controlling phytoplankton abundance.

The effects of zooplankton upon effluent quality at Gumeracha were manifested through the reduction of phytoplankton standing crop. *D. carinata* contributed to major reductions in BOD, SS, and TOC in pond 2 during late March-April 1977 and in both ponds during the same period during 1978. It was shown in chapter 2 that reduction of BOD, SS, and TOC was highest in the Gumeracha ponds during the winter months. This was related to periods of macrophyte development in chapter 3. Highest reduction of organic parameters also coincided with periods of high *D. carinata* population density. However, percentage reduction of BOD, SS, and TOC in pond 1 was high throughout June-November 1977 even though *D. carinata* was absent. The standing crop of *P. ochreatus* in pond 1 was high during that period. Despite a high standing crop of *D. carinata* in pond 2 during June-November 1977, percentage reduction of BOD, SS, and TOC was lower in that pond than in pond 1. This was consistent with a lower standing crop of *P. ochreatus* in pond 2. However, *D. carinata* contributed to improvement in effluent quality during periods of grazing as evidenced by increased reduction of BOD, SS, and TOC in pond 2 during March and April 1977. The growing season of *P. ochreatus* in that pond did not commence until May 1977.

That *D. carinata* did not contribute greatly to the reduction of organic parameters during winter is not unexpected. After the decline of phytoplankton standing crops, *D. carinata* (a facultative browser) foraged on the bottom and ingested the sediments. Consequently, less time would have been spent filtering in the water column. As the chief mode of BOD and SS reduction by cladocerans appears to be the filtration of sestonic particles, the shift in feeding behaviour of *D. carinata*

would decrease its contribution to BOD and SS reduction. Loedolff (1965) reported a good inverse correlation between BOD and total cladoceran standing crop in WSPs in southern Africa. It is likely, however, that high standing crops of phytoplankton were present throughout the year in Loedolff's ponds (c.f. Shillinglaw and Pieterse, 1977). Under such conditions, phytoplankton standing crop, and therefore BOD, would reflect grazing pressure.

Removal of NO_3^- and soluble and total $\text{PO}_4\text{-P}$ was highest in the Gumeracha ponds during phytoplankton blooms. Consequently, grazing by *D. carinata* resulted in a reduction in nitrogen and phosphorus removal. Elster (1965) reported that grazing by *Daphnia* in WSPs resulted in high nitrogen and phosphorus concentrations in effluents. The data of Loedolff (1965) also showed that effluent phosphate was highest when standing crop of cladocerans was maximal. Removal of NH_3 , TKN, and org-N was highest in pond 1 at Gumeracha during the latter half of 1977 when *D. carinata* was absent. Removal was lower in pond 2 during the same period even though density of *D. carinata* was high. Removal in pond 2 during 1977 increased with the onset of *P. ochreatus* growth. As for organic parameters, *P. ochreatus* was the major agent of reduction of nitrogenous compounds in the Gumeracha ponds during the winter of 1977. However, a comparison of influent and effluent concentrations does not accurately reflect the importance of a population as a nutrient store. The nutrient store represented by annual net production of *D. carinata* and *S. exspinosus* in the Gumeracha ponds is compared with the amount of nutrient retained in the ponds annually in subsequent sections of this chapter.

4.3 Population Dynamics and Production of *Daphnia carinata*

4.3.1 Methods

4.3.1.1 Size Distribution. Information on the age and size structure of a population is essential for an accurate analysis of population fluctuations. It is difficult to describe the age structure of *Daphnia* populations as members of this genus do not exhibit any age-specific characters. Individuals may be aged in the laboratory by following moulting and instar duration. Such a technique is impractical in the field. The appearance and development of successive generations may be followed in the field by monitoring the changes in numbers of animals in arbitrarily defined size classes. This approach was adopted during the present study.

Body length of *D. carinata* was measured after Anderson (1932) as the longest distance from the top of the head to the base of the caudal spine (see Mitchell, 1978). Measurements were made at 20 times magnification using a micrometer eyepiece. At this magnification, 10 eyepiece units were equivalent to 0.526 mm. Post embryonic animals (juveniles and sexually mature adults) were placed into 9 length classes each of 10 micrometer units in width (Table 4.7); the lower limit of the first juvenile size class was 15 eyepiece units. The lower limit of size class 4 corresponded to carapace length at the onset of reproduction.

Immature or embryonic stages (passed in the brood chamber) of *D. carinata* were also assigned to size classes for length - dry weight determinations. The development of the parthogenetic eggs of *D. carinata* has been described by Murugan and Venkataraman (1977). The developmental sequence is identical to that of *D. pulex* described by Edmondson (1955). For convenience, Edmondson's classification was adopted during the present study. Embryonic stages were classed as follows: early - eggs round or slightly elongate; middle - embryo

Table 4.7

Length classes for mature *D. carinata*

		Length class	Micrometer units	mm	Mid-class length (mm)
Juvenile	{	1	15 - 25	0.759 - 1.325	1.04
		2	25 - 35	1.325 - 1.855	1.59
		3	35 - 45	1.855 - 2.385	2.12
Sexually mature	{	4	45 - 55	2.385 - 2.915	2.65
		5	55 - 65	2.915 - 3.445	3.18
		6	65 - 75	3.445 - 3.975	3.71
		7	75 - 85	3.975 - 4.505	4.24
		8	85 - 95	4.505 - 5.035	4.77
		9	95 - 105	5.035 - 5.565	5.30

elongate with distinct head bulge, separate antennal rami bearing terminal setae, and developing carapace and caudal spine; late - embryo with well developed eye pigment and differentiated thoracic appendages. The late embryonic stage is clearly distinguishable from the first adult stage as in the former the caudal spine is curled ventro-anteriorly between the carapace valves.

Embryos ($n = 339$) were dissected out of the brood chambers of female *D. carinata* collected from pond 1 on 21 May, 1976. Each embryo was classified according to the scheme above and measured using a micrometer eyepiece. The mean length of each stage was: early, 0.249 mm ($\pm$ standard error equal to 2.0% of the mean, $n = 95$); middle, 0.378 mm ($\pm$ standard error equal to 2.4% of the mean, $n = 115$); late, 0.616 mm ($\pm$ standard error equal to 1.9% of the mean, $n = 129$). To check this procedure, embryos were assigned to 0.02 mm length classes; length-frequency analysis revealed peaks in number at lengths of 0.27, 0.37, and 0.63 mm. These peaks corresponded closely with the mean lengths of Edmondson's embryonic stages. The upper length limit of the late embryonic stage was 14.5 eyepiece units and the length of the newly hatched neonate was 0.759 mm. Neonate length of *D. carinata* at Gumeracha was slightly higher than the value of 0.57 mm reported for the same species by Murugan and Venkataraman (1977). Neonate length of *D. carinata* at Gumeracha was midway between that of *D. thomsoni* (maximum body length 4.8 mm) and *D. magna* (maximum body length 6.0 mm) (from Green, 1956).

After the number of animals per sample had been counted for each sampling date, the 9 samples were pooled and subsampled volumetrically as in 4.2.1. At least 150 animals were measured (or total number if less than 150) and assigned to length classes. The mean length of sexually mature adults (size classes 4-9) on each sampling date was calculated from the number of animals per size class (N) and

the mid-length of each size class (L). That is, mean body length of the adult population was equivalent to

$$\frac{\Sigma[(N_1 \cdot L_1) + (N_2 \cdot L_2) + \dots (N_n \cdot L_n)]}{\Sigma N}$$

4.3.1.2 Reproduction. The number of females in reproductive condition (carrying eggs, middle or late stage embryos, and ephippia) in each of the 9 samples, was noted for each sampling date. The abundance of ovigerous and ephippial females was expressed as the percentage of the total number of mature females.

Loss of eggs from the brood chamber occurs when *Daphnia* are preserved in formalin (e.g. Prepas, 1978; Prepas and Rigler, 1978). Live material was, therefore, used where possible for the determination of brood size. Animals were collected by oblique hauls from the pond bottom with a zooplankton net (25 cm mouth diameter, 150 μ m mesh). When preserved material was used, only animals with carapace valves close together and showing no apparent signs of disturbance were selected. Only females carrying eggs (not middle or late stage embryos) were selected. For each sampling date at least 50 ovigerous females were measured and the number of eggs counted (after dissection out of the brood chamber). In the case of preserved animals, loose eggs were not included in counts. Brood size (and conceivably, the number of ovigerous females) may, therefore, have been slightly underestimated on some occasions. This would have resulted in a slight underestimation of birth and mortality rates, turnover time, and, therefore, production. Mean brood size on each sampling date was calculated from the total number of eggs counted divided by the total number of ovigerous females.

4.3.1.3 Population Parameters. *D. carinata* reproduces continuously; birth and death rates cannot be determined solely from counts, as can be done with cohort breeders. The egg-ratio method,

devised for rotifers by Edmondson (1960), provides a technique for expressing reproductive intensity in animals that carry their eggs. This technique has been applied to populations of *Daphnia* by Kwik and Carter (1975), Clark and Carter (1974), George and Edwards (1974), Cummins et al. (1969), Wright (1965), and Hall (1964), and was employed during the present study.

If the number of eggs in the population (E) and the initial population size (N_0) are known, and egg development time (D) is measured experimentally, the finite birth rate (B), or the number of newborn per individual per day, can be calculated from

$$B = \frac{E}{D \cdot N_0} \cdot$$

An estimate of the instantaneous (potential) population growth rate (b'), or the rate at which the population would increase if it maintained birth rate B, can be calculated from

$$b' = \log_e (1 + B) \cdot$$

This formula slightly underestimates b' (Edmondson, 1972). The prime sign has been used to indicate that population parameters have been calculated from estimates of population number. The calculation of b' assumes zero mortality and a stable age distribution, but may be applied to non-steady-state populations as an approximation (George and Edwards, 1974; Edmondson, 1968). If successive pairs of population densities are known, the actual or net rate of population growth (r') can be calculated from

$$r' = \frac{\log_e N_t - \log_e N_0}{t},$$

where N_0 is initial population density, and N_t is population density after time t .

The difference between instantaneous (or potential) population growth rate and actual population growth rate is a measure of

instantaneous mortality rate (d'), or

$$d' = b' - r' .$$

That is, the observed population change is subtracted from the predicted population increase to reveal mortality from natural causes and predation.

If the population is in a steady state, d' equals b' . If the population is increasing, b' exceeds d' , while if the population is decreasing d' exceeds b' . In both cases d' is positive. A negative d' value indicates that the observed population growth rate exceeds the potential population growth rate. Such a situation could possibly be associated with the increased survival of non-reproductive adults, but is more likely to reflect errors in density estimates (Cummins *et al.*, 1969) or the underestimation of birth rate due to the hatching of ephippial eggs (Clark and Carter, 1974). The least reliable statistic associated with the egg-ratio method is d' as it is based upon two quantities already calculated with error (Edmondson, 1974).

The number of eggs in the population (E) on each sampling date was calculated from the number of ovigerous females per litre multiplied by mean brood size on that date. Egg development times were determined in the laboratory.

4.3.1.4 Calculation of Production: Population Turnover-time Model.

Net production of *D. carinata* was calculated using population turnover rates as derived from birth rates. This method has been used to calculate the production of *Daphnia* populations by George and Edwards (1974), Cummins *et al.* (1969), and Wright (1965). In this method, instantaneous mortality rate (d') is converted to a finite death rate (D), or deaths per finite time interval, from

$$D = 1 - e^{-d'} .$$

The turnover time of the population (T), or the time for the population to replace itself, is calculated from

$$T = \frac{1}{D} \text{ (days) .}$$

Percentage turnover per day is thus $\frac{1}{T} \cdot 100$. Net production rate (exclusive of respiration) can then be calculated by multiplying daily percentage turnover by standing crop biomass.

Standing crop biomass on each sampling date was determined from the number of post-embryonic individuals in each size-class per litre and the mean weight of each size class. The relationship between length and dry weight for *D. carinata* was determined in the laboratory.

4.3.1.5 Egg Development Time. A direct method was used to determine the development time of parthenogenetic eggs of *D. carinata*. The time interval between the release of eggs into the brood chamber and the emergence of neonates was measured. Development time is influenced mainly by temperature; maternal nutrition after egg release has little effect (Edmondson and Winberg, 1971). Differences in egg size between populations of a species may influence development time (Bottrell et al., 1976; Munro and White, 1975). For the determination of development time, *D. carinata* in both the Gumeracha ponds was treated as a single population.

Ovigerous females were collected from the ponds, returned to the laboratory within the hour, and only individuals bearing eggs in the earliest stages of development (that is, eggs spherical and in undivided state: after Murugan and Venkataraman, 1977) were selected. Brood size was counted and each female was placed in a 20 ml petri dish filled with pond water which had been filtered and examined microscopically to ensure that no neonates were present. A small amount of sediment and 5 drops of an algal suspension (*Scenedesmus* cultured from pond 2) were added to each petri dish. Petri dishes (plus lids) were placed in constant

temperatures cabinets ($\pm 0.5^{\circ}\text{C}$; 9 hour dark - 15 hour light cycle) at the temperatures at which animals had been collected in the field. Experiments were run at 10, 13, 16, 18 and 23°C . Two separate experiments, each consisting of 10 females, were run at all temperatures. Developing eggs were examined at 12 hourly intervals except during the later stages of development when observations were more frequent.

In applying laboratory determined egg development times to a field situation, allowance must be made for the thermal history of eggs if the animal exhibits marked vertical migration over a wide temperature range (Prepas and Rigler, 1978). The Gumeracha ponds were isothermal on many occasions and during periods of thermal stratification maximum temperature differences between the epi- and hypolimnion were 5°C . Under these conditions the ponds could be treated as a single layer and depth-averaged water temperature was an adequate representation of the thermal history of eggs (after Edmondson and Winberg, 1971). Keen (1979) has shown that different thermal regimes, even if mean temperature is constant, can produce significant differences in egg development time. However, even fluctuations of up to 8°C only produced a development time difference of 1.8 hours. In view of the other assumptions involved in the turnover-time method of production calculation, such an error is insignificant.

In the present study, an attempt was made to select eggs in the earliest stage of development for the determination of egg development time. Obviously, eggs had been in the brood chamber for some time prior to the commencement of experiments. A correction factor of an extra 3 hours for each 4°C decrease in temperature from 29°C (calculated from Murugan and Venkataraman: 1977, and Edmondson: 1955) was used to compensate for the period of time between the deposition of eggs in the brood chamber and the commencement of experiments. The actual corrections were as follows:

23°C, laboratory time plus 0.31 days,

18°C, laboratory time plus 0.46 days,

16°C, laboratory time plus 0.53 days,

13°C, laboratory time plus 0.59 days,

10°C, laboratory time plus 0.69 days.

4.3.1.6 Length - Dry Weight Relationship. Female *D. carinata* were collected from the Gumeracha ponds at various times during the study, returned to the laboratory, washed with distilled water, and sorted into size classes. Ovigerous and non-ovigerous adults (above size class 4) were sorted independently. Animals were placed into small, pre-weighed aluminium foil cups, the number per cup depending upon size. The larger size class animals (classes 7 and 8) could be weighed individually. For size classes 1 to 3, the number of animals pooled in a cup ranged from 11 to 509, but was generally about 50. For size classes 4 to 7, the number per cup ranged from 3 to 93, but was generally about 25. Embryonic stages were also weighed after dissection out of the brood chamber. The number of embryonic stages per cup ranged from 30 to 163, but was generally about 50. All weights represented averages for several animals. Animals were dried at 60°C for 24 hours. Higher temperatures were not used to avoid volatilization and decomposition of fats and, therefore, weight underestimation (after Edmondson and Winberg, 1971). Cups plus dried animals were placed in a dessicator over silica gel and then weighed on a Cahn gram electrobalance (model G).

4.3.1.7 Calculation of Production: Biomass Turnover Model:

Certain problems are associated with the use of the population turnover-time model for calculating production (see Waters, 1977; Edmondson, 1974). Principally, the underlying assumptions of the model (that b' , r' and d' are constant during the interval between sampling, and that the population is in a steady-state with a stable age distribution) are

rarely, if ever, met in a field situation. Steady-state populations of *Daphnia* may be obtained only temporarily in the laboratory (Slobodkin, 1954). The turnover-time method is, therefore, an approximation. In view of these problems, a second method which made no assumptions concerning population demography was also used to calculate the production of *D. carinata*.

The second method, developed by Winberg *et al.* (1965), is based upon biomass turnover-time or the time taken for an animal to pass through successive developmental stages. The turnover-time of each stage is, therefore, equivalent to its duration. This method has generally been used to calculate the production of cohort breeders, e.g. copepods (Burgis, 1974), but has been applied to populations of *Daphnia* (Duncan, 1975; Hillbricht-Ilkowska *et al.*, 1966) and other continuously reproducing cladocerans (Lim and Fernando, 1978; Janicki and DaCosta, 1977; Pedersen *et al.*, 1976).

In this method, developmental stages may be instars or arbitrarily defined size classes. The latter were used in the present study and were the same as above. The duration of each size class (T) can be measured in the laboratory. From the length-dry weight relationship, the weight change upon passing through each size class (ΔW) can be calculated. If the density of animals in each size class (N) is known, daily production of each size class is then equivalent to standing crop biomass divided by duration. Net production of the population on each sampling date is the sum of the production of all size classes present, that is,

$$\Sigma \left[\frac{N_1 \cdot \Delta W_1}{T_1} + \frac{N_2 \cdot \Delta W_2}{T_2} + \dots + \frac{N_n \cdot \Delta W_n}{T_n} \right] .$$

The only assumption made in applying this method is that laboratory development times are similar to those in the field. Therefore, food quality and quantity in the experimental situation will be important.

Egg production must be estimated separately in the biomass turnover method. For this purpose, all embryonic stages were classed as one developmental stage and the initial weight of an egg was assumed to be zero.

4.3.1.8 Growth. The duration of successive size classes of *D. carinata* was determined in the laboratory at 10, 14.5, 18 and 24.5°C. Animals used in experiments at 10°C and 14.5°C were collected from the field at the same temperatures. Animals used in experiments at 18°C and 24.5°C were collected at lower temperatures (10–15°C) and acclimated for 5 days with gradual temperature increases. Experimental animals were collected during June, July, and August, 1978, when chlorophyll *a* concentrations were extremely low. At those times, *D. carinata* would have been foraging amongst the sediments.

Five females of varying length, the smallest being early size class 1 (15 eyepiece units in length), were measured as in 4.3.1.1 and placed in a 130 ml pomade jar containing 1 cm of pond sediment and 85 ml of filtered pond water. Jar tops were covered but not sealed. 6 replicates were run at each temperature (i.e. 30 females). Jars were placed in constant temperature ($\pm 0.5^\circ\text{C}$) cabinets under constant illumination. Animals were removed and measured daily, the water in the jars agitated, and animals replaced. The intestines of animals were dark brown throughout the experiments and animals were observed foraging amongst the sediments. Mature females released young during moulting; all neonates were removed.

Animals could be maintained in the experimental situation for about 30 days. Therefore, the observed daily growth increments of different animals were added sequentially to provide overall growth curves. Each daily point on the length versus time curve was a mean of several values. The duration of successive size classes was read directly off the growth curves.

4.3.1.9 Nitrogen and Phosphorus Content. Total nitrogen content of *D. carinata* (as percentage of dry weight) was determined using a Kjeldahl digestion technique (as for *P. ochreatus*, 3.2.4). Animals were collected from the ponds during August, 1976, and March, May, and June 1977. Animals from all size classes were pooled, washed with distilled water, dried at 60°C for 24 hours, and homogenised in a tissue grinder. A known weight of *D. carinata* tissue was then digested in potassium sulphate and sulphuric acid.

Total phosphorus content of *D. carinata* (as percentage of dry weight) was determined after APHA (1976). Animals were collected from the ponds during March and April 1977, and treated as above. A known weight of tissue was digested in sulphuric acid and 10% copper sulphate, and phosphate determined using the molybdate/acid technique.

4.3.2 Results

4.3.2.1 Size Distribution. Length-frequency histograms for *D. carinata* in pond 1 are presented in Figure 4.19, and are discussed in relation to population density curves (Fig. 4.5). The high proportion of juveniles (size class 1) in early July, 1976, indicated a period of marked recruitment. Throughout August, September and October, 1976, size classes 1 to 4 were fairly equally represented and the size distribution was fairly constant; the population was thus in a fairly stable state, although some variation occurred. A period of recruitment (high proportion of juveniles) commenced in early November, 1976, after a decline in population density, and continued through December. The proportion of animals in size classes 5 and above fell off rapidly during the latter half of 1976 indicating that mortality in those classes was high.

Recruitment from the hatching of ephippial eggs occurred during early February, 1977, and the proportion of juveniles was high on 16 February. All size classes were represented on that date and,

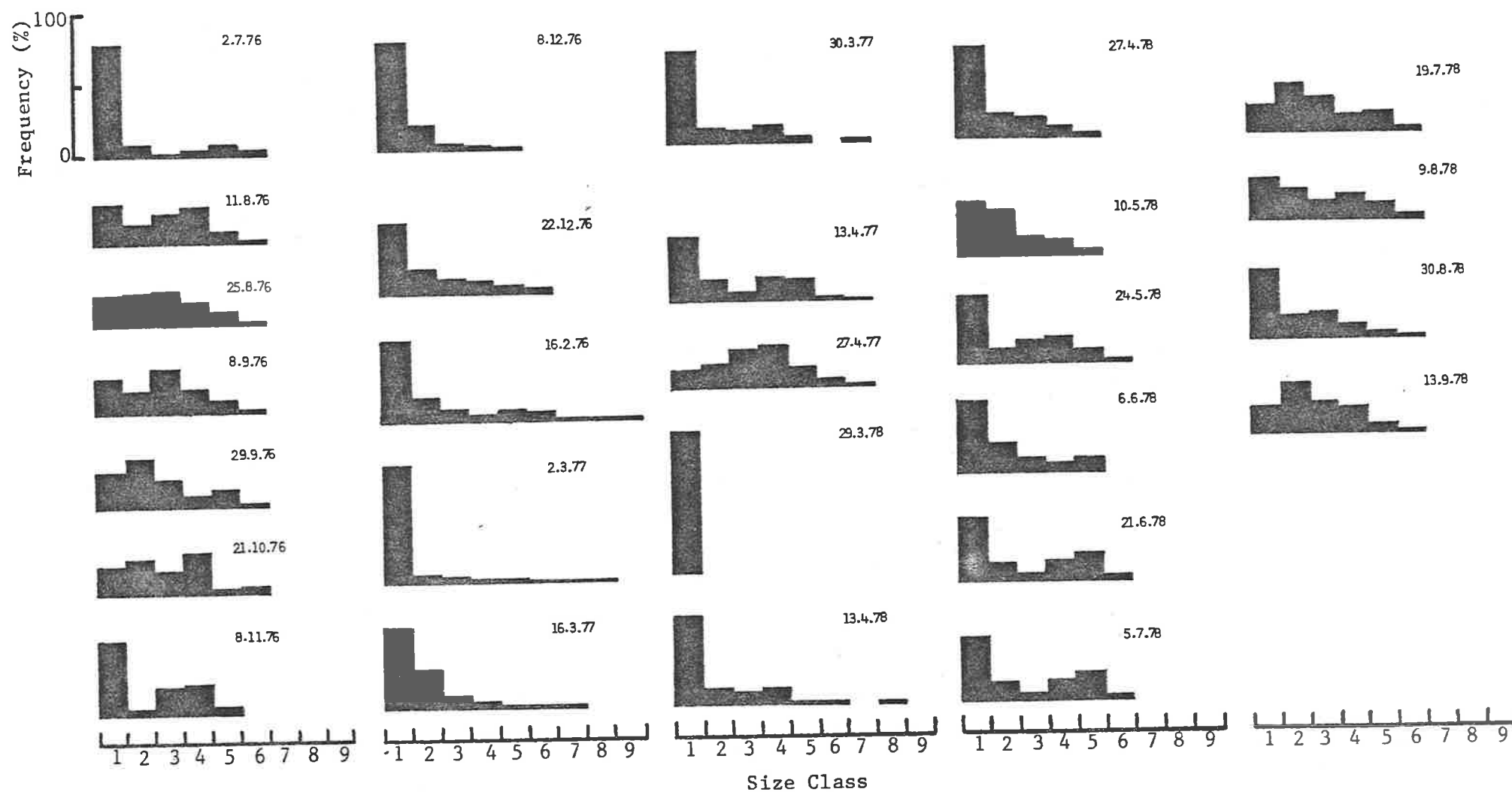


FIGURE 4.19 Length-frequency distribution of *D. carinata* in pond 1.

therefore, some of the juveniles present would have hatched from parthenogenetic eggs. *D. carinata* was not recorded in samples on 2 February, 1977. The presence of size class 9 individuals on 16 February indicated that growth had been extremely rapid or that sampling error had occurred on 2 February. Recruitment was high throughout March, 1977, as population density reached a peak. Mortality of larger size classes was high. Maximum population density during 1977 occurred when the population was composed largely of juveniles. A similar situation has been reported for *D. hyalina* (George and Edwards, 1974). Growth of the population through successive length classes can be followed from early March until late April, 1977, although recruitment was continuous. Recruitment decreased in late April (size classes 3 and 4 became most abundant) just prior to a population decline. Mortality was high during May and the population entered a diapause phase.

Recruitment from the hatching of ephippial eggs occurred in mid-late March, 1978. A period of high recruitment from parthenogenetic eggs continued through April as population density increased. As in early 1977, a period of rapid growth in length occurred early in the population cycle, although sampling error could also have been involved. High population densities during 1978 occurred when the proportion of juveniles in the population was high. Recruitment was continuous and fairly constant during May and June, 1978, declined slightly during July, and increased during late August, 1978. Recruitment decreased during mid-September, 1978, just prior to a population decline. A period of high mortality occurred during late September as the population entered summer diapause.

Length-frequency histograms for *D. carinata* in pond 2 are presented in Figure 4.20, and are discussed in relation to population density curves (Fig. 4.6). Recruitment from the hatching of ephippial eggs occurred during mid-March, 1977; some of the juveniles on 30 March

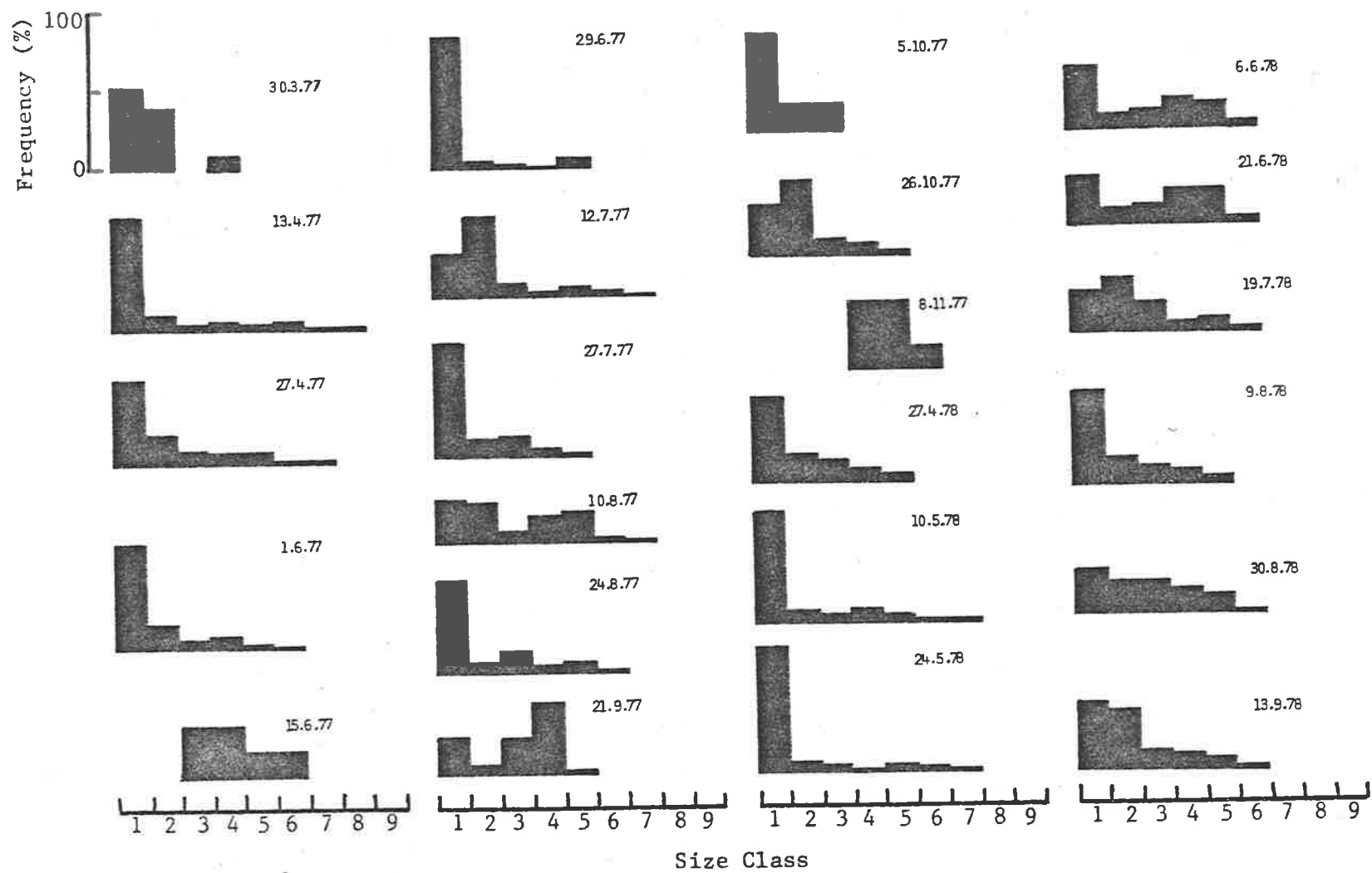


FIGURE 4.20 Length-frequency distribution of *D. carinata* in pond 2.

could have hatched from parthenogenetic eggs as sexually mature females were present at that time. Recruitment was high during early April as population density increased. Maximum population density occurred during late April when the proportion of juveniles in the population was high. As in pond 1, mortality of the larger size classes was high. Recruitment ceased altogether (no juveniles) in mid-June during a significant decline in population density. Recruitment was high during late June and late July, 1977, as population density increased. Growth of the population through successive length classes could be followed from late July to mid-September. Recruitment was continuous from July to October, 1977, but varied in intensity. Recruitment decreased during late October, and ceased altogether during early November, 1977. At that time the population was senescent (composed of older animals), and mortality was high as the population entered summer diapause.

Recruitment from the hatching of ephippial eggs occurred during mid-April, 1978. Juveniles hatched from parthenogenetic eggs probably also contributed to recruitment by late April (sexually mature females present). Recruitment was high during May, 1978, as population density increased and reached a maximum. Mortality amongst larger animals was very high during May. Recruitment decreased during late June and July, 1978, as population density decreased. Recruitment increased during early September as population density increased, but declined somewhat at the end of that month. Although juveniles were present in late September, the population had declined by early October. Thus, a period of high mortality occurred just after 30 September, 1978, as the population entered summer diapause.

Seasonal variation in mean body length of mature female *D. carinata* (size class 4 and above) in the Gumeracha ponds is shown in

Figure 4.21. Mean body length of mature animals in pond 1 varied between 2.76 mm and 3.40 mm; maxima occurred during mid-February, 1977 (3.40 mm; depth averaged water temperature was 23.5°C), and early July, 1978 (3.27 mm; average water temperature was 9.0°C). In pond 2, mean body length of mature animals varied between 2.65 mm and 3.36 mm; maxima occurred during mid-April, 1977 (3.30 mm; average water temperature was 16.7°C), early July, 1977 (3.26 mm; average water temperature was 10.3°C), and late May, 1978 (3.36 mm; average water temperature was 12.5°C). The range of mean body length was similar in both ponds and during both 1977 and 1978. Mean body length maxima were also similar but occurred at different times in each pond.

One female (size class 3) carrying eggs was collected from pond 1 on 16 March, 1977. This was the only occasion on which an ovigerous female smaller than size class 4 was recorded from the Gumeracha ponds. Size class 8 and 9 females were recorded from pond 1 during February and March, 1977. The peak in mean body length during mid-February may have reflected increased growth rates at high temperatures due to reduced instar duration (Green, 1956). Generally, body length at the onset of maturity remained constant. Therefore, mean body length maxima at much lower temperatures reflected increased longevity and continued moulting in adults, even though growth rate would have been lower. This pattern of growth has been recorded in *D. hyalina* (George and Edwards, 1974) and *D. magna* (Green, 1956).

Longevity in *Daphnia* is temperature dependent (Hebert, 1978c). Mean body length of mature *D. carinata* in the Gumeracha ponds has, therefore, been plotted against average water temperature in Figure 4.22. A linear regression of mean body length on average water temperature for pooled data showed that variation in temperature accounted for none of the variance in mean body length. The effect of lag is important when considering the influence of temperature upon the growth of individuals

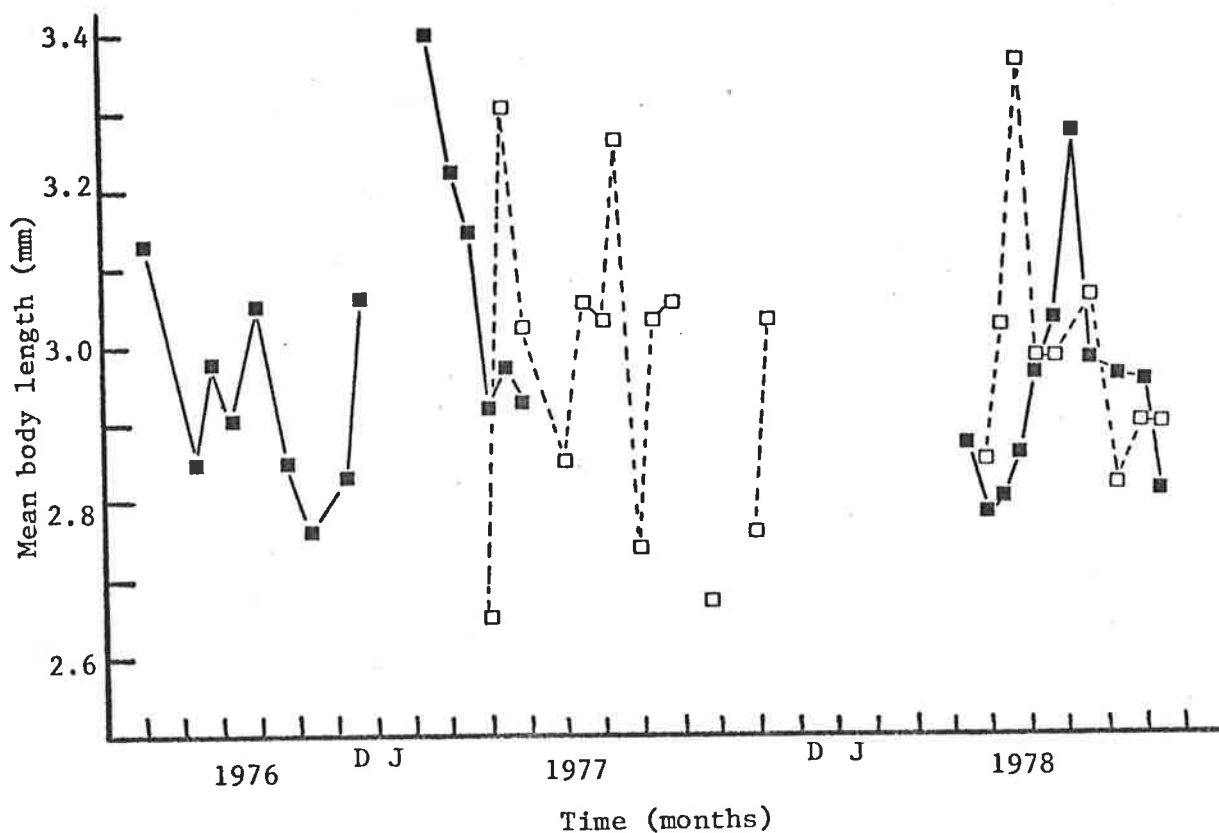


FIGURE 4.21 Mean body length of adult *D. carinata* in pond 1 (■) and pond 2 (□).

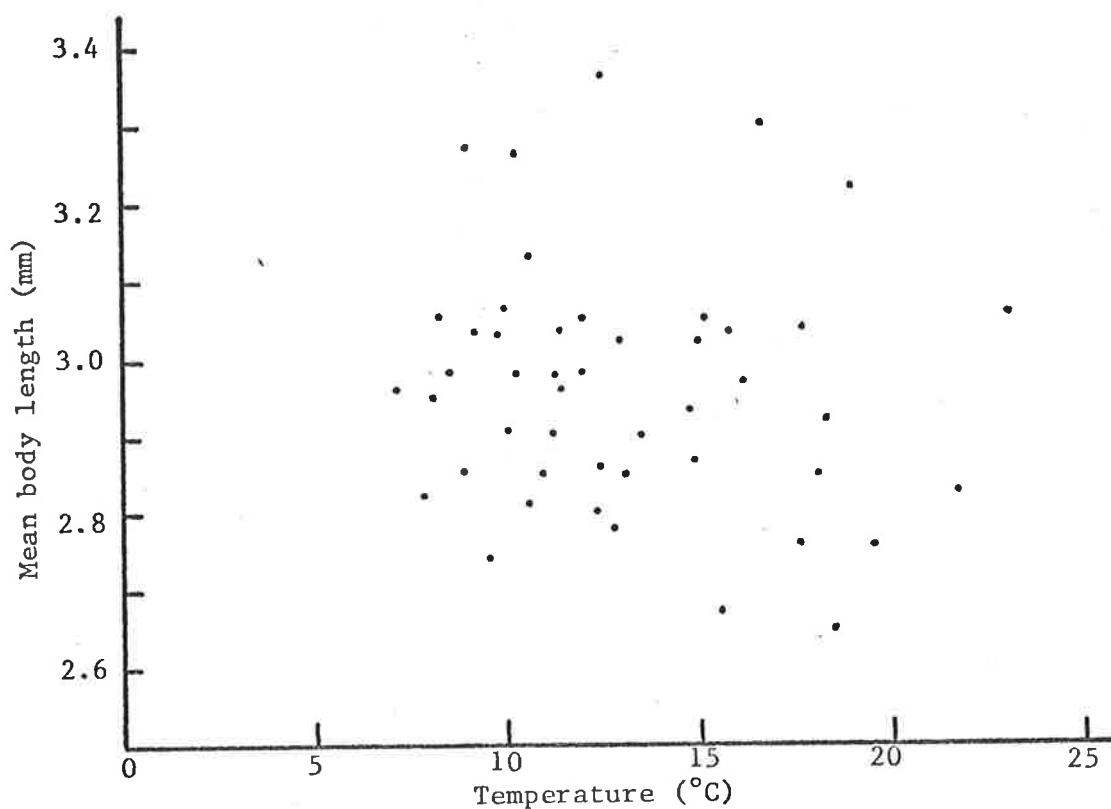


FIGURE 4.22 Mean body length of adult *D. carinata* versus depth-averaged water temperature in the Gumeracha ponds.

and populations (Hazelwood and Parker, 1963; Deevey, 1960). Deevey showed that the size of adult copepods was more strongly correlated with average temperature during the month preceding sampling than with temperature at the time of sampling. A linear regression of mean body length of *D. carinata* on mean monthly depth-averaged water temperature (for month prior to sampling; data pooled for both ponds during 1977 and 1978) showed that variation in mean monthly water temperature accounted for only 1% of the variance in mean body length.

A lack of oxygen may retard growth in *Daphnia* (Green, 1956). Minimum mean body length of *D. carinata* in pond 1 during 1978 occurred on 27 April. Dissolved oxygen concentration was very low on that date due to a decline in phytoplankton standing crop. However, mean body length minima occurred in pond 2 during periods of high dissolved oxygen concentration (1977 and 1978).

Food is also an important determinant of growth. However, no significant correlation (Spearman's ρ) was found between mean body length of *D. carinata* and chlorophyll a concentration in either pond during 1977 or 1978. *D. carinata* foraged amongst the sediments during most of the population cycle. Although temporal variation in the nutritional value of sediments may occur in large lakes (e.g. Bowen, 1979), this was considered unlikely in the Gumeracha ponds due to the constancy of organic inputs.

4.3.2.2 Reproduction. Seasonal variation in the number of ovigerous and ehippial female *D. carinata*, expressed as percentage of mature adults, in the Gumeracha ponds is presented in Figure 4.23. The percentage of females carrying middle and late stage embryos was always greater than the percentage carrying eggs. The early stages of egg development were, therefore, more rapid. A peak in the percentage of ovigerous females occurred in pond 1 in early November, 1976, during a period of recruitment and increasing population density. Ehippial

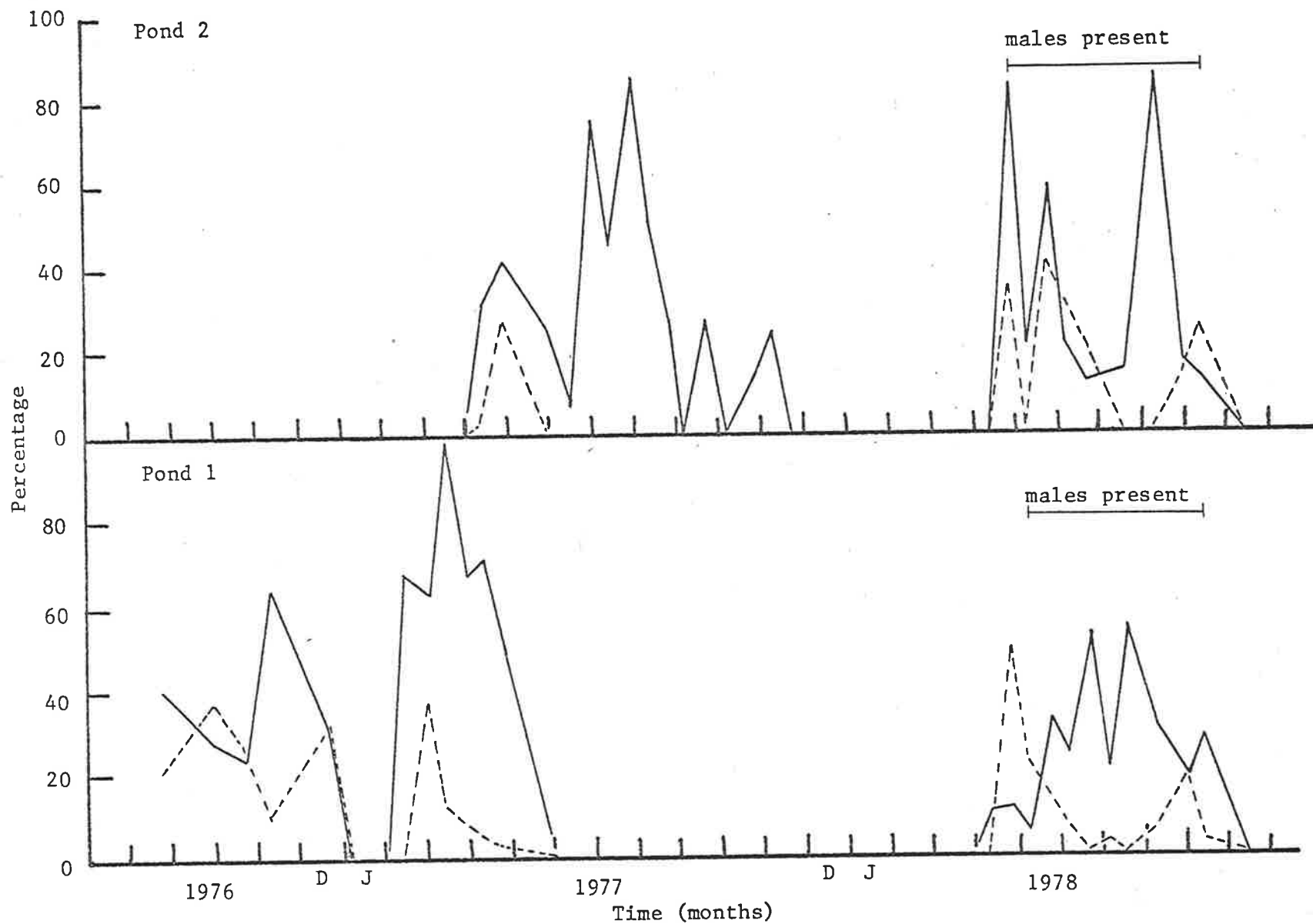


FIGURE 4.23 The number of ovigerous (—) and ehippial (----) *D. carinata* expressed as a percentage of the number of adult females in the Gumeracha ponds.

females were present throughout the latter part of 1976. The percentage of ehippial females reached a peak in late September, 1976 during a decrease in population density, and also increased in late December prior to the population decline. The percentage of ovigerous females increased rapidly during February and March, 1977 when recruitment was high and population density increasing. A small increase in the percentage of ovigerous females occurred in early April, 1977, just prior to an increase in population density. Ehippial females were present in pond 1 from mid-February, 1977, peaked in early March, and declined gradually thereafter. Several peaks in the percentage of ovigerous females occurred in pond 1 during 1978. The peak in late May occurred prior to an increase in population density; peaks in late June, late July, and early September occurred during periods of declining population density. The percentage of ehippial females peaked in late April and late August during population density peaks. During 1978, the percentage of ovigerous and ehippial females exhibited an inverse relationship. Males were generally rare but from late April, 1978, constituted 1-2% of the total *D. carinata* population; the percentage of males peaked at 6% of the total population during mid-September. Thus, a pronounced sexual phase occurred during the latter part of the *D. carinata* population cycle in pond 1, 1978.

Several peaks in the percentage of ovigerous females occurred in pond 2 during 1977. The peak in late April coincided with a peak in population density. The percentage of ovigerous females declined to 7% during mid-June. No juveniles were present in the population at that time; that is, recruitment had ceased. The percentage of ovigerous females increased markedly in late June and late July during periods of high recruitment and increasing population density. No ovigerous females were recorded in early September or early October. However, population density did not decrease at those times suggesting increased survival of

larger animals. Juveniles were present even though no females in the population were carrying eggs. This suggested that some recruitment occurred from the hatching of ephippial eggs. Peaks in the percentage of ovigerous females in pond 2 during 1978 occurred in late April, late May, and early August during periods of high recruitment and increasing population density. The decrease in percentage of ovigerous females in June and July, 1978 was reflected in reduced recruitment (increase in proportion of larger size classes) and a decrease in population density. The percentage of ovigerous females also decreased during late August and September; the population became senescent and declined at that time. Peaks in the percentage of ephippial females in late April and late May, 1978, were coincident with peaks in the percentage of ovigerous females. The percentage of ephippial females also increased during early September as the population was declining (percentage of ovigerous females and recruitment both decreasing). As in pond 1, males were rare in pond 2 until April of 1978. After that time, males constituted 1-2% of the total population but increased to 5% of the population in mid-September.

Seasonal variation in mean brood size of *D. carinata* (animals from both ponds pooled) is shown in Figure 4.24. Mean brood size fluctuated from 3.0 to 35.2 per female in 1977 and from 4.0 to 48.3 per female in 1978. Seasonal variation was similar during 1977 and 1978. Highest mean brood size occurred in February, 1977, and April, 1978, at the commencement of population cycles as population density increased rapidly. Mean brood size decreased markedly as population density approached maximal values and remained low thereafter. Small increases in brood size occurred during periods of population density increase in July, 1977, and August, 1978. Mean brood size would have been high in pond 2 during early April, 1977. As animals from both ponds were pooled, low brood sizes in pond 1 masked true brood size in pond 2. However,

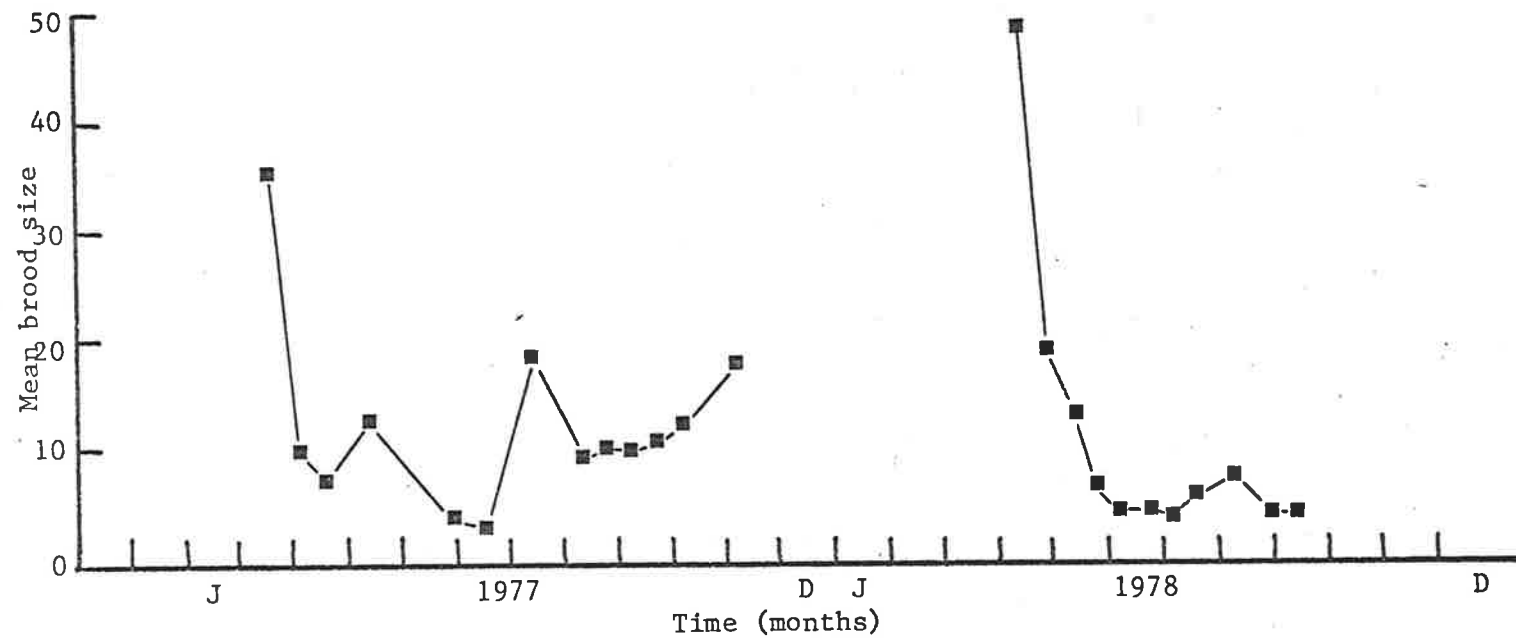


FIGURE 4.24 Mean brood size of *D. carinata* in both Gumeracha ponds.

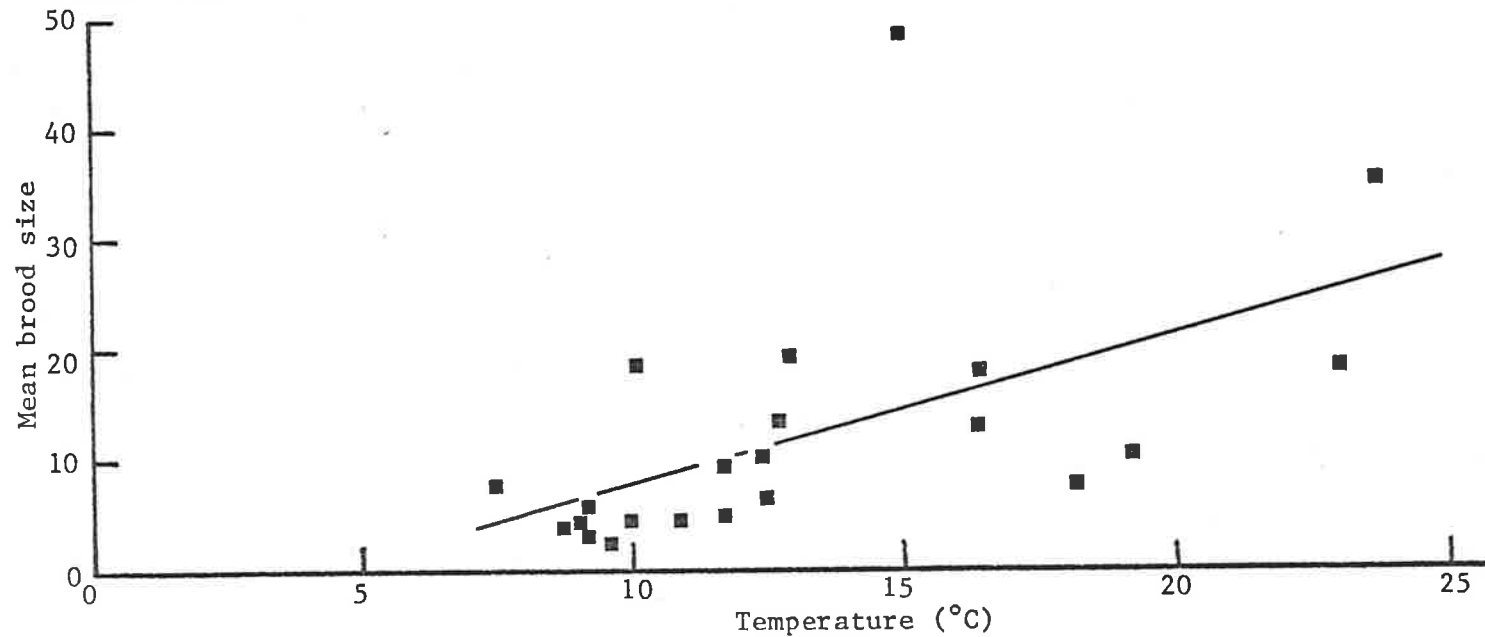


FIGURE 4.25 Mean brood size of *D. carinata* versus depth-averaged water temperature.

the increase in mean brood size in mid-April, 1977 probably reflected the contribution of high values from pond 2 animals.

Brood size in *Daphnia* is influenced by temperature, body size, and food; conditions which favour growth also favour egg production (Green, 1956). Brood size was determined from animals carrying eggs in the earliest stages of development. It is unlikely that eggs had been in the brood chamber longer than about 12 hours when collected, even at lowest water temperatures (see 4.3.1.5). Depth-averaged water temperature on the date of collection was, therefore, an adequate representation of the thermal history of eggs. Mean brood size in *D. carinata* during 1977 and 1978 has been plotted against depth-averaged water temperature in Figure 4.25. A linear regression of mean brood size on average temperature yielded a relationship of the form, $\text{mean brood size} = -5.29 + 1.32 \cdot \text{temperature}$, $r^2 = 0.29$. That is, variation in water temperature accounted for only 29% of the variance in mean brood size.

Egg number is positively correlated with body size in several species of *Daphnia* (George and Edwards, 1974; Green, 1956). Log mean brood size per size class (averaged over the entire study period) is plotted against mid size class length (mm) in Figure 4.26. A linear regression of log average brood size on body length yielded a relationship of the form, $\log \text{brood size} = -0.64 + 0.52 \cdot \text{body length}$, $r^2 = 0.99$. Variation in body length accounted for 99% of the variance in log brood size. Brood size increased continuously as body length increased. Maximum brood size recorded for an individual female *D. carinata* from the Gumeracha ponds was 147 (size class 9). Seasonal variation in average brood size per size class is shown in Figure 4.27. It can be seen that increases in mean brood size of the whole population were due to increases in the number of eggs carried by mature females of all sizes. Mean brood size of the population generally increased when mean

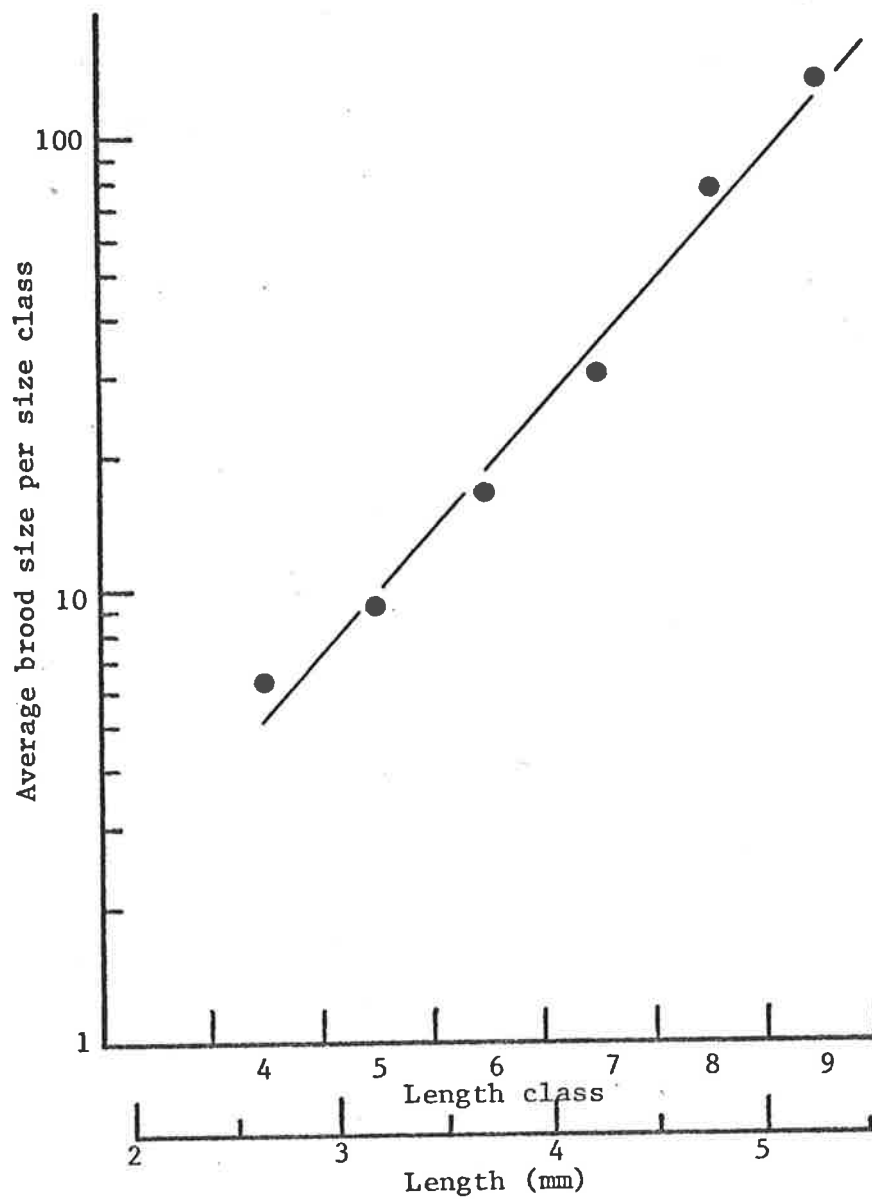


FIGURE 4.26 Average brood size per size class versus mid-size class length in *D. carinata*.

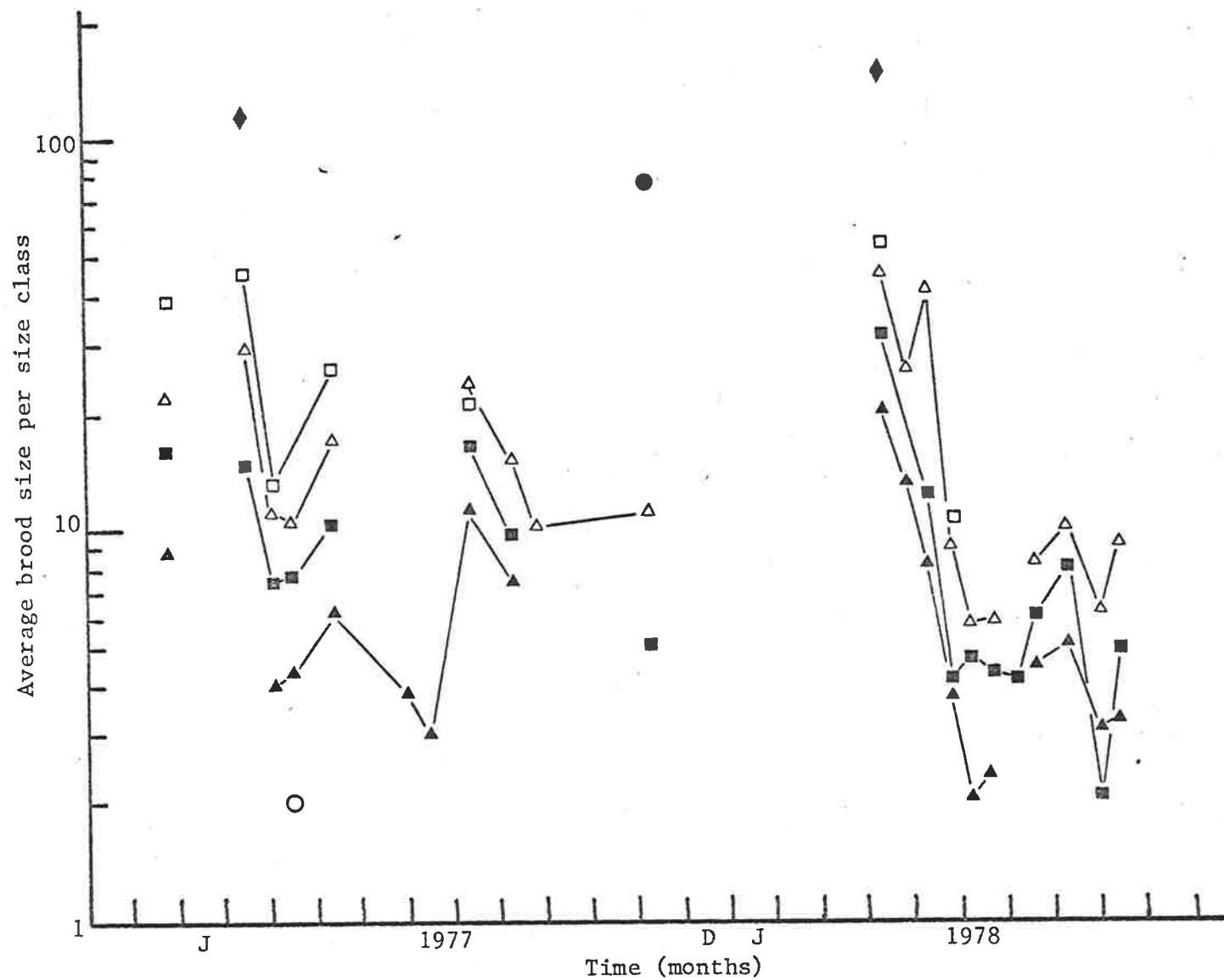


FIGURE 4.27 Average brood size per size class of *D. carinata* in the Gumeracha ponds.

body length in pond 1 and/or pond 2 increased. Average brood size per size class also increased when mean body length was high; mean brood size maxima occurred in 1977 and 1978 when size-class 9 ovigerous females were present. That is, the egg laying capacity of the population decreased as mean body length decreased.

Within a suitable temperature range, the number of eggs produced by *Daphnia* appears to be proportional to food availability (Vivjerberg, 1976; Hall, 1964; Ingle, Wood and Banta, 1937). A minimum food level may exist below which egg production ceases entirely (Lampert, 1978). Food quality affects egg production in a manner analogous to food quantity (Vivjerberg, 1976; Arnold, 1971). The feeding behaviour of *D. carinata* changed during the course of population cycles; it is, therefore, difficult to relate brood size to food availability. Mean brood size of *D. carinata* in 1978 was highest when chlorophyll a concentrations were high and declined as phytoplankton standing crops decreased and animals switched to foraging amongst the sediments. However, mean brood size in pond 1 during February, 1977, was high despite low chlorophyll a concentrations. Mean body length was also high in pond 1 at that time. Mean brood size in *D. carinata* at Gumeracha did not appear to be dependent upon food type. The effect of food availability will be discussed further in section 4.3.3.

4.3.2.3 Egg Development Time. The mean duration of development (plus 95% confidence limits) of *D. carinata* eggs is shown in Figure 4.28, together with values corrected for time in the brood chamber prior to incubation. Both curves have been drawn by eye. The number of observations (eggs hatched) at each temperature were: 10°C, n = 95; 13°C, n = 183; 16°C, n = 114; 18°C, n = 72; 23°C, n = 234. Egg development time decreased as temperature increased. The relationship between egg development time and temperature is best described by a curvilinear logarithmic function (that is, a second order polynomial)

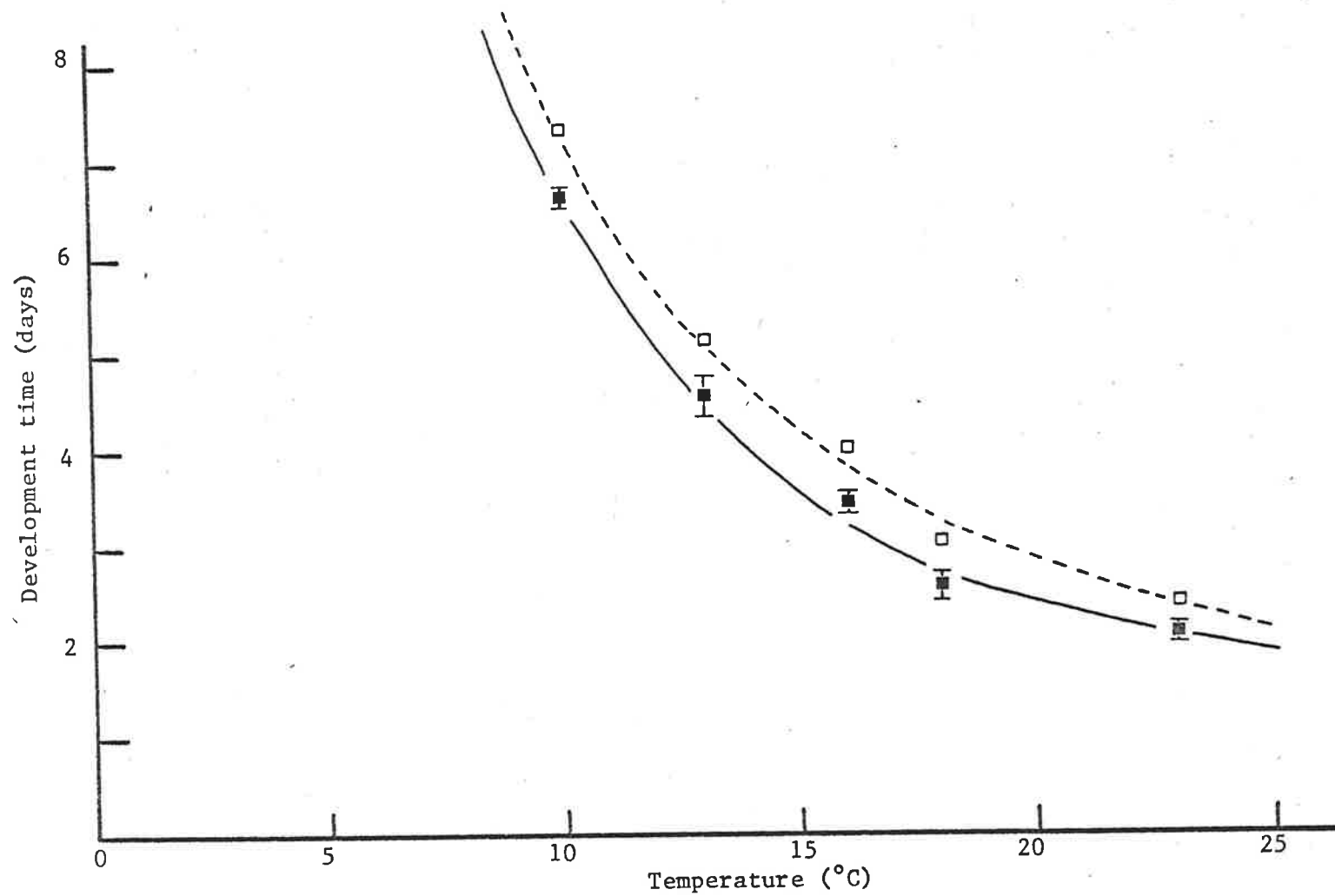


FIGURE 4.28 Measured development time (■), plus 95% confidence limits, and corrected development time (□) for the parthenogenetic eggs of *D. carinata*.

(Bottrell et al., 1976). Such a relationship could not be determined for the data presented above as data points were not equally spaced. The corrected curve was very similar to the general familial curve presented by Bottrell et al. (1976).

4.3.2.4 Population Parameters. Seasonal variation in instantaneous (or potential) growth rate, b' , actual growth rate, r' , and estimated instantaneous death rate, d' , for *D. carinata* in pond 1 is shown in Figure 4.29. Maximum b' values preceded population density maxima. b' was high early in population cycles but decreased as cycles proceeded. b' and r' both decreased as population density declined. r' values were high and positive at the commencement of population cycles but decreased and became negative as cycles proceeded. Population declines in late March, 1977 and early May, 1978 were due to a fall in b' (or birth rate). The decrease in b' in early May 1978 corresponded with a decrease in the percentage of ovigerous females in the population. b' declined gradually from June to September, 1978. b' was very high in mid-May, 1977 and the demise of the population in pond 1 at that time appeared to be fundamentally different from the decline observed in late 1978 when b' was low.

Changes in death rate generally paralleled changes in birth rate. High mortality in late February, 1977, and late March, 1978, was associated with high proportions of juveniles. However, high mortality in late April to mid-May, 1977, and late September, 1978, occurred when larger size classes were more abundant. That is, mortality of juveniles appeared to be high during periods of increasing population density while adult mortality was responsible for population declines. d' also includes prenatal mortality (George and Edwards, 1974). Highest mortality occurred during periods of increasing population density when mean brood size was high. This suggested that egg mortality may have contributed considerably to d' values.

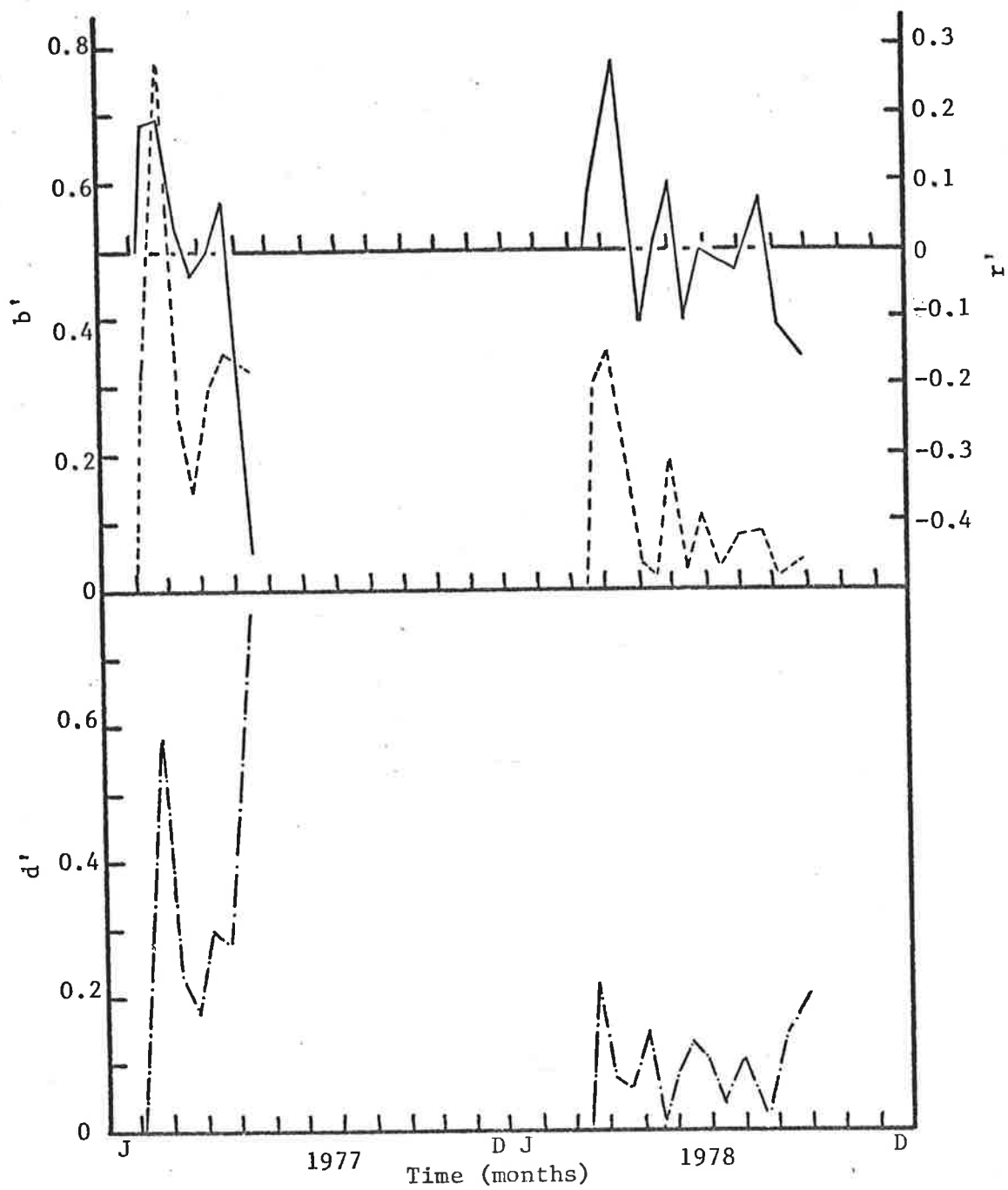


FIGURE 4.29 Population parameters b' (---), r' (—), and d' (— · —) for *D. carinata* in pond 1.

High juvenile mortality in pond 1 during February, 1977 and March-April, 1978, coincided with peaks in abundance of *M. leuckarti*. Birth rates were high at those times suggesting that predation may have contributed to decreased r' values in March, 1977, and April, 1978. However, d' was not significantly correlated with population density of *M. leuckarti* in pond 1 during 1977 ($\rho = -0.11$, $p > 5\%$). A positive correlation existed between d' and population density of *M. leuckarti* during 1978 ($\rho = 0.54$) but this was not significant at the 5% level. Very high mortality of *D. carinata* in May 1977 was associated with a reduced birth rate and a decline in recruitment.

Seasonal variation in b' , r' and d' of *D. carinata* in pond 2 is shown in Figure 4.30. As in pond 1, maximum b' values generally preceded peaks in population density; from initial high values, b' declined as population cycles proceeded. b' increased as the population entered a second major cycle during the latter half of 1977. This followed a significant decrease in population density during May. Population declines in May-June, 1977, and June-August, 1978, were associated with decreases in b' . However, b' was extremely high during the population decline in mid-November, 1977.

Although d' increased during the population decline in May-June, 1977, this was not marked. The population decline at that time was due to a decrease in the percentage of ovigerous females (and therefore b') and the cessation of recruitment. b' and d' were both very high during the population decline in November, 1977. However, no juveniles were recorded on 8 November, 1977 suggesting that egg mortality was high. The population decline during June-July, 1978 was also due to a decrease in the percentage of ovigerous females, as reflected in reduced b' values, and a decrease in recruitment. d' values increased during that period but were not high. b' increased during August, 1978 prior to an increase in population density. During

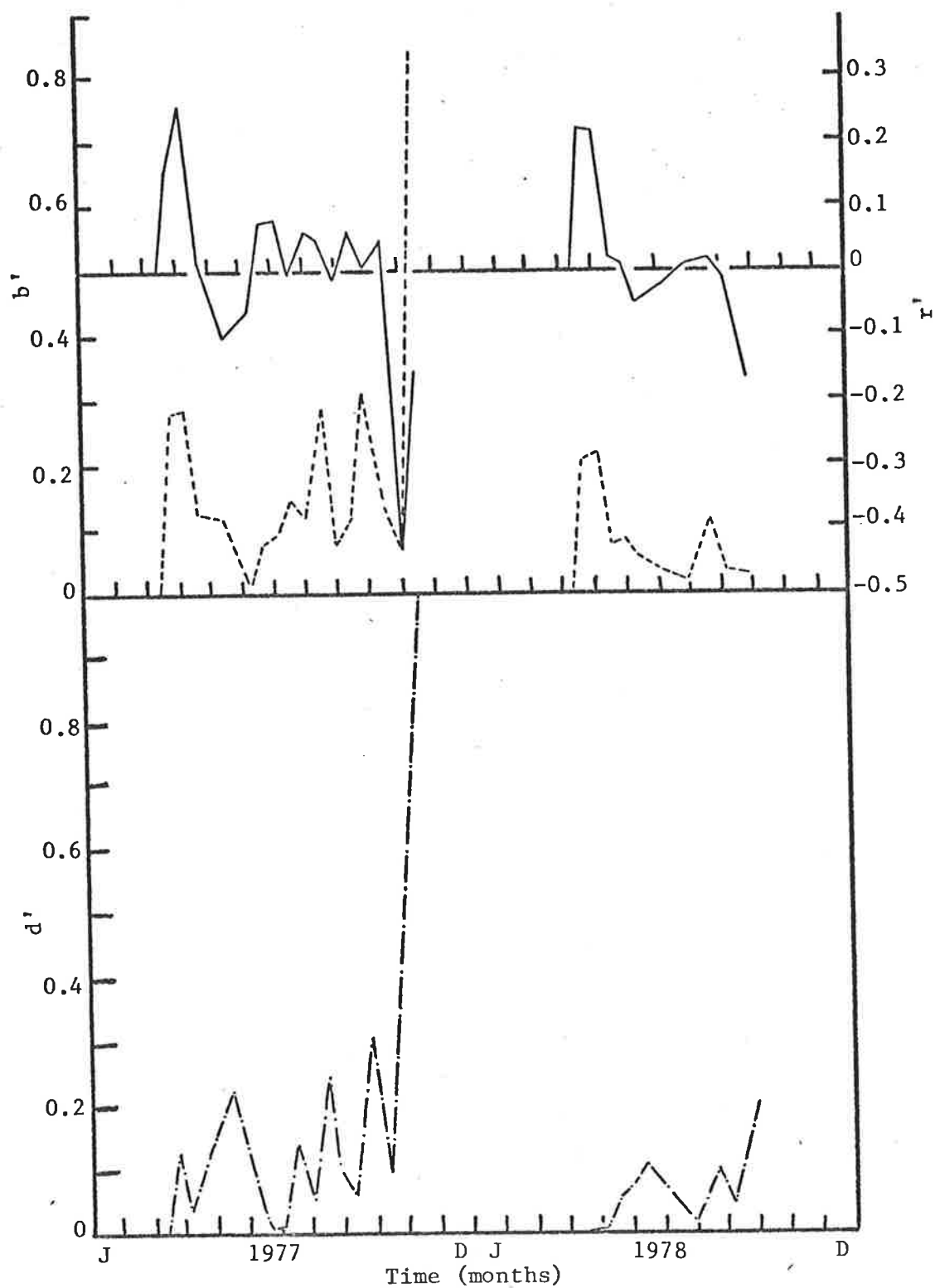


FIGURE 4.30 Population parameters b' (—), r' (---), and d' (— · —) for *D. carinata* in pond 2.

the population decline in late September, 1978, d' increased, b' decreased (percentage of ovigerous females decreased), recruitment decreased, and the population became senescent.

d' was not significantly correlated with density of *M. leuckarti* during 1977 ($\rho = 0.06$, $p > 5\%$) or during 1978 ($\rho = 0.11$, $p > 5\%$). Population peaks of *M. leuckarti* in pond 2 occurred prior to the commencement of *D. carinata* population cycles. Density of *M. leuckarti* in pond 2 was lower than in pond 1.

Mean and maximum values of the population parameters b' , r' , and d' for *D. carinata* in the Gumeracha ponds during 1977 and 1978 are presented in Table 4.8. Mean and maximum b' , r' , and d' values in both ponds were higher in 1977 than in 1978. Although maximum values of b' , r' , and d' in pond 2 were greater than in pond 1 during 1977, mean values in pond 1 were higher. Both mean and maximum values of b' , r' , and d' were higher in pond 1 during 1978.

4.3.2.5 Length-Dry Weight Relationship. A double logarithmic plot of mean dry weight (μg) per size class (plus 95% confidence limits) on mid-size class length (mm) for embryonic, juvenile and adult *D. carinata* from Gumeracha is presented in Figure 4.31. Mean dry weights of ovigerous and non-ovigerous adult females have been plotted separately. A linear regression of the natural logarithm of mean dry weight (W) on the natural logarithm of mid-size class length (L) for embryonic stages yielded a relationship of the form, $\ln W = 1.6335 + 0.0941 \cdot \ln L$, $r^2 = 0.26$. Variation in length accounted for only 26% of the variance in mean dry weight of embryonic stages. Confidence limits for the weight of embryonic stages overlapped and weight did not change significantly during embryonic development. Linear regressions of $\ln$ mean dry weight on $\ln$ mid-size class length for adults yielded relationships of the form, $\ln W = 1.3877 + 2.8335 \cdot \ln L$, $r^2 = 0.99$ for ovigerous females, and $\ln W = 1.4011 + 2.7476 \cdot \ln L$, $r^2 = 0.99$ for

Table 4.8

Mean and maximum values of population parameters b' , r' and d' , for *D. carinata* in the Gumeracha ponds during 1977 and 1978

		POND 1		POND 2	
		1977	1978	1977	1978
b'	$\bar{x}$	0.331	0.111	0.191	0.072
	Max.	0.778	0.348	0.834	0.212
r'	$\bar{x}^*$	0.119	0.110	0.077	0.051
	Max.	0.193	0.271	0.252	0.211
d'	$\bar{x}$	0.337	0.101	0.191	0.072
	Max.	0.766	0.210	0.994	0.196

* Mean positive r'

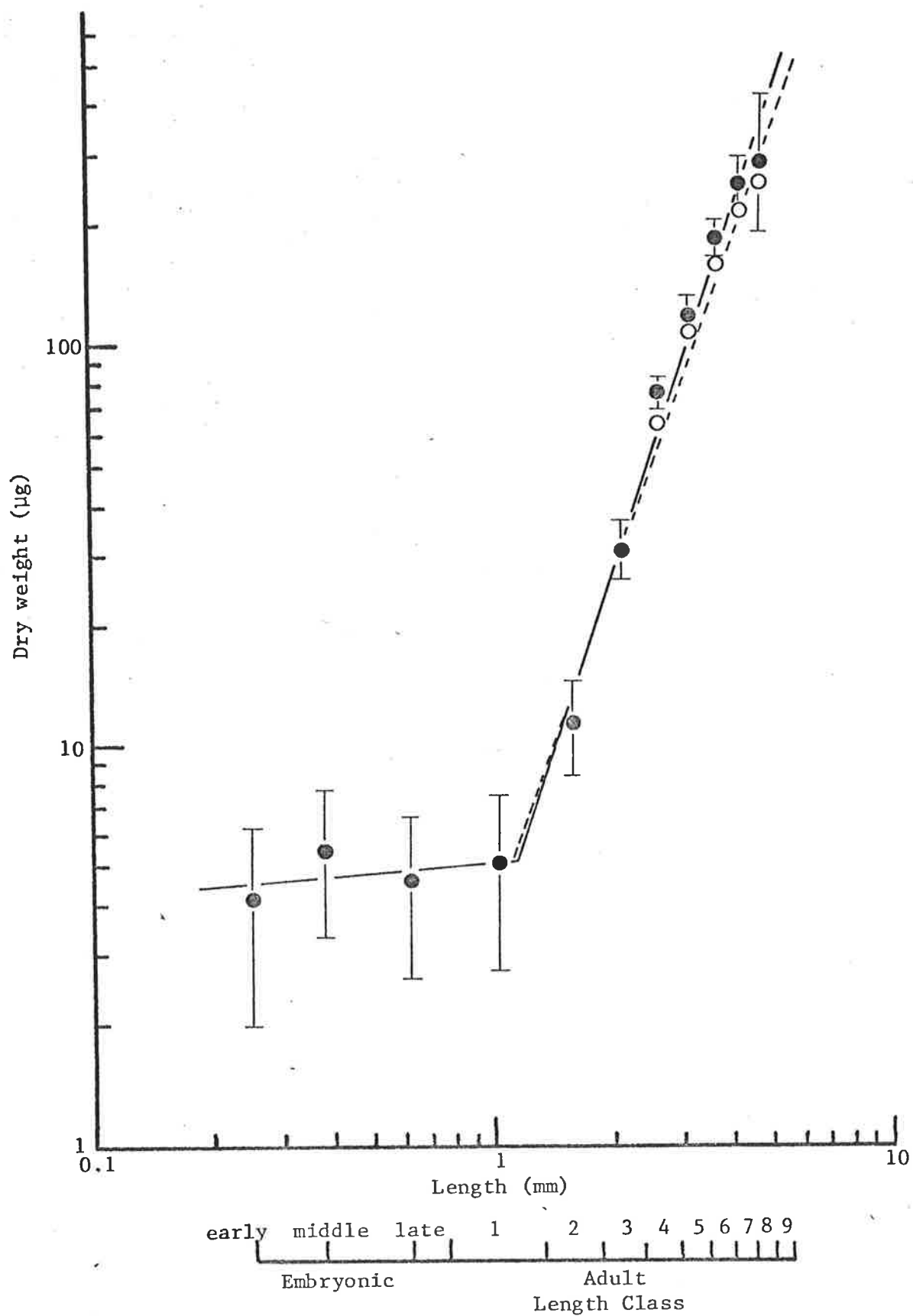


FIGURE 4.31 Mid-size class length-dry weight relationship for ovigerous (●) and non-ovigerous (○) *D. carinata*.

non-ovigerous females. Slope coefficients less than 3 indicated that, for adult *D. carinata*, weight increases were relatively smaller as length increased (Daborn, 1974). The mean weight of ovigerous females, averaged over all mature size classes, was 8.8% ($\pm$ a standard error equivalent to 18% of the mean) greater than for non-ovigerous females.

The relationships between mean dry weight and length for *D. carinata* from Gumeracha were similar to length-weight relationships for other members of the genus from a wide variety of habitats (summarized by Bottrell et al., 1976). The weight data presented above has been averaged over time and, therefore, masks any seasonal variation that may have occurred in the length-weight relationship.

4.3.2.6 Growth. Mean length (eyepiece units and mm) of female *D. carinata* has been plotted against time (days) for each temperature in Figure 4.32. Growth curves were asymptotic (or nearly so) as is typical for species of *Daphnia* (e.g. Munro and White, 1975; Anderson et al., 1937; Anderson, 1932; MacArthur and Bailie, 1929). Size class duration (read directly from growth curves) and cumulative duration at each temperature is shown in Figure 4.33. Growth was most rapid in early size classes; growth rate decreased and size class duration increased as mature animals aged. Growth rate increased as temperature increased up to 18°C. Consequently the duration of size classes decreased as temperature increased. Animals attained a greater size at higher temperatures but lived longer at lower temperatures. This pattern of growth has been reported for other species of *Daphnia* (Munro and White, 1975; Anderson et al., 1937). Had it been possible to maintain animals in the laboratory for longer periods, animals at lower temperatures may have reached larger final sizes despite lower growth rates (e.g. Green, 1956; MacArthur and Bailie, 1929). Growth rate of *D. carinata* at 24.5°C was low (between rates at 10°C and 14.5°C); the duration of length-classes increased at 24.5°C. *D. magna* and *D. pulex*

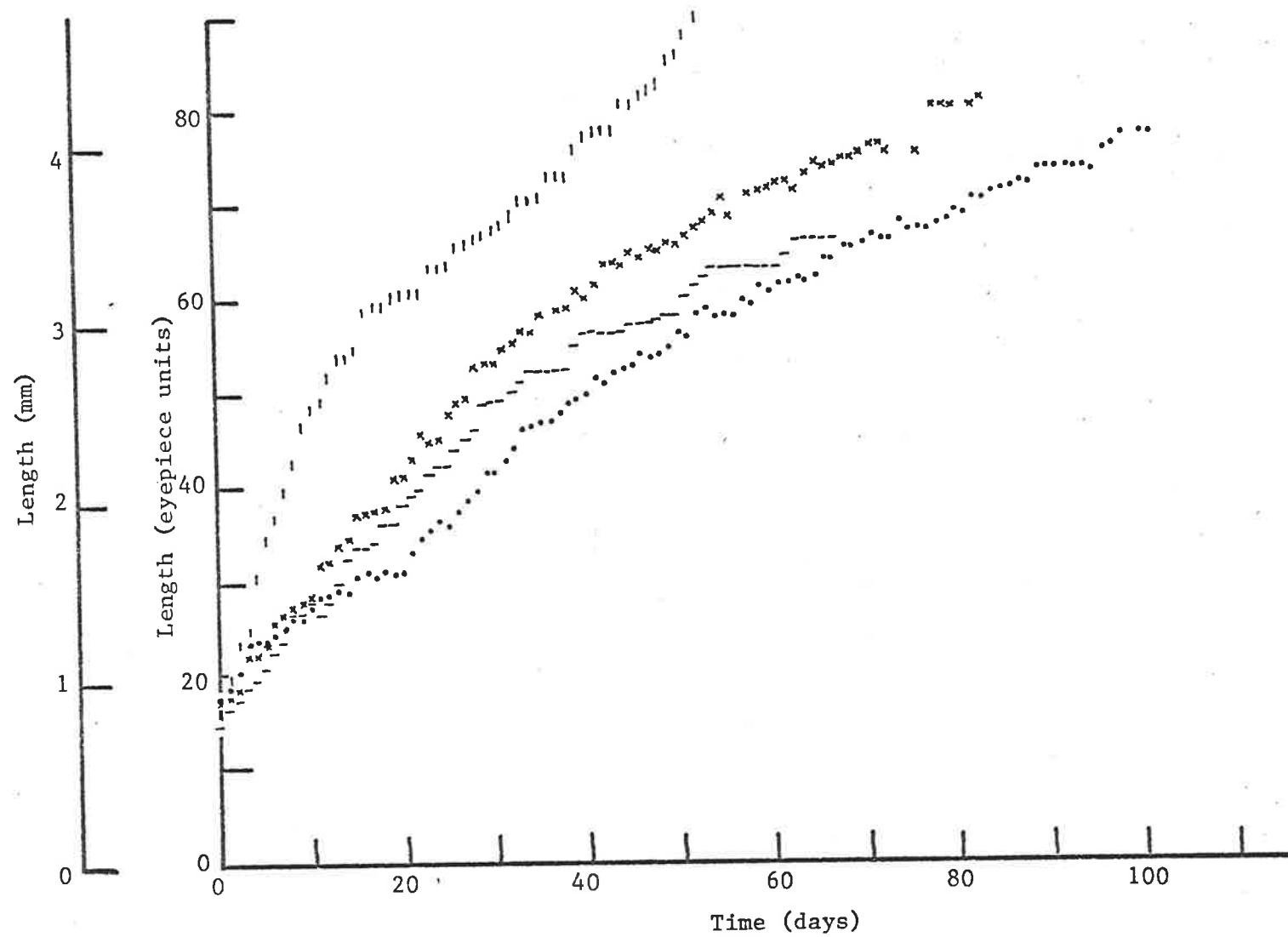


FIGURE 4.32 Growth of *D. carinata* at 10°C (•), 14.5 C°(×), 18°C (|), and 24.5 C°(—).

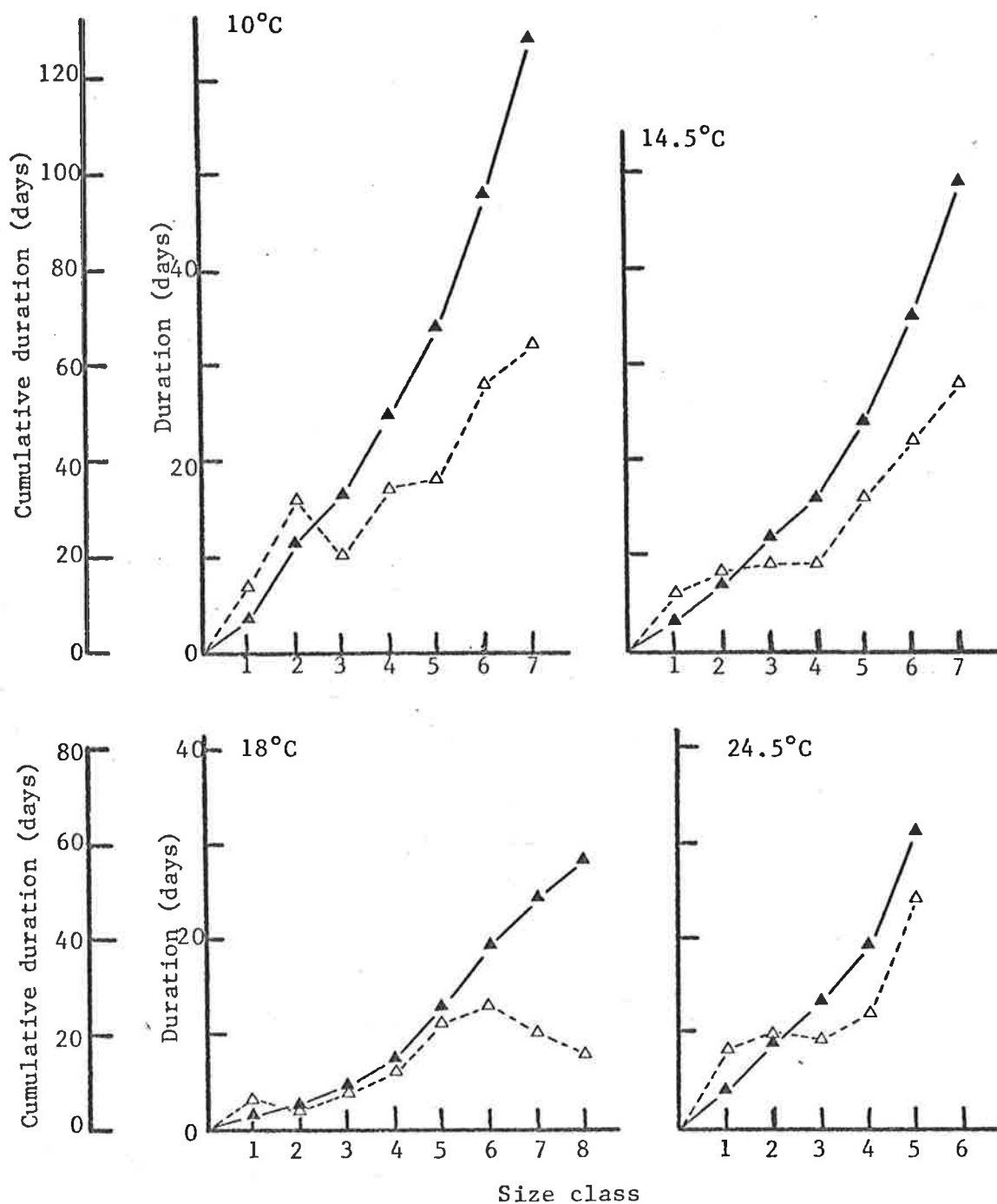


FIGURE 4.33 Size class duration (Δ), and cumulative duration ($\blacktriangle$) for *D. carinata*.

both exhibit lower growth rates at 30°C than at 25°C (Brown, 1929).

Survivorship of *D. carinata* (percentage of animals remaining alive) is plotted against time for each temperature in Figure 4.34. Mortality was similar at 10°C, 14.5°C, and 18°C, but increased markedly at 24.5°C. High temperatures were detrimental to the survival of *D. carinata* and laboratory observations were supported by field studies of seasonal occurrence. Growth experiments at temperatures between 18°C and 24°C would be required to determine the exact critical temperature above which thermal stress caused high mortality. Although growth rate was highest in the laboratory at 18°C, field studies suggested that the optimum temperature for the growth of *D. carinata* (as evidenced by peak population densities) was about 15°C.

4.3.2.7 Nitrogen and Phosphorus Content. Mean phosphorus content for *D. carinata* (all size classes pooled) from Gumeracha was 1.3% of dry weight ($\pm$ standard error equivalent to 6.1% of the mean). Mean nitrogen content of *D. carinata* was 6.6% of dry weight ($\pm$ standard error equal to 6.5% of the mean). The nutrient content of *D. carinata* was similar to that reported for *D. catawba* from a temperate, oligotrophic lake (Makarewicz and Likens, 1979). Nitrogen content of *D. carinata* was considerably lower than has been reported for zooplankton (including *Daphnia*) elsewhere (Vivjerberg and Frank, 1976; Khan and Siddiqui, 1971; Krishnamurthy, 1967; calculated from Blazka, 1966). However, variation in analytical methodology and the expression of results renders these studies less directly comparable. Phosphorus content of *D. carinata* was lower than reported for *Daphnia* by Vivjerberg and Frank (1976) but greater than reported for mixed freshwater zooplankton by Khan and Siddiqui (1971). Sufficient comparable data is not available at present to determine whether the nutrient content of zooplankton is related to habitat nutrient status.

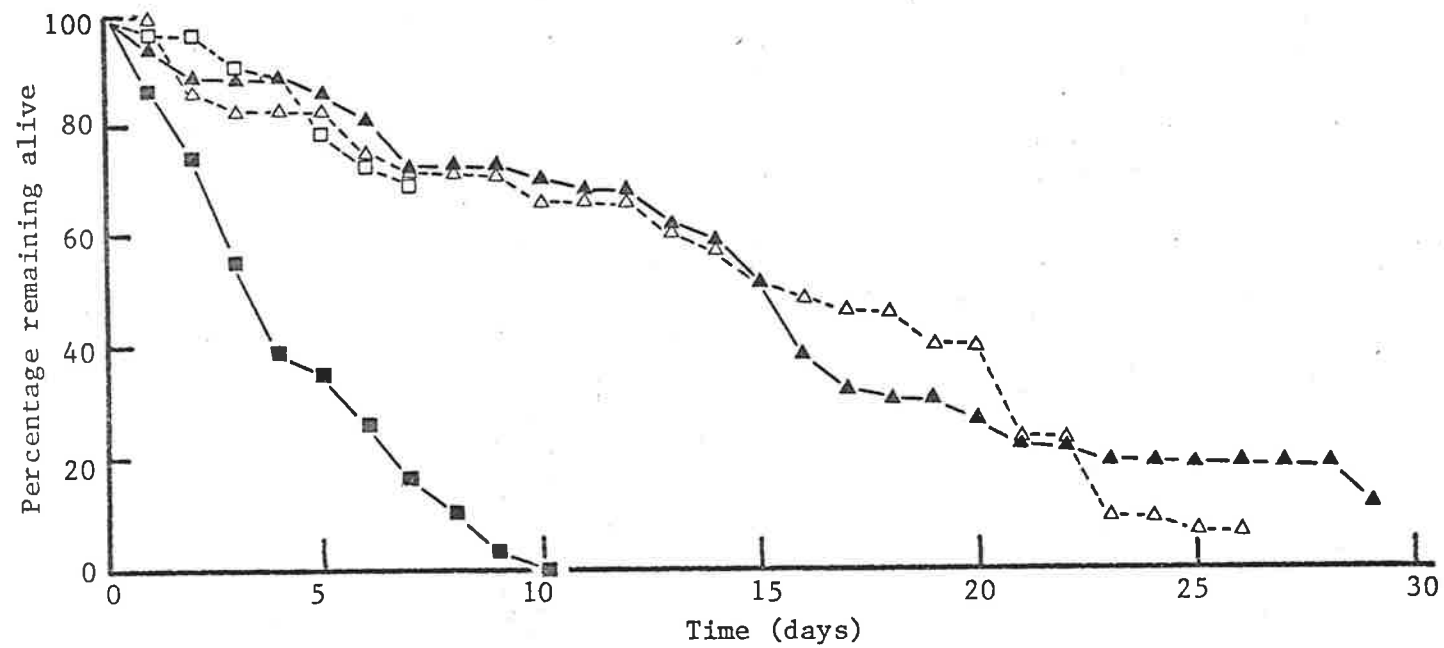


FIGURE 4.34 Survivorship (percentage remaining alive) for *D. carinata* at 10°C (▲), 14.5°C (△), 18°C (□), and 24.5°C (■).

4.3.2.8 Production

Population Turnover-time Method. Seasonal variation in standing crop biomass (mg dry weight/l) and net daily production rate (mg dry weight/l/day) of *D. carinata* in the Gumeracha ponds are shown in Figure 4.35. Production calculations, based on the population turnover-time method, for *D. carinata* in both ponds are presented in Appendix 4.

Biomass in pond 1 was low during February and March, 1977, despite high population density. This resulted from a high proportion of juveniles in the population. Maximum biomass occurred in April, 1977, coincident with a population density peak and higher proportions of larger size classes. In pond 1 during 1978, biomass peaks coincided with population density maxima. Maximum biomass in both 1977 and 1978 occurred some months after the decline of phytoplankton standing crops. Mean and maximum daily biomass in pond 1 were 8.459 mg dry weight/l and 29.529 mg dry weight/l respectively in 1977, and 9.223 mg dry weight/l and 29.106 mg dry weight/l respectively in 1978. Mean and maximum biomass were similar during both years. Net daily production followed a pattern very similar to biomass. Production has been calculated over the time interval between sampling dates and plotted at the mid-point of the sampling interval. Although mean biomass between sampling dates was used to calculate production, actual biomass on each sampling date has been plotted. Therefore, production increases appear to lag behind biomass increases. Peaks in net daily production occurred at times of population density maxima. Net daily production rate in pond 1 varied from zero to 7.896 mg dry weight/l/day in 1977 and from zero to 2.439 mg dry weight/l/day in 1978. The range of net daily production to biomass ratios (P/B) in 1977 was 0.126-0.535; mean daily P/B was 0.282, equivalent to an average biomass turnover-time during the growing season of 3.5 days. The range of daily P/B ratios in 1978 was 0.003-0.250; mean daily P/B was 0.099, equivalent to an

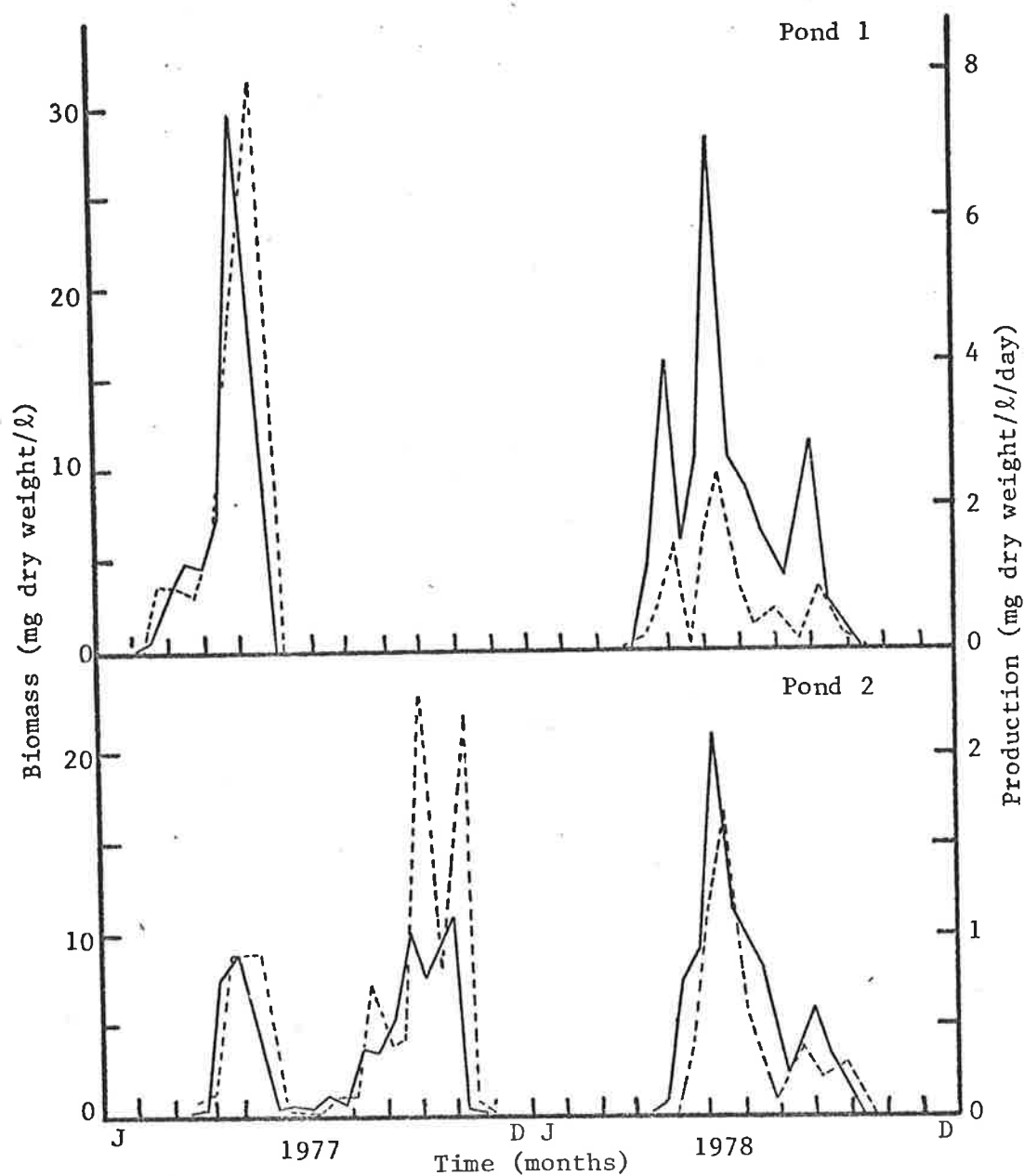


FIGURE 4.35 Standing crop biomass and daily production of *D. carinata* (population turnover-time method) in the Gumeracha ponds. Biomass (—), production (---).

average biomass turnover time of 10.1 days. Maximum daily production in pond 1 was higher in 1977 than in 1978. Although mean daily biomass was similar in both years, average turnover time was shorter in 1977.

In pond 2 during 1977 and 1978, biomass peaks coincided with population density maxima, and occurred after the decline of phytoplankton standing crops. Mean and maximum daily biomass in pond 2 were 3.738 mg dry weight/l and 10.986 mg dry weight/l respectively in 1977, and 7.713 mg dry weight/l and 21.105 mg dry weight/l respectively in 1978. Maximum and mean biomass in pond 2 were lower in 1977 than in 1978, and lower than in pond 1 during both years. Net daily production followed a pattern very similar to biomass, and production peaks occurred at times of population density maxima. Net daily production rate in pond 2 varied from zero to 2.315 mg dry weight/l/day in 1977, and from zero to 1.679 mg dry weight/l/day in 1978. The range of daily P/B ratios in 1977 was 0.004-0.630; mean daily P/B was 0.153, equivalent to an average biomass turnover time of 6.5 days. The range of daily P/B ratios in 1978 was 0.001-0.178; mean daily P/B was 0.068, equivalent to an average biomass turnover time of 14.7 days. Maximum daily net production in pond 2 was greater in 1978 than in 1977. Although average biomass turnover time was longer in 1978, mean daily biomass was much higher than in 1977. Maximum daily production rate in pond 1 was higher than in pond 2 during 1977 and 1978. This reflected higher mean daily biomass and shorter turnover times in pond 1 during both years. A linear regression of pooled daily P/B ratios from both ponds during 1977 and 1978 on depth-averaged water temperature showed that variation in temperature accounted for only 23% of the variance in P/B ratio.

Total monthly and annual net production (mg dry wt/l) of *D. carinata* in the Gumeracha ponds was calculated by determining the area under the net daily production rate curves using an Ott compensating polar planimeter, type 30 115. Total net production was converted to

g dry weight/m² of pond surface area; weighted mean monthly biomass (g dry weight/m²) was calculated by measuring the area under the daily biomass curves and dividing the total by the number of days per month. The results, together with monthly and annual P/B ratios, are presented in Table 4.9.

In pond 1 during 1977, monthly net production was highest in May; this reflected a peak in daily net production just prior to a rapid population decline. In 1978, monthly net production was highest in May but decreased gradually thereafter. In pond 2 during 1977, peaks in monthly net production occurred in May and August and coincided with times of population density peaks. In 1978, monthly net production was highest in June, coincident with a peak in population density. Annual net production in both ponds during 1977 was higher than during 1978. The *D. carinata* population in each pond turned over much more rapidly in 1977. Annual net production of *D. carinata* in pond 1 during both years exceeded production in pond 2. In 1977, annual P/B ratio in both ponds was similar but average biomass was much higher in pond 1. In 1978, average biomass in both ponds was similar but annual P/B ratio was higher in pond 1. Higher annual production of *D. carinata* in pond 1 was, therefore, due to the same rate of turnover of a higher biomass in 1977, and more rapid turnover of a similar biomass in 1978.

Biomass Turnover Method. Growth of *D. carinata* in the laboratory was most rapid at 18°C. However, field studies suggested that the optimal temperature for growth was closer to 15°C. Therefore, in the calculation of net production using the biomass turnover method, size-class duration at field temperatures was determined from the duration observed in the laboratory at 14.5°C and the formula (based on Krogh's curve) presented in Edmondson and Winberg (1971, p. 20). Although this formula is generally applied in the calculation of egg development, the relationship between temperature and developmental rate is similar for zooplankton

Table 4.9

Total monthly and annual net production (P, g dry weight/m²) based on population turnover-time method, mean monthly and annual biomass (B, g dry weight/m²), and P/B ratios for *D. carinata* in the Gumeracha ponds during 1977 and 1978

	POND 1						POND 2					
	P		B		P/B		P		B		P/B	
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978
Jan.	-	-	-	-	-	-	-	-	-	-	-	-
Feb.	14.4	-	1.1	-	13.1	-	-	-	-	-	-	-
March	30.4	*	4.9	*	6.2	-	*	-	*	-	-	-
April	115.2	17.9	16.0	8.2	7.2	2.2	17.9	*	7.0	*	2.6	-
May	184.6	28.4	15.2	11.4	12.1	2.5	25.0	13.8	4.9	8.8	5.1	1.6
June	-	60.4	-	20.3	-	3.0	1.7	44.0	0.3	16.9	5.7	2.6
July	-	16.8	-	8.4	-	2.0	1.9	12.7	0.7	9.2	2.7	1.4
Aug.	-	9.1	-	7.7	-	1.2	15.3	9.3	3.7	4.4	4.1	2.1
Sept.	-	19.0	-	4.8	-	4.0	32.8	8.8	8.5	3.9	3.9	2.3
Oct.	-	1.5	-	0.2	-	7.5	42.9	1.1	10.3	0.3	4.2	3.7
Nov.	-	-	-	-	-	-	25.7	-	1.4	-	18.4	-
Dec.	-	-	-	-	-	-	-	-	-	-	-	-
Annual	344.6 ¹	153.1	9.3 ²	8.7	37.1 ³	17.6	163.2	89.7	4.6	7.3	35.5	12.3

* Too small to be measured planimetrically

¹ Total annual production (ΣP)

² Mean annual biomass ($\bar{B}$)

³ $\frac{\Sigma P}{\bar{B}}$

eggs and adults (McLaren, 1963). The critical temperature above which thermal stress reduced growth rate and increased mortality could not be fixed accurately from laboratory growth experiments. It was assumed that the relationship between temperature and development rate was constant over the temperature range encountered by *D. carinata* in the field. This assumption appeared to be justified as egg development was more rapid at 23°C than at 18°C. However, if the critical temperature for *D. carinata* was substantially lower than 24°C, growth and therefore production, will have been overestimated at higher temperatures. As production was highest during periods of low water temperature this was not considered a serious source of error.

Seasonal variation in daily net production (mg dry weight/ℓ/day) of *D. carinata* in the Gumeracha ponds is shown in Figure 4.36. Production calculations, based on the biomass turnover method, for *D. carinata* are presented in Appendix 5. Net daily production rate in pond 1 varied from zero to 2.707 mg dry weight/ℓ/day in 1977 and from zero to 1.374 mg dry weight/ℓ/day in 1978. The range of daily P/B ratios in 1977 was 0.136-0.709; mean daily P/B was 0.272, equivalent to an average biomass turnover time of 3.7 days. The range of daily P/B ratios in 1978 was 0.018-1.163; mean daily P/B was 0.155, equivalent to an average biomass turnover time of 6.5 days. Net daily production rate in pond 2 varied from zero to 1.453 mg dry weight/ℓ/day in 1977 and from zero to 0.809 mg dry weight/ℓ/day in 1978. The range of daily P/B ratios in 1977 was 0.002-0.186; mean daily P/B was 0.079, equivalent to an average biomass turnover time of 12.6 days. The range of daily P/B ratios in 1978 was 0.012-0.329; mean daily P/B was 0.079, equivalent to an average biomass turnover time of 12.6 days. Highest daily P/B ratios occurred in both ponds during the onset of population cycles.

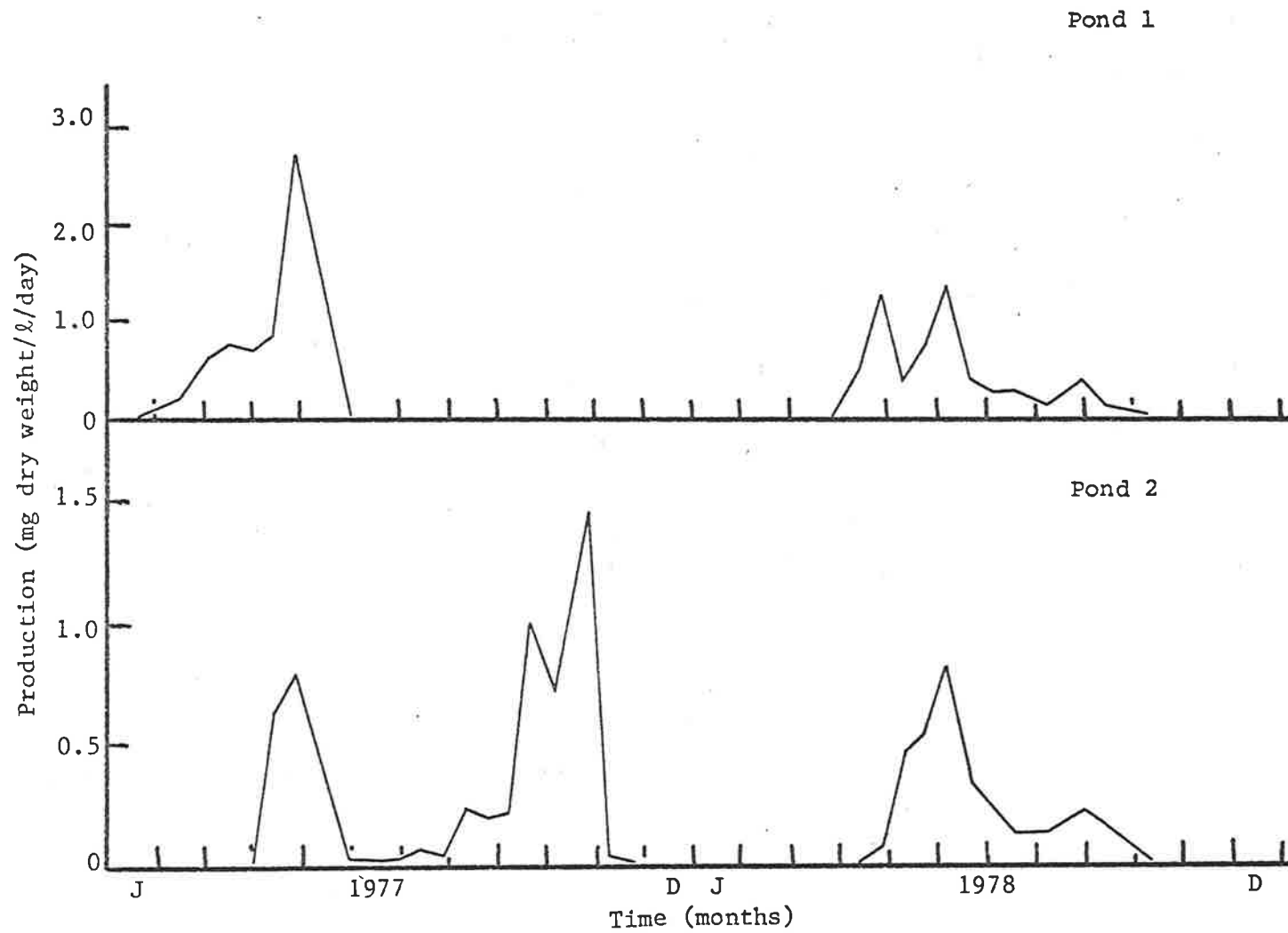


FIGURE 4.36 Daily production of *D. carinata* (biomass turnover method) in the Gumeracha ponds.

Daily net production rates calculated using the population turnover-time method always exceeded daily rates calculated using the biomass turnover method. Differences between daily net production rates were most marked in pond 1 during late April-May, 1977, and mid-June, 1978, and in pond 2 during late September-late October, 1977, and early June, 1978. These periods coincided with high population densities and large numbers of eggs in the population (and therefore high b' values), but low recruitment (that is, low r' values).

Daily net production rates calculated using the biomass turnover method showed that egg production often made the largest contribution to population production of all size classes. Daily net production of eggs, expressed as percentage of daily net production of the total population, ranged from 31 to 77% (mean = 51%, $\pm$ standard error equivalent to 12% of the mean) in pond 1 during 1977, 6 to 74% (mean = 27%, $\pm$ standard error equivalent to 22% of the mean) during 1978, and from 9 to 61% (mean = 31%, $\pm$ standard error equivalent to 26% of the mean) in pond 2 during 1977, and from 8 to 66% (mean = 25%, $\pm$ standard error equivalent to 25% of the mean) during 1978. Highest percentage contribution to total population production generally occurred at the commencement of population cycles. The contribution to total population production generally decreased with increasing size class.

Total monthly and annual net production of *D. carinata* was determined from the curves of daily production rate (calculated using the biomass turnover method) by planimetry. Total net production (g dry weight/m^2) is presented with weighted mean monthly biomass and monthly and annual P/B ratios in Table 4.10. Total annual net production in both ponds was higher in 1977 than in 1978, and during both years total annual net production in pond 1 was greater than in pond 2. Annual production patterns were the same as indicated by the population turnover-time method. Total annual net production calculated using the

Table 4.10

Total monthly and annual net production (P, g dry weight/m²) based on biomass turnover method, mean monthly and annual biomass (B, g dry weight/m²), and P/B ratios for *D. carinata* in the Gumeracha ponds during 1977 and 1978

	POND 1						POND 2					
	P		B		P/B		P		B		P/B	
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978
Jan.	-	-	-	-	-	-	-	-	-	-	-	-
Feb.	7.5	-	1.1	-	6.8	-	-	-	-	-	-	-
March	23.7	*	4.9	*	4.8	-	*	-	*	-	-	-
April	48.1	25.2	16.0	8.2	3.0	3.1	18.1	0.4	7.0	*	2.6	-
May	41.8	23.1	15.2	11.4	2.8	2.0	12.1	15.1	4.9	8.8	2.5	1.7
June	-	26.1	-	20.3	-	1.3	0.2	16.8	0.3	16.9	0.7	1.0
July	-	7.5	-	8.4	-	0.9	1.3	5.2	0.7	9.2	1.9	0.6
Aug.	-	7.1	-	7.7	-	0.9	5.8	5.0	3.7	4.4	1.6	1.1
Sept.	-	6.0	-	4.8	-	1.3	20.9	4.7	8.5	3.9	2.5	1.2
Oct.	-	0.2	-	0.2	-	1.0	36.0	0.2	10.3	0.3	3.5	0.7
Nov.	-	-	-	-	-	-	4.5	-	1.4	-	3.2	-
Dec.	-	-	-	-	-	-	-	-	-	-	-	-
Annual	121.1 ¹	95.2	9.3 ²	8.7	13.0 ³	10.9	98.9	47.4	4.6	7.3	21.4	6.5

* Too small to be measured planimetrically

¹ Total annual production (ΣP)

² Mean annual biomass ($\bar{B}$)

³ $\frac{\Sigma P}{\bar{B}}$

population turnover-time method was, on average, twice as high as total annual net production calculated using the biomass turnover method.

Mean and maximum daily P/B ratios based on the biomass turnover method were similar to, or slightly higher than, mean and maximum daily P/B ratios based on the population turnover-time method. However, daily net production rates calculated using the population turnover-time method greatly exceeded daily rates calculated using the biomass turnover method when population density (and biomass) was high and a large number of eggs were present in the population. The biomass turnover method showed that egg production made a significant contribution to total population production. Therefore, when egg or embryo mortality was underestimated production would have been greatly overestimated. The population turnover-time model assumes a stable age distribution, that is, that mortality of all size classes is constant. Seasonal variation in the number of eggs (calculated from percentage of ovigerous females and mean brood size) and the number of juveniles (size-class 1) in the populations of *D. carinata* at Gumeracha is shown in Figure 4.37. Comparison of egg number curves with population density curves showed that the rate of decline in the number of eggs was often more rapid relative to the decline in numbers of adults. This suggested departure from a stable age distribution with increased mortality of eggs or embryos (c.f. Threlkeld, 1979a). Comparison of egg numbers with the numbers of juveniles showed that considerable mortality of eggs or neonates occurred in pond 1 in April, 1977, and late May, late June, and July-August, 1978, and in pond 2 in late April, early July, early August, late September and early October, 1977, and early August, 1978. These periods generally coincided with high b' values and preceded peaks in daily production rate calculated using the population turnover-time method. High mortality (40-90%) between eggs and neonates of *Daphnia* has been reported elsewhere (Prepas and Rigler,

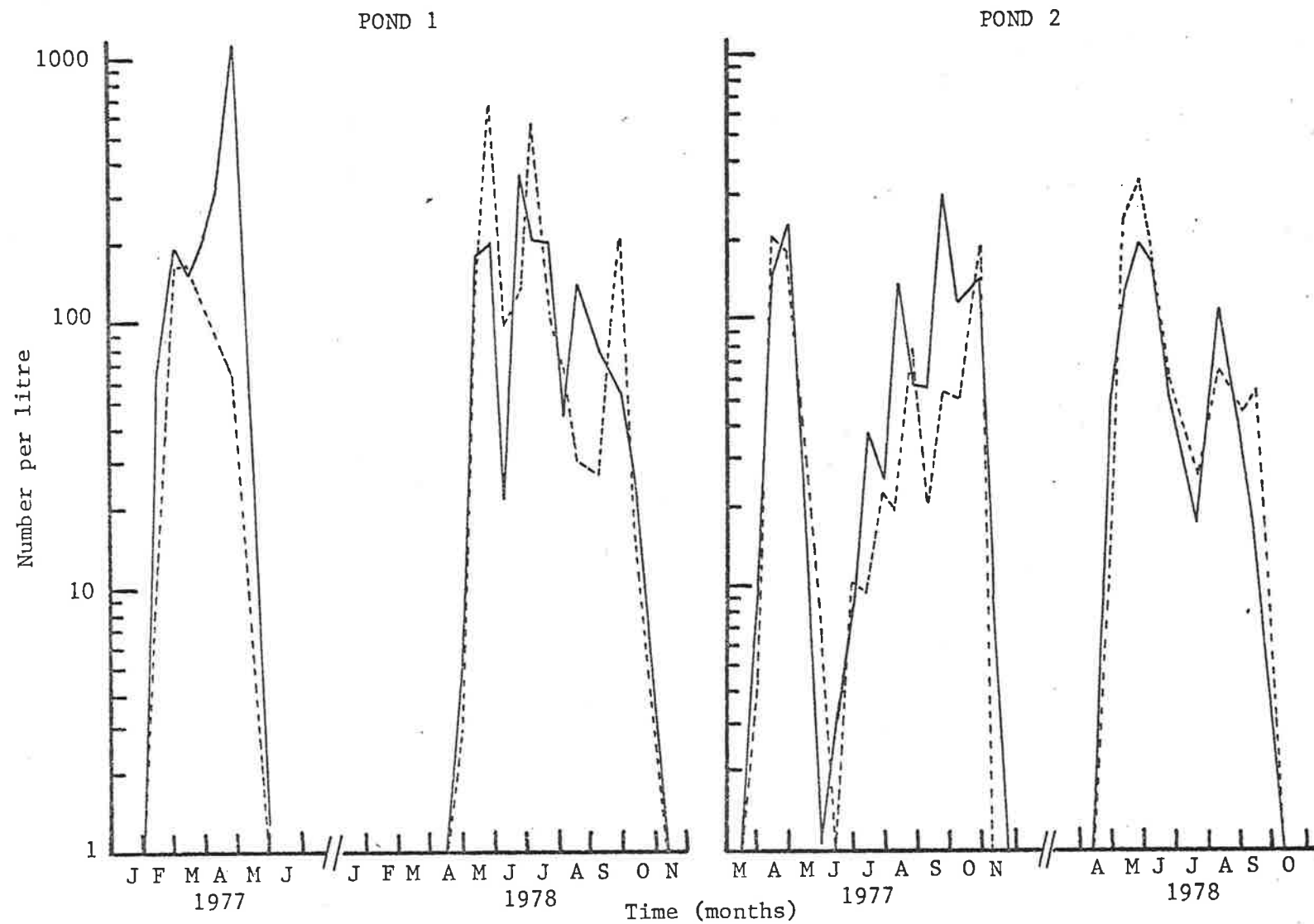


FIGURE 4.37 The number of eggs (—) and juveniles (---) of *D. carinata* in the Gumeracha ponds.

1978; Hall, 1964). Mortality may have occurred during embryonic stages (in the brood chamber) or amongst newly hatched neonates. Female *Daphnia* may abort eggs, although this generally occurs in response to high temperatures (Threlkeld, 1979b). Thus, the population turnover-time method of production calculation overestimated production of *D. carinata* during periods of increased egg mortality and departure from a stable age distribution.

On several occasions the number of juveniles of *D. carinata* in the Gumeracha ponds exceeded the number of eggs in the population. This could have resulted from the underestimation of brood size (e.g. due to egg loss on preservation) or repeated recruitment from the hatching of ephippial eggs. Vijayaraghavan (1970) has suggested that continuous recruitment from the hatching of ephippial eggs may be characteristic of *D. carinata* and the present study seems to support this. This phenomenon appears to occur in other *Daphnia* species (Duncan, 1975). Temperature changes or desiccation may not be necessary to induce hatching in the ephippial eggs of *Daphnia* (Wood and Banta, 1937, 1933).

The biomass turnover method appeared to provide more realistic estimates of annual net production than the population turnover-time method. Total annual net production of *D. carinata* during 1977 was 174.384 kg dry weight in pond 1 and 123.131 kg dry weight in pond 2. Total annual net production of *D. carinata* in pond 1 represented a nutrient store equivalent to 4.63% of total $\text{PO}_4\text{-P}$ retained in the pond during 1977, and 2.20% of TKN and 1.32% of total nitrogen ($\text{NO}_3^- + \text{TKN}$) retained during 1977. Total annual net production of *D. carinata* in pond 2 represented a nutrient store equivalent to 3.06% of total $\text{PO}_4\text{-P}$ and 17.56% of total nitrogen ($\text{NO}_3^- + \text{TKN}$) retained in the pond during 1977. Harvest of *D. carinata* did not represent a significant pathway for nutrient removal from the Gumeracha ponds.

Total annual net production of *D. carinata* in pond 1 during 1977 was equivalent to 5% of total annual net primary production and 425% of total annual net phytoplankton production. The latter result is not surprising as during most of the population cycle *D. carinata* obtained nutrition from the sediments. Total annual net production of *D. carinata* in pond 2 during 1977 was equivalent to 3.68% of total annual net primary production and 3.94% of total annual net phytoplankton production.

4.3.3 Discussion

Two types of population cycle are common amongst Nearctic and Palaearctic species of *Daphnia* (subgenus *Daphnia*) (Hebert, 1978c). In both types, *Daphnia* may overwinter or hatch from ehippial eggs in spring. During early spring a high proportion of females are ovigerous and mean brood size is high. Population density increases rapidly to reach a peak in early summer but during the latter phase of the population increase both brood size and the proportion of reproductive females decline. From peak summer densities populations may (1) collapse, and then undergo one or more similar cycles later in the year, or (2) decline slightly but remain fairly stable until the onset of winter. In both cases there is a transition from low density spring populations with high mean brood size to high density summer populations with lower egg production.

The population cycle of *D. carinata* (subgenus *Ctenodaphnia*) at Gumeracha was, in form, similar to the general cycle exhibited by Nearctic and Palaearctic *Daphnia* and conformed with (1) above. After an initial, rapid increase in density the population declined (to a varying degree) and then underwent a secondary increase and similar cycle later in the year. During the onset of the population cycle the percentage of ovigerous females and mean brood size were high but both decreased as population density increased. However, the population

cycle of *D. carinata* differed fundamentally from Holarctic species in seasonality. *D. carinata* was a cold water form and population peaks occurred in late autumn-early winter. *D. carinata* was not present during summer and populations were reestablished from diapausing ephippial eggs in autumn. At Gumeracha, the populations of *D. carinata* were intermittent in a permanent habitat. High summer temperatures, rather than low winter temperatures, were unfavourable for this species.

In pond 1 during May and July, 1978, and in pond 2 during April to June, 1977, and May to June, 1978, a dramatic reduction in reproduction occurred shortly after peaks in population density. b' and r' (and population density) decreased at those times while d' was little altered. This pattern of population change is characteristic of *Daphnia* in food-limited situations (e.g. George and Edwards, 1974). *D. carinata* foraged amongst the sediments during most of the population cycle. As discussed in section 4.2.3, it is unlikely that *D. carinata* could have depleted the sediments to a limiting level. It is more likely that a relative resource limitation occurred due to large numbers of animals attempting to feed on the sediments simultaneously. Populations of *D. pulex* (a facultative browser) in aerated WSPs may also be food-limited at times (Daborn et al, 1978). Although Frank et al. (1957) reported density-dependence of b' and r' in laboratory cultures of *D. pulex*, this was unlikely at the densities of *D. carinata* encountered at Gumeracha.

During the population decline in pond 1 in late April and May, 1977, and in pond 2 in early November, 1977, events differed considerably from the above situation in that d' increased markedly while b' remained high. This suggested that predation by *M. leuckarti* may have contributed to the population decline. However, mortality of neonates could have been caused by other factors, for example, a relative food shortage; while sufficient food could be obtained by

adults to produce eggs, those eggs may have been unable to survive past hatching. *M. leuckarti* is carnivorous only as late stage copepodids and adults (Gophen, 1977). Therefore, total numbers are not an accurate reflection of the predation pressure exerted by this species. In the absence of more detailed information on the age structure of *M. leuckarti* in the Gumeracha ponds, the lack of correlation between the density of this species and the density of *D. carinata* is not surprising.

Although carnivorous cyclopoids include smaller cladocerans in their diet (Lane, 1978; Gophen, 1977; Kerfoot, 1977a) they appear to exhibit extreme selectivity for the nauplii and copepodids of other copepods, even if cladocerans are more abundant (Brandl and Fernando, 1975; Confer, 1971). Dodson (1974) has divided cyclomorphic plankters into three groups: (1) organisms too small to experience vertebrate predation (less than 1 mm in length) and which elaborate spines or other structures to frustrate invertebrate predators; (2) intermediate sized organisms (1-2 mm) that face both vertebrate and invertebrate predation and which reduce the visible part of their body by elaborating helmets to avoid vertebrate predators; and (3) large cladocerans (greater than 2 mm) which can live only in the absence of intense vertebrate predation and resemble truly cyclomorphic forms only in small, immature stages. *D. carinata* should obviously fall within category (3). If *D. carinata* was subject to predation by *M. leuckarti*, the immature stages might be expected to exhibit cyclomorphic changes. However, the present author has shown that juvenile and primiparous stages of *D. carinata* at Gumeracha maintain constant carapace width to body length ratios throughout the year despite morphological changes in adults (see Mitchell, 1978). This suggested that predation by *M. leuckarti* did not significantly influence the populations of *D. carinata* at Gumeracha. In this regard, hemipterans and odonatans also prey upon *Daphnia* (McArdle and Lawton, 1979; Johnson, 1973) and

notonectid predation exerts considerable influence upon the morphology of adult *D. carinata* (O'Brien and Vinyard, 1978). Hemipterans and odonatans occurred in the Gumeracha ponds but were not studied quantitatively, although *Agraptocorixa* sp. and *Anisops* sp. appeared to be most abundant from late spring through summer. The intensity of this form of invertebrate predation pressure at Gumeracha remains unknown.

Population declines in both ponds during late 1978 were accompanied by gradual decreases in b' and r' and a gradual increase in d' . Populations became senescent at that time as reproduction gradually decreased in response to unfavourable environmental conditions. That is, temporal changes in *D. carinata* populations at Gumeracha resembled those operating for other species of *Daphnia* in natural habitats often characterized by variable food supplies and predation pressure.

Variation in mean brood size of *D. carinata* at Gumeracha was typical of *Daphnia* in food-limited situations (c.f. Daborn et al., 1978; de Bernardi and Canali, 1975; George and Edwards, 1974; Clark and Carter, 1974; Wright, 1965). In such situations, brood size is highest at the commencement of population cycles, declines rapidly thereafter and remains fairly constant with some minor fluctuations. Brood size is dependent upon energy intake and fecundity reflects food availability. Low mean brood size is, therefore, expected in a population that has reached the carrying capacity of its environment (Clark and Carter, 1974; Hall, 1964). Generally, the reduction of brood size to a low, constant level occurs in Nearctic and Palaearctic *Daphnia* during the summer suggesting that populations are in equilibrium with their food supplies (Hebert, 1978c; Hall, 1964). However, equilibrium is unlikely to occur for long periods (if at all) in the field (Slobodkin, 1954). In *D. carinata*, equilibrium conditions may have occurred briefly during winter.

b' values for *D. carinata* at Gumeracha were similar to those for *D. pulex* in aerated WSPs (Daborn et al , 1978). However r' values for *D. carinata* were generally lower, and d' values therefore, higher. The finding that r', b' and d' values for *D. carinata* in pond 1 exceeded values for pond 2 agreed with the results of Daborn et al. (1978) who reported lower values in the second pond of a two-pond series. r', b' and d' values for *D. carinata* at Gumeracha were generally high compared to other studies of *Daphnia* in natural water bodies; b' and d' values during 1977 were higher than reported in most studies while 1978 values were lower (c.f. Kwik and Carter, 1975; Clark and Carter, 1974; George and Edwards, 1974; Wright, 1965; Hall, 1964).

Population density of *D. carinata* at Gumeracha was similar to that of *D. pulex* in aerated WSPs (Daborn et al , 1978) but greatly exceeded that reported for *Daphnia* in any natural water body (c.f. Allan, 1977; de Bernardi and Canali, 1975; Kwik and Carter, 1975; Clark and Carter, 1974; George and Edwards, 1974; Korinek, 1966; Wright, 1965; Hall, 1964). Accordingly, mean and maximum biomass of *D. carinata* at Gumeracha greatly exceeded that previously reported for any member of the genus (c.f. George and Edwards, 1974; Duncan, 1975; Wright, 1965). Annual production of cladoceran populations has been reported from 0.7 to 110 g dry weight/m², the usual maximum being 30 g dry weight/m² (see review by Waters, 1977). Prior to this study, the maximum annual production calculated for a population of *Daphnia* using the population turnover-time method was 110 g dry weight/m² for *D. galeata mendotae* (Cummins et al., 1969). Mean annual net production of *D. carinata* in the Gumeracha ponds, calculated using the population turnover-time method, was 188 g dry weight/m². Thus, mean annual net production of *D. carinata* at Gumeracha is the highest yet recorded for any species of *Daphnia* or any species of planktonic cladoceran. Total annual net

production of *D. carinata* in pond 2 during 1978 was less than that reported for *D. galeata mendotae* by Cummins et al. (1969). Annual P/B ratios for *D. carinata* in both ponds during 1977 were very high, but the 1978 value in pond 1 was closer to average (approximately 20) (c.f. Waters, 1977). Annual P/B for *D. carinata* in pond 2 during 1978 was below average.

As discussed above, b' , r' and d' values for *D. carinata* from Gumeracha were lower than reported for some natural populations of *Daphnia*. Average and maximum mean brood size of *D. carinata* exceeded values reported in other studies of *Daphnia* from natural situations (c.f. Allan, 1977; de Bernardi and Canali, 1975; Kwik and Carter, 1975; George and Edwards, 1974; Wright, 1965; Hall, 1964). High brood size in *D. carinata* from Gumeracha could reflect the large size of the species. However, mean brood size of *D. carinata* was similar to that of *D. pulex* (a smaller species: Green, 1956) in aerated WSPs (c.f. Daborn et al., 1978). Brood size of *D. pulex* from natural habitats is much lower than reported by Daborn et al. (1978) (see Hebert, 1978a; Green, 1956). While average brood size for size class 8 and 9 females of *D. carinata* from Gumeracha was higher than previously recorded maxima for the species (Hebert, 1978c), brood sizes of size class 4 to 7 females were lower than recorded for females of the same length from other habitats (Hebert, 1978c; Navaneethakrishnan and Michael, 1970). Thus, high food conditions in WSPs appear to result in increased brood sizes, although this may be related to more favourable conditions for growth.

An increase in brood size will increase the number of eggs in the population and, therefore, increase b' . If r' is constant, d' will also increase. The turnover-time of the population will decrease, and daily percentage turnover, and therefore production, will increase. Thus, high fecundity, resulting in rapid turnover of a very high

standing crop biomass appeared to be responsible for the high production of *D. carinata* at Gumeracha during 1977. This was reflected in high annual P/B ratios. High fecundity in *D. carinata* appears to be a specific trait, but some environmental modification may have occurred in the Gumeracha ponds due to high food conditions. High production in 1978 resulted from moderate turnover of a high biomass.

Mean annual net production of *D. carinata*, calculated using the biomass turnover method, was 91 g dry weight/m². Total annual production of *D. carinata* in both ponds during 1977 and in pond 1 during 1978 exceeded the production (but not greatly) of *D. cucullata* in a eutrophic European lake calculated using the same method (Hillbricht-Ilkowska et al., 1966). Total annual production of *D. carinata* in pond 2 during 1978 was similar to that reported for *D. cucullata*. Annual P/B ratios for *D. carinata* were low compared to values presented by Hillbricht-Ilkowska et al. (1966). Daily net production rates of *D. carinata* in both ponds were much higher than reported for three species of *Daphnia* in a London reservoir (Duncan, 1975) calculated using the biomass turnover method.

The major assumption of the biomass turnover model is that growth in the laboratory is similar to that in the field under natural conditions. Food quality and quantity in the experimental situation is, therefore, of paramount importance. In growth experiments conducted during the present study, *D. carinata* was fed on pond sediment. Although the relative nutritional value of different algae for *Daphnia* has been investigated (e.g. Arnold, 1971; Schindler, 1971), no comparison has been made of the relative nutritional qualities of algae and detritus. Van Heyningen (1954) suggested that detritus had no nutritional value for *D. pulex*. This is not in accord with the finding of Horton et al. (1979) that *D. pulex* frequently utilizes the sediments

when suspended food is low. Pacaud (in Hutchinson, 1967) reported that *Daphnia* fared better on a diet of flagellates than detritus. However, as Horton *et al.* (1979) have shown, the ability of different species of *Daphnia* to utilize the sediments varies. Maximum biomass of *Daphnia* appears to occur when food quality is highest; this may even occur prior to the development of highest numerical density (George and Edwards, 1974). On this basis, detritus may have been a higher quality food for *D. carinata* than algae; maximum biomass at Gumeracha occurred several weeks after the decline of phytoplankton standing crops. It is likely the growth rate, and thus production rate, of *D. carinata* would have varied while feeding on phytoplankton.

Growth rate and longevity of *Daphnia* in laboratory cultures may both decrease as density increases (Frank *et al.*, 1957; Pratt, 1943). In growth experiments conducted during the present study, the density of *D. carinata* was equivalent to 60 animals per litre. This density would not have been high enough to cause a depression in growth rate (c.f. Frank *et al.*, 1957). In fact, experimental densities were much lower than commonly encountered at Gumeracha. Thus, in the experimental situation food may have been superabundant and growth rates may have been overestimated.

The present study showed that the population turnover-time method of production calculation gave annual production values for *D. carinata* that were about twice as high as given by the biomass turnover method. This resulted from the overestimation of daily production rates during periods of high egg or neonate mortality. The generality of this finding must await further investigation and will probably depend upon the prevalence of periods of departure from a stable age distribution. Both methods of production calculation involve assumptions, those for the biomass turnover method probably being least unrealistic. Obviously, the above finding has important implications

for all studies involving estimates of secondary production. It would be desirable for future studies to incorporate both methods, or to estimate the prevalence of egg mortality. If this is impractical, and only the population turnover-time method is used, it must be realised that calculated total annual production may be overestimated by up to 100%.

4.4 Population Dynamics and Production of *Simocephalus exspinosus*

4.4.1 Methods

Body length of *S. exspinosus* was measured (at 20 times magnification) as the longest distance from the top of the head to the tip of the posterior carapace protuberance. Mature animals were placed into 13 size classes, each being 5 eyepiece units or 0.265 mm in width (Table 4.11). The lower limit of size class 4 corresponded to carapace length at the onset of reproduction. That is, animals less than 1.325 mm in length were never observed to carry eggs. Two immature (embryonic) stages were recognised and designated "early" (including eggs) and "late". Length frequency distributions and mean length of adults on each sampling date were determined as in 4.3.1.1.

The percentage of mature adult females in reproductive condition and mean brood size on each sampling date (after 29 June, 1977) were determined as in 4.3.1.2. The population parameters b' , r' , and d' were calculated as in 4.3.1.3, and daily net production (mg dry weight/l/day) determined using the population turnover-time method as in 4.3.1.4.

The development time of parthenogenetic eggs of *S. exspinosus* was not measured directly in the present study. Length of the hatched embryo of *S. exspinosus* (having moulted the nauplius membrane) at Gumeracha (0.398 mm) and mean length of neonates (0.663 mm) were similar to values for *S. vetulus* (Hoshi, 1950) and *S. acutirostris* (Murugan and Sivaramakrishnan, 1973). Temperature-corrected egg development times

Table 4.11

Length classes for *S. exspinosus*

Length class		Micrometer units	mm	Mid-class length (mm)
Embryonic	Early	0- 5	0 -0.265	0.133
	Late	5-10	0.265-0.530	0.398
Juvenile	1	10-15	0.530-0.795	0.663
	2	15-20	0.795-1.060	0.928
	3	20-25	1.060-1.325	1.193
Sexually mature	4	25-30	1.325-1.590	1.458
	5	30-35	1.590-1.855	1.723
	6	35-40	1.855-2.120	1.988
	7	40-45	2.120-2.385	2.253
	8	45-50	2.385-2.650	2.518
	9	50-55	2.650-2.915	2.783
	10	55-60	2.915-3.180	3.048
	11	60-65	3.180-3.445	3.313
	12	65-70	3.445-3.710	3.578
	13	70-75	3.710-3.975	3.843

for *S. vetulus* and *S. acutirostris* were very similar (calculated from Murugan and Sivaramakrishnan, 1973; Hoshi, 1950). Egg development times for *S. serrulatus* reported by Ang and Fernando (1973) were much shorter at high temperatures. Therefore, egg development times for *S. exspinosus* were calculated from the figure of 1.92 days for *S. acutirostris* at 29°C (from Murugan and Sivaramakrishnan, 1973) using the equation (based on Krogh's curve) presented in Edmondson and Winberg (1971, p. 168). This equation was found to overestimate measured egg development times for *D. carinata* by a mean value of 0.16 days; egg development times for *S. exspinosus* were corrected accordingly.

The relationship between mid-size class length and mean size class dry weight for *S. exspinosus* was determined on pooled ovigerous and non-ovigerous females (collected from Gumeracha during August, 1977) as in 4.3.1.6.

4.4.2 Results

S. exspinosus occurred only briefly in pond 2 during January, 1977; the following concerns only population cycles in pond 1.

4.4.2.1 Size Distribution. Length-frequency histograms for *S. exspinosus* in pond 1 during 1977 are shown in Figure 4.38. In late October - early November, 1976, recruitment from the hatching of resting eggs initiated the population cycle. Recruitment decreased and mortality amongst larger size classes was reduced in December, 1976. Recruitment increased during January, 1977, and large numbers of juveniles contributed to the population density peak in mid-January. Recruitment continued during February while juveniles from the mid-January peak increased in length. Mortality of the larger size classes was high during that period. Recruitment occurred during March and April, 1977, but mortality of larger size classes was extremely high. Population density declined to less than 1 animal per litre at that time.

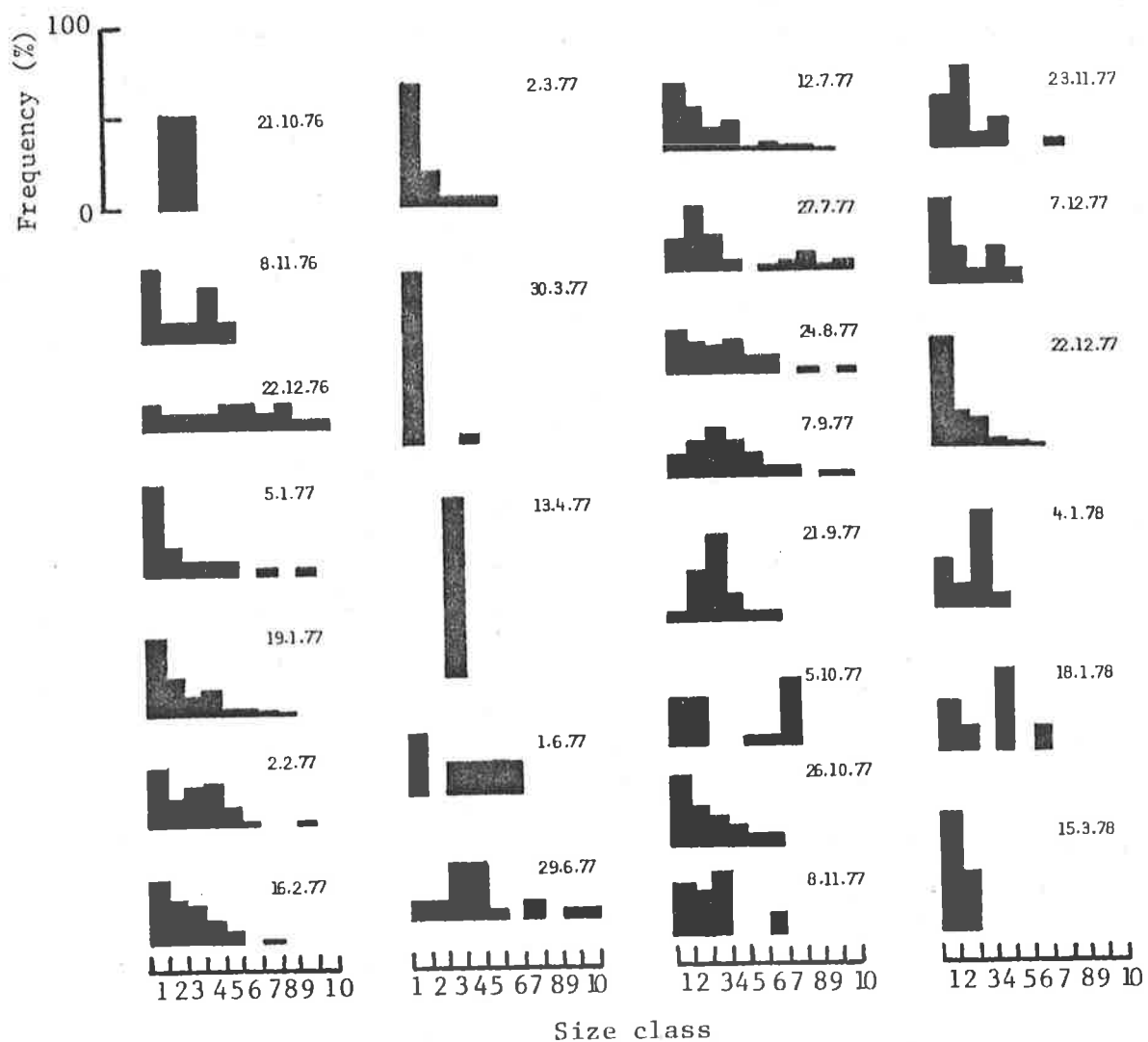


FIGURE 4.38 Length-frequency distribution of *S. exspinosus* in pond 1.

Recruitment decreased during June and animals increased in length. Recruitment increased somewhat during early July, contributing to an increase in population density, but declined thereafter and remained low until late October. Although recruitment was low from July to October, mortality amongst the larger size classes also decreased and population density remained fairly constant. Recruitment increased during October–December but mortality of larger size classes also increased. Peak population density in late December, 1977, was due to large numbers of juveniles. Recruitment declined during January, 1978, and mortality of larger size classes was high. Both factors contributed to the population decline in January and February. A small burst in recruitment occurred from the hatching of ephippial eggs in March, 1978. However, high mortality prevented the development of large numbers. Recruitment in *S. exspinosus* was continuous. However, reproduction appeared to be synchronized to some extent in that periodic bursts of recruitment (and high adult mortality) were interspersed with periods of reduced recruitment and low adult mortality.

Seasonal variation in mean body length of mature female *S. exspinosus* in pond 1 during 1977 is shown in Figure 4.39. Mean body length of *S. exspinosus* ranged from 1.46 to 2.35 mm. Maxima occurred in late December, 1976 (2.13 mm: depth averaged water temperature was 23.0°C), early August, 1977 (2.35 mm: depth averaged water temperature was 12.0°C), and early October, 1977 (2.16 mm: depth averaged water temperature was 16.1°C). It appeared that, as was the case for *D. carinata*, high mean body length in *S. exspinosus* could occur at high temperatures due to rapid growth, or at low temperatures due to increased longevity.

Mean body length of mature *S. exspinosus* has been plotted against depth-averaged water temperature on the date of sampling in Figure 4.40. A linear regression of mean body length on water

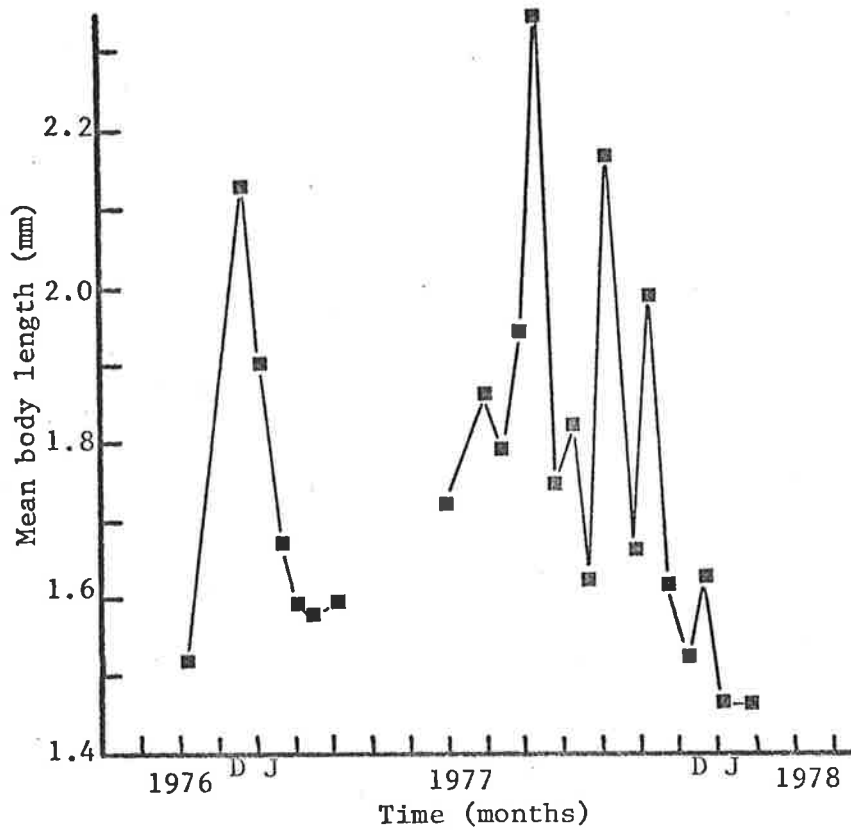


FIGURE 4.39 Mean body length of adult *S. exspinosus* in pond 1.

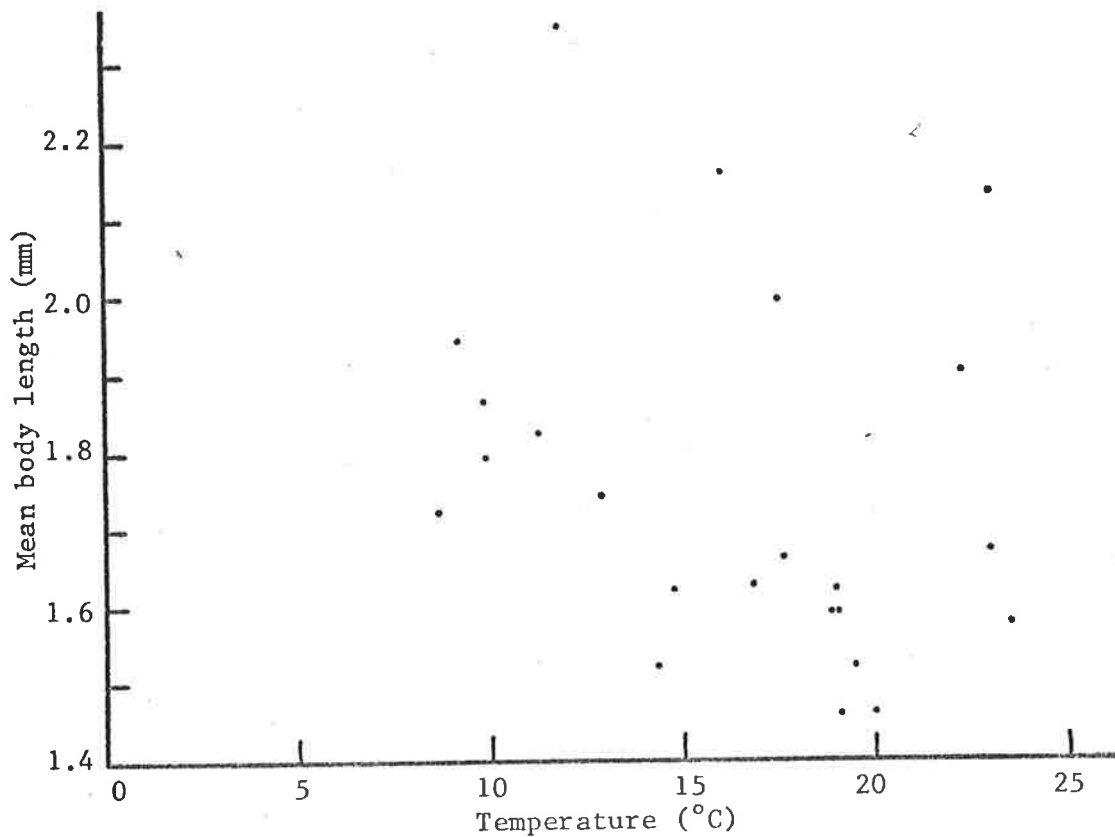


FIGURE 4.40 Mean body length of *S. exspinosus* versus depth-averaged water temperature in pond 1.

temperature showed that variation in temperature accounted for only 7% of the variance in mean body length. A linear regression of mean body length on depth-averaged water temperature over the month prior to sampling showed that variation in mean monthly water temperature accounted for only 14% of the variance in mean body length. These results contrast with the finding of Green (1966) that mean body length of *S. vetulus* is negatively correlated with water temperature above 18°C. Mean body length was negatively correlated with chlorophyll a concentration ($\rho = -0.56$, $5\% > p > 1\%$).

4.4.2.2 Reproduction. Seasonal variation in the number of ovigerous and ehippial female *S. exspinosus* (expressed as percentage of number of mature adults) in pond 1 is shown in Figure 4.41. The percentage of ovigerous females reached peaks in late October, 1976, early January, early November, and late December, 1977, during periods of pronounced recruitment prior to population density increases. The percentage of ovigerous females decreased from late January to early April, 1977 (3%) during a major decline in population density. Ovigerous females increased in April and May during a period of pronounced recruitment but only gradually increasing population density (high mortality amongst larger animals). Although the percentage of ovigerous females (and therefore recruitment) declined during June, 1977, population density increased in late June due to increased survival of larger animals. Ovigerous females peaked in late July but decreased in August. Ovigerous females increased during October and early November. Although recruitment was high, mortality of larger animals increased and population density was little altered. The percentage of ovigerous females declined markedly in late November - early December and population density decreased slightly; confidence limits were very wide at that time. No ovigerous females were present after January, 1978. Recruitment in mid-March was from ehippial eggs.

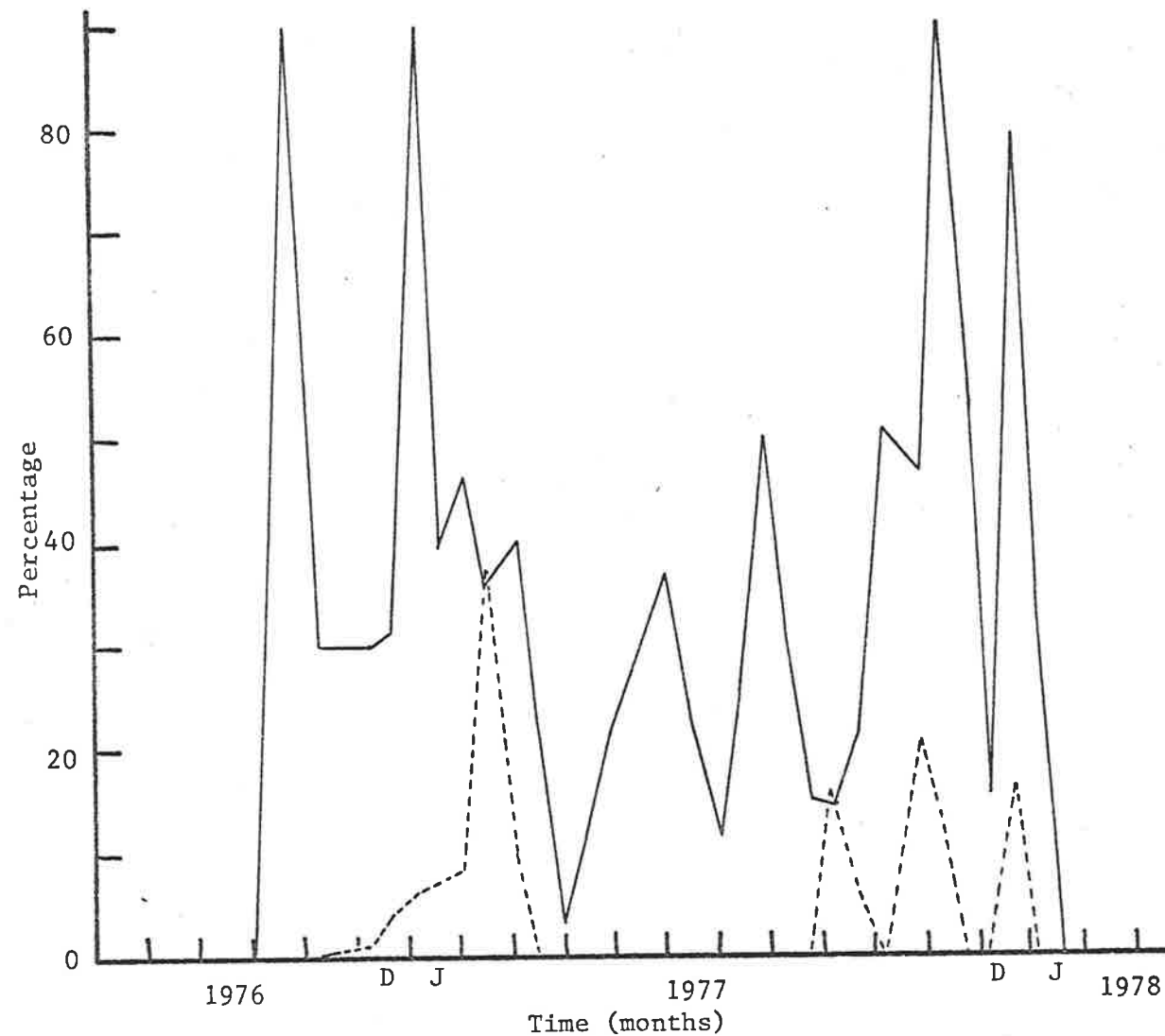


FIGURE 4.41 The number of ovigerous (—) and ehippial (---) *S. exspinosus* expressed as a percentage of the number of adult females in pond 1.

Peaks in the percentage of ehippial females coincided with, or occurred just prior to, decreases in population density.

Variation in mean brood size of *S. exspinosus* in pond 1 from late June, 1977, is shown in Figure 4.42. Mean brood size decreased rapidly during July; thereafter, mean brood size showed a less rapid but continued decrease until the population declined in January, 1978. Although maximum mean brood size of *D. carinata* was much higher than that of *S. exspinosus*, average mean brood size of the two species were not significantly different during 1977 (Mann-Whitney U test, $p > 0.05$).

Body size, temperature, and food are all important factors influencing brood size in *Simocephalus* (Green, 1966). Brood size, determined individually on live *S. exspinosus* collected in June and July, 1977, has been plotted against body length (mm) in Figure 4.43. A linear regression of brood size on body length gave a relationship of the form, $\text{brood size} = 24.85 \cdot \text{length} - 39.88$, $r^2 = 0.79$. That is, variation in body length accounted for 79% of the variance in brood size. The intercept on the X-axis (1.6 mm) showed close agreement with body length at the onset of reproduction (1.45 mm). The maximum individual brood size recorded for *S. exspinosus* from Gumeracha was 42 in a size class 12 female (2.92 mm body length).

Log mean brood size per size class, averaged over the entire study period, has been plotted against mid-size class length (mm) in Figure 4.44. A linear regression of log average brood size on mid-size class length gave a relationship of the form, $\log \text{mean brood size} = 0.49 \cdot \text{length} - 0.29$, $r^2 = 0.97$. That is, variation in mid-size class length accounted for 97% of the variance in average brood size per size class. A strong positive relationship existed between body length and brood size in *S. exspinosus*. However, in the field, mean brood size and mean body length were not significantly correlated ($\rho = 0.68$, $p > 5\%$).

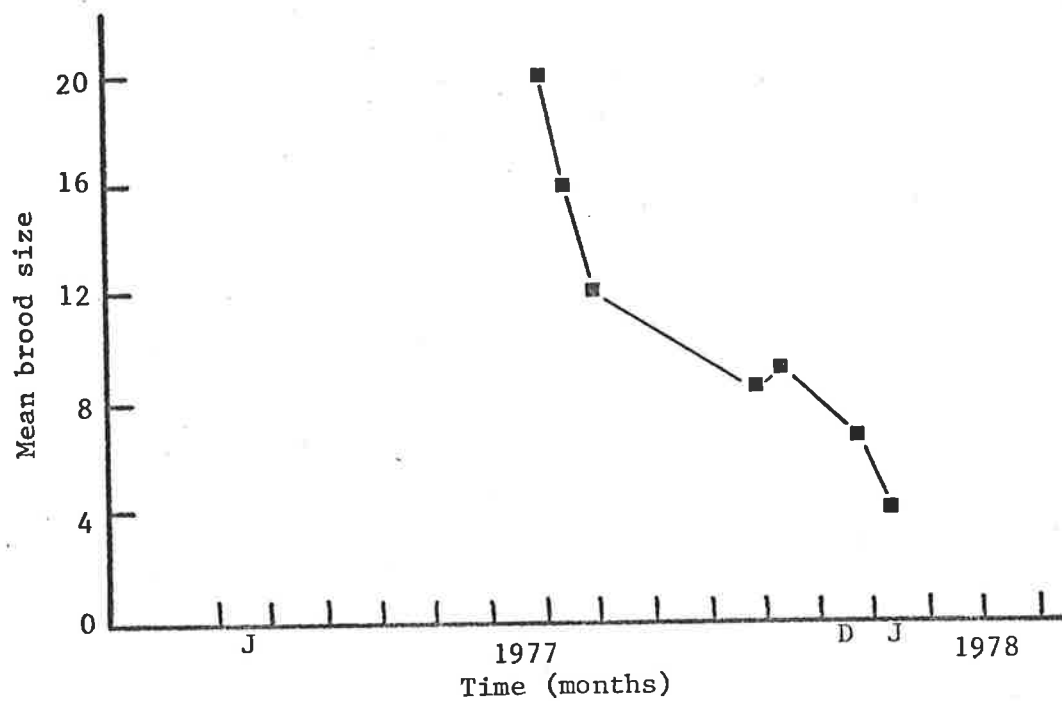


FIGURE 4.42 Mean brood size of *S. exspinosus* in pond 1.

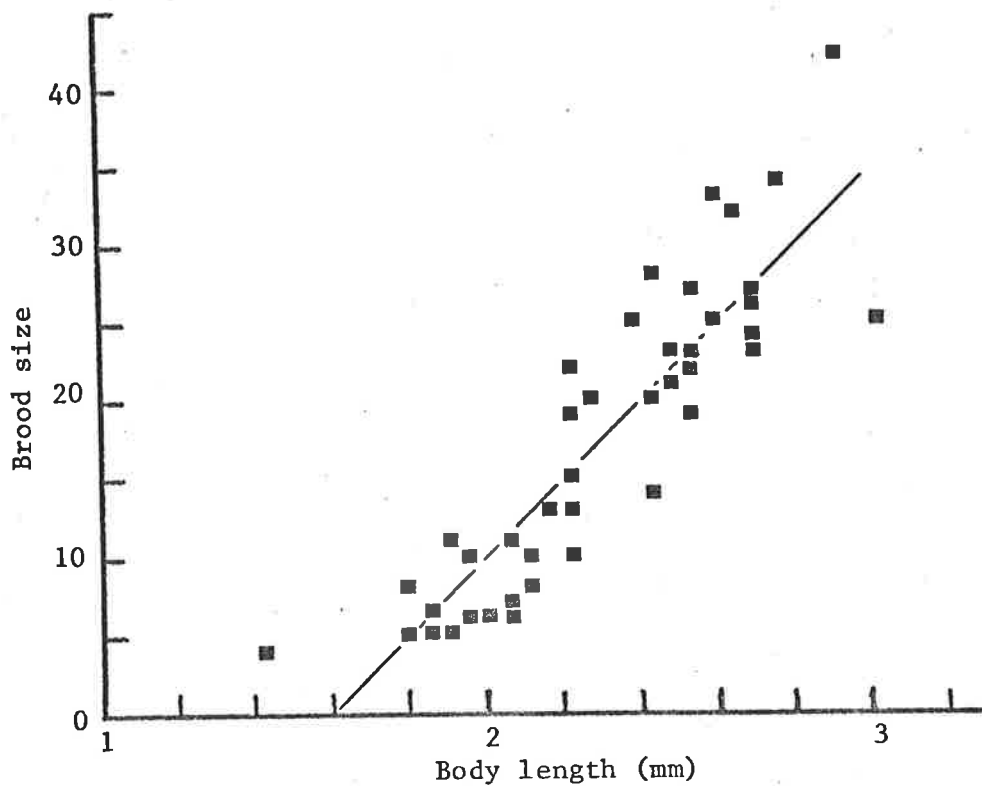


FIGURE 4.43 Brood size versus body length of *S. exspinosus* in pond 1.

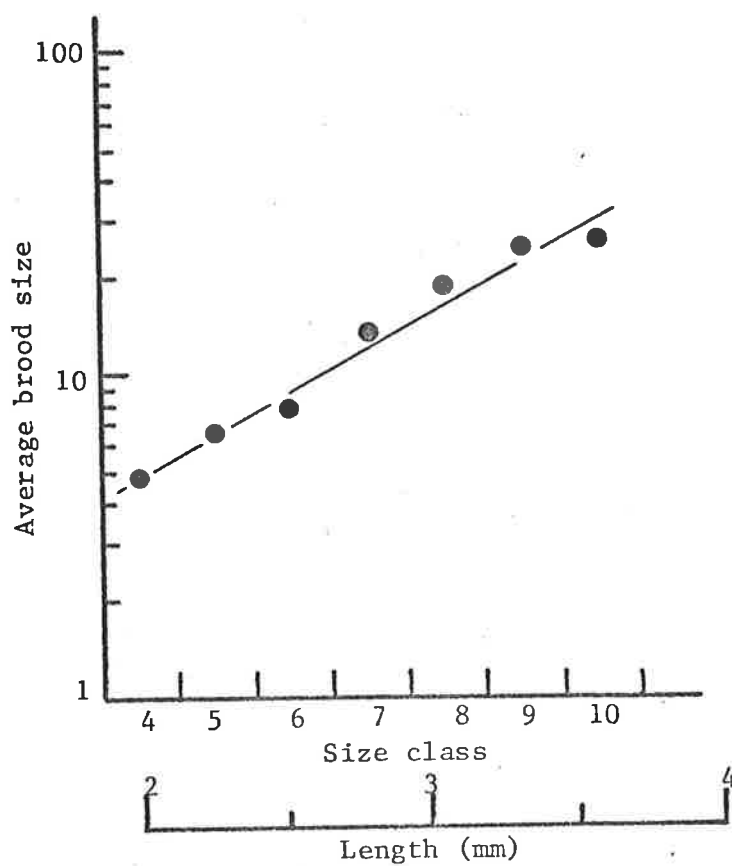


FIGURE 4.44 Average brood size per size class versus mid-size class length of *S. exspinosus*.

A strong negative correlation was found between mean brood size of *S. exspinosus* and chlorophyll a concentration (on the date of sampling) ($\rho = -0.96$, $p < 0.1\%$). This suggested that *S. exspinosus* may also have gained nutrition from the sediments.

Log mean brood size of *S. exspinosus* has been plotted against depth-averaged water temperature on the date of sampling in Figure 4.45. A linear regression of log mean brood size on average water temperature gave a relationship of the form, $\log \text{ mean brood size} = 1.64 - 0.05 \cdot \text{temperature}$, $r^2 = 0.78$. That is, variation in average water temperature accounted for 78% of the variance in log mean brood size. Thus, a strong negative relationship existed between mean brood size and water temperature. On a seasonal basis in the field, this appeared to override the relationship between brood size and body length. Low mean brood size in *S. vetulus* also occurs at high temperatures as females become mature at a smaller size thereby restricting egg-laying capacity (Green, 1966). For the calculation of population parameters, mean brood size on each sampling date from November, 1976, until June, 1977, was back-calculated from the relationship between log mean brood size and depth-averaged water temperature.

4.4.2.3 Population Parameters. Seasonal variation in instantaneous growth rate, b' , actual growth rate, r' , and instantaneous death rate, d' , of *S. exspinosus* in pond 1 is shown in Figure 4.46. Peaks in r' during mid-January, late June, and mid-December, 1977, corresponded with periods of high recruitment and, therefore, high or increasing population density. The population decline in March, 1977, was due to a decrease in the percentage of ovigerous females and concomitant reductions in b' and r' . r' was low from July to November, 1977; recruitment was generally low and survival of the larger size classes high during that period. Maximum

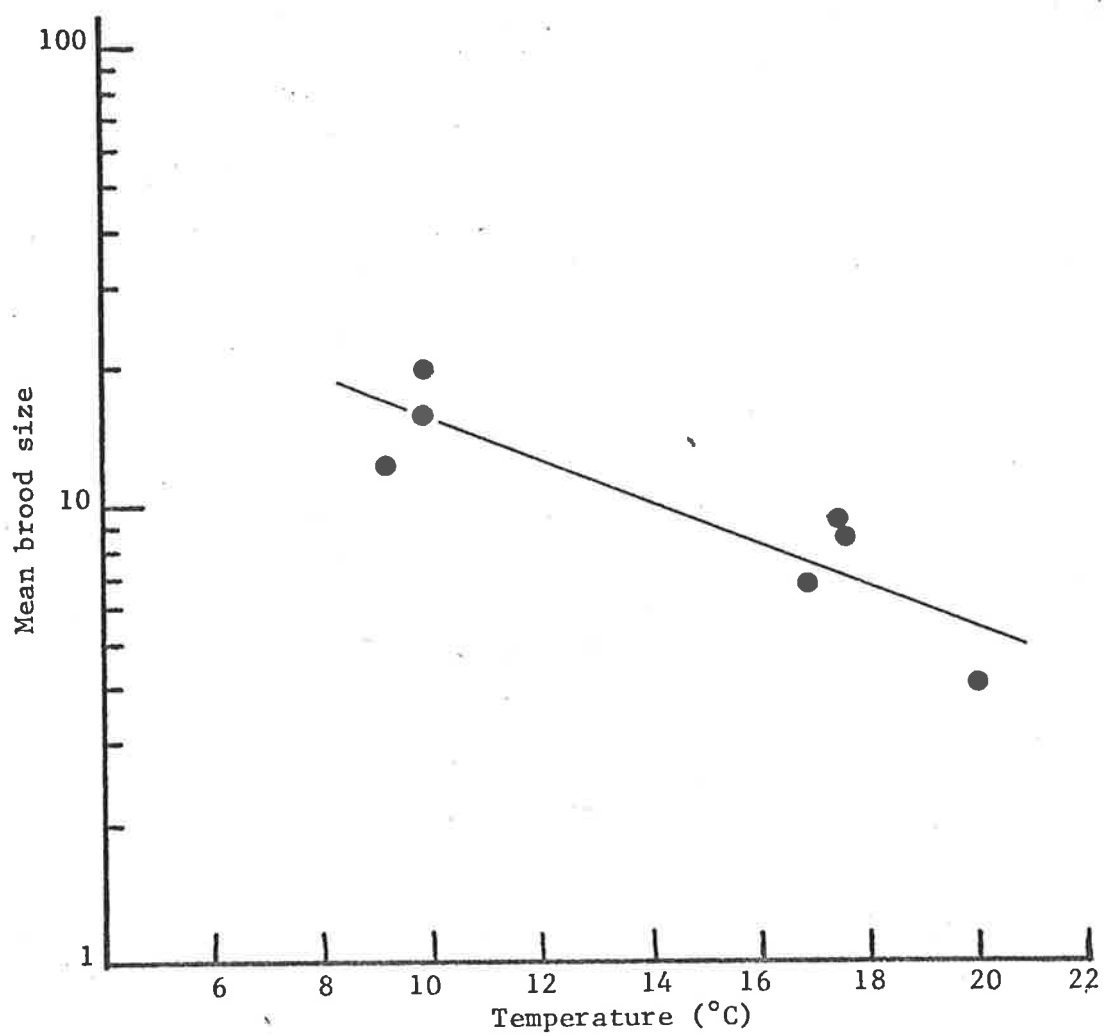


FIGURE 4.45 Mean brood size of *S. exspinosus* versus depth-averaged water temperature in pond 1.

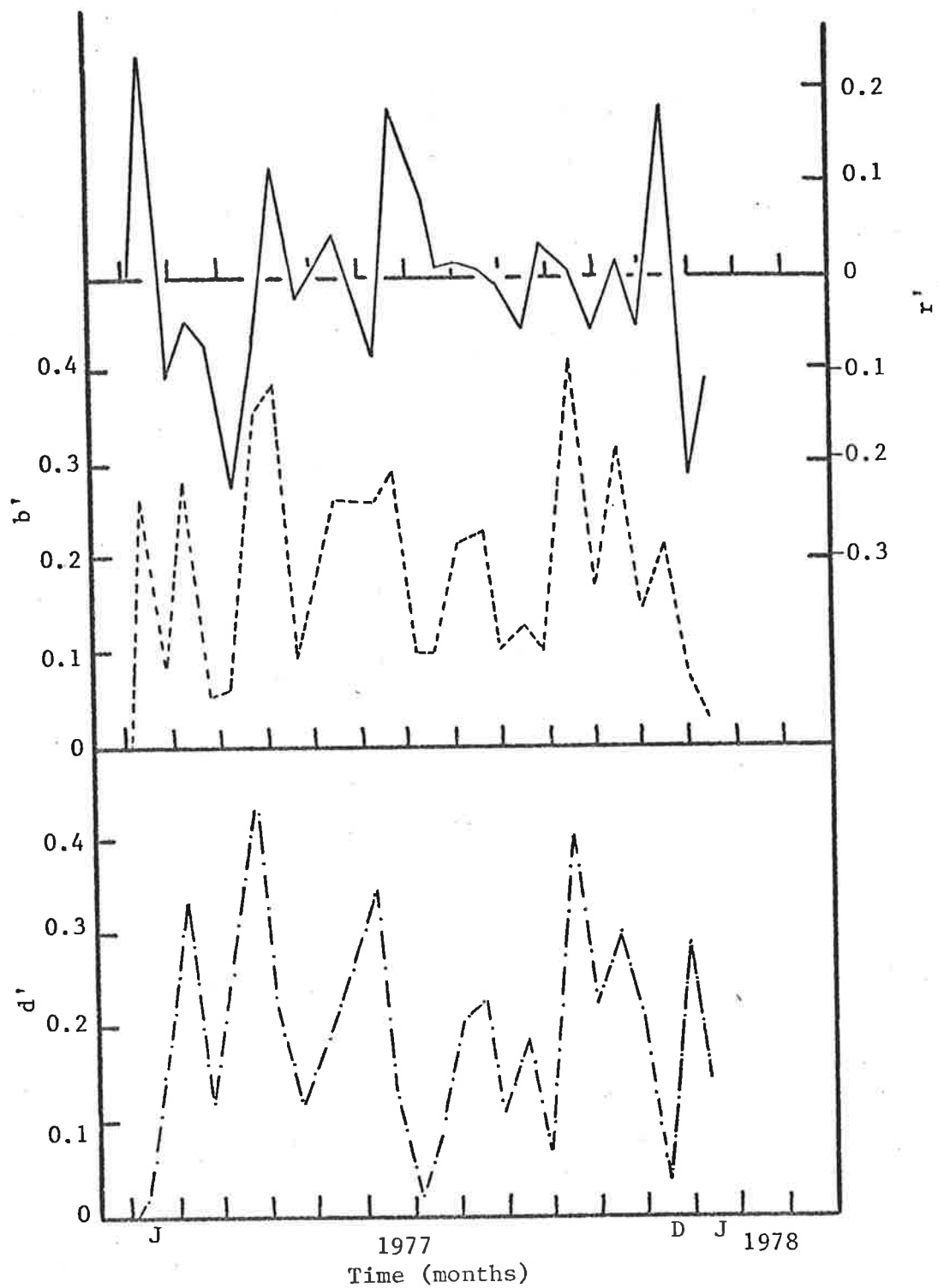


FIGURE 4.46 Population parameters b' (---), r' (—), and d' (-.-) for *S. exspinosus* in pond 1.

r' was 0.238, and mean positive r' was 0.077. Mean and maximum b' values were 0.214 and 0.410 respectively. Seasonal change in d' generally followed a similar pattern to b' . Mean and maximum d' values were 0.197 and 0.432 respectively.

The decline of b' and r' during February and early March, 1977, coincided with an increase in abundance of *D. carinata*. However, b' increased during late March, 1977, while *D. carinata* was still present. r' increased markedly in late June after the decline of *D. carinata*. However, neither b' , r' , nor d' was significantly correlated with population density of *D. carinata* during 1977 (Spearman's ρ , $p > 0.05$). The percentage of ovigerous females in the population of *S. exspinosus* decreased markedly in January and March, 1977. A high percentage of non-reproductive adults is common in food-limited populations of *Daphnia* (Hebert, 1978c; Slobodkin, 1954). Events in the population of *S. exspinosus* during the early part of 1977 resembled those in the food-limited *D. carinata* populations. b' of *D. carinata* was significantly greater than b' of *S. exspinosus* during 1977 (Mann-Whitney U test, $p > 0.05$). Although maximum r' of *S. exspinosus* was greater than maximum r' of *D. carinata*, mean positive r' values of both species were not significantly different (Mann-Whitney U test, $p > 0.05$). d' values for both species were only just not significantly different during 1977 (Mann-Whitney U test, $p > 0.05$).

The peak in d' of *S. exspinosus* in mid-February, 1977, coincided with a peak in population density of *M. leuckarti*. However, during January, 1978, d' decreased as the density of *M. leuckarti* increased. d' of *S. exspinosus* and population density of *M. leuckarti* were not significantly correlated during 1977 ($\rho = 0.34$; $p > 5\%$).

The number of eggs and juveniles (size class 1) in the population of *S. exspinosus* in pond 1 during 1977 is shown in Figure 4.47. The rate of decrease in egg number exceeded the rate of decline

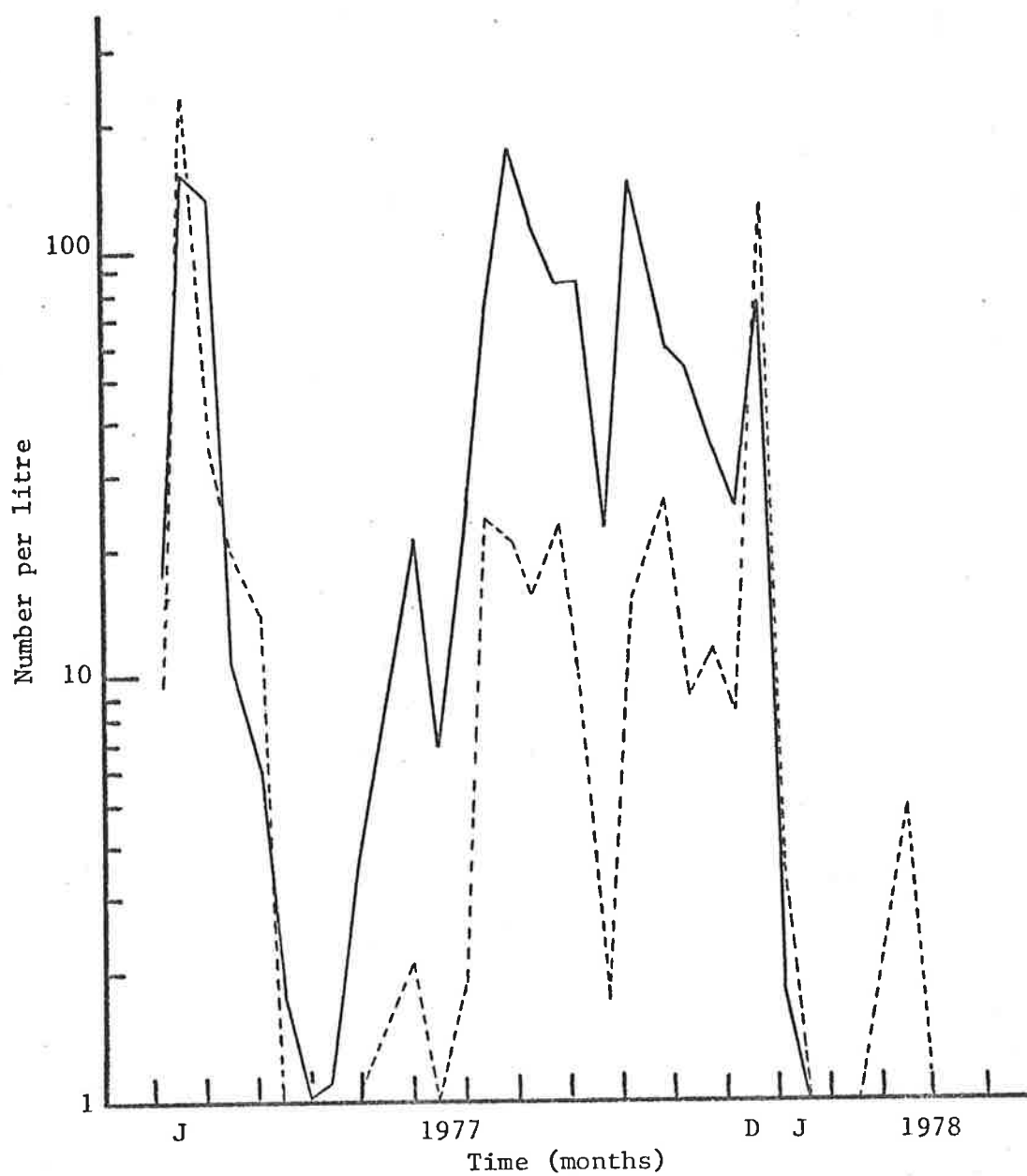


FIGURE 4.47 Number of eggs (—) and juveniles (---) of *S. exspinosus* in pond 1.

in population density during February, August and September, October and November, and late December, 1977. This suggested departure from a stable age distribution at those times. Comparison of egg number with the number of juveniles showed that considerable mortality of eggs or neonates occurred in early February, late March, and from April to early December, 1977. This explained low r' values during the latter period. Low numbers of juveniles and the presence of larger size class females from April to December suggested starvation of neonates under low food conditions even though some females were still able to obtain sufficient food for growth and egg production (e.g. Neill, 1975).

4.4.2.4 Length-Dry Weight Relationship. A double logarithmic plot of mean dry weight (μg) per size class on mid-size class length (mm) for embryonic, juvenile, and adult *S. exspinosus* from pond 1 is presented in Figure 4.48. A linear regression of the natural logarithm of mean dry weight (W) on the natural logarithm of mid-size class length (L) for embryonic stages yielded a relationship of the form, $\ln W = 0.8585 - 0.0971 \cdot \ln L$, $r^2 = 0.31$. That is, variation in length accounted for only 31% of the variance in weight of embryonic stages. Some weight loss appeared to occur in late embryonic stage animals. However, confidence limits for the weight of embryonic stages overlapped and weight changes were not significant. A weight loss may occur during the embryonic development of some cladocerans (Green, 1956).

A linear regression of the natural logarithm of mean dry weight on the natural logarithm of mid-size class length for ovigerous and non-ovigerous females yielded a relationship of the form, $\ln W = 2.1423 + 2.8460 \cdot \ln L$, $r^2 = 1.00$. Slope coefficients for the regression line of weight on length for *D. carinata* and *S. exspinosus* were similar. However, the intercept for *S. exspinosus* was higher than for *D. carinata*. Larger intercepts generally occur as body size decreases among cladocerans (Bottrell et al., 1976). Weight of the embryonic stages and

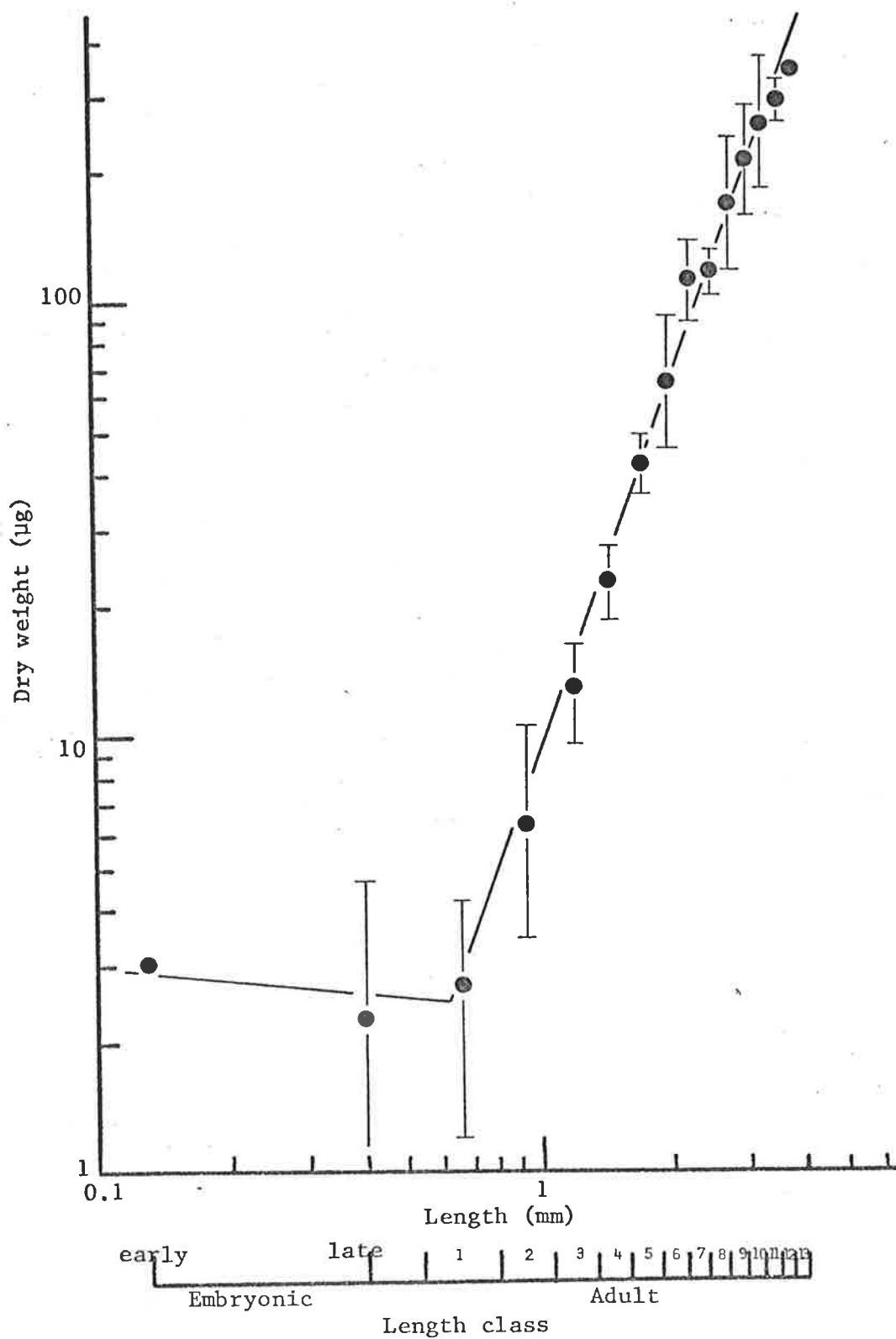


FIGURE 4.48 Mid-size class length-dry weight relationship for pooled ovigerous and non-ovigerous *S. exspinosus*.

neonate of *D. carinata* were higher than for the corresponding stages in *S. exspinosus*. However, above a length of 0.9 mm, *S. exspinosus* was more than twice as heavy as *D. carinata* of the same length even though *D. carinata* attained a larger maximum body length. That is, *S. exspinosus* was a shorter, stouter animal. *Simocephalus* has a heavier exoskeleton than *Daphnia* (Hutchinson, 1967).

4.4.2.5 Production

Population Turnover-Time Method. Seasonal variation in standing crop biomass (mg dry weight/ℓ) and daily net production rate (mg dry weight/ℓ/day) of *S. exspinosus* in pond 1 during 1977 is shown in Figure 4.49. Production calculations, based on the population turnover-time method, for *S. exspinosus* are presented in Appendix 6. Biomass peaks coincided with population density maxima. Biomass was highest (7.349 mg dry weight/ℓ) in January, 1977, when population density was maximal. Mean biomass during 1977 was 1.093 mg dry weight/ℓ. Maximum and mean biomass of *S. exspinosus* were much lower than for *D. carinata* in pond 1 during 1977 due to lower population densities. Daily net production rate closely followed biomass fluctuations. Net production rate varied from 0.004 to 0.785 mg dry weight/ℓ/day, and was approximately one order of magnitude lower than for *D. carinata*.

The range of net daily production to biomass ratios was 0.020 to 0.385; mean daily P/B ratio was 0.176, equivalent to an average biomass turnover-time of 5.7 days. Mean daily P/B ratio for *D. carinata* in pond 1 during 1977 was higher than for *S. exspinosus* and average biomass turnover-time was 3.5 days. However, daily P/B ratios for the two species were not significantly different during 1977 (Mann-Whitney U test, $p > 0.05$). Thus, the higher production of *D. carinata* resulted from the same rate of turnover of a much higher standing crop biomass.

A linear regression of daily P/B ratio for *S. exspinosus* on depth-averaged water temperature showed that variation in temperature

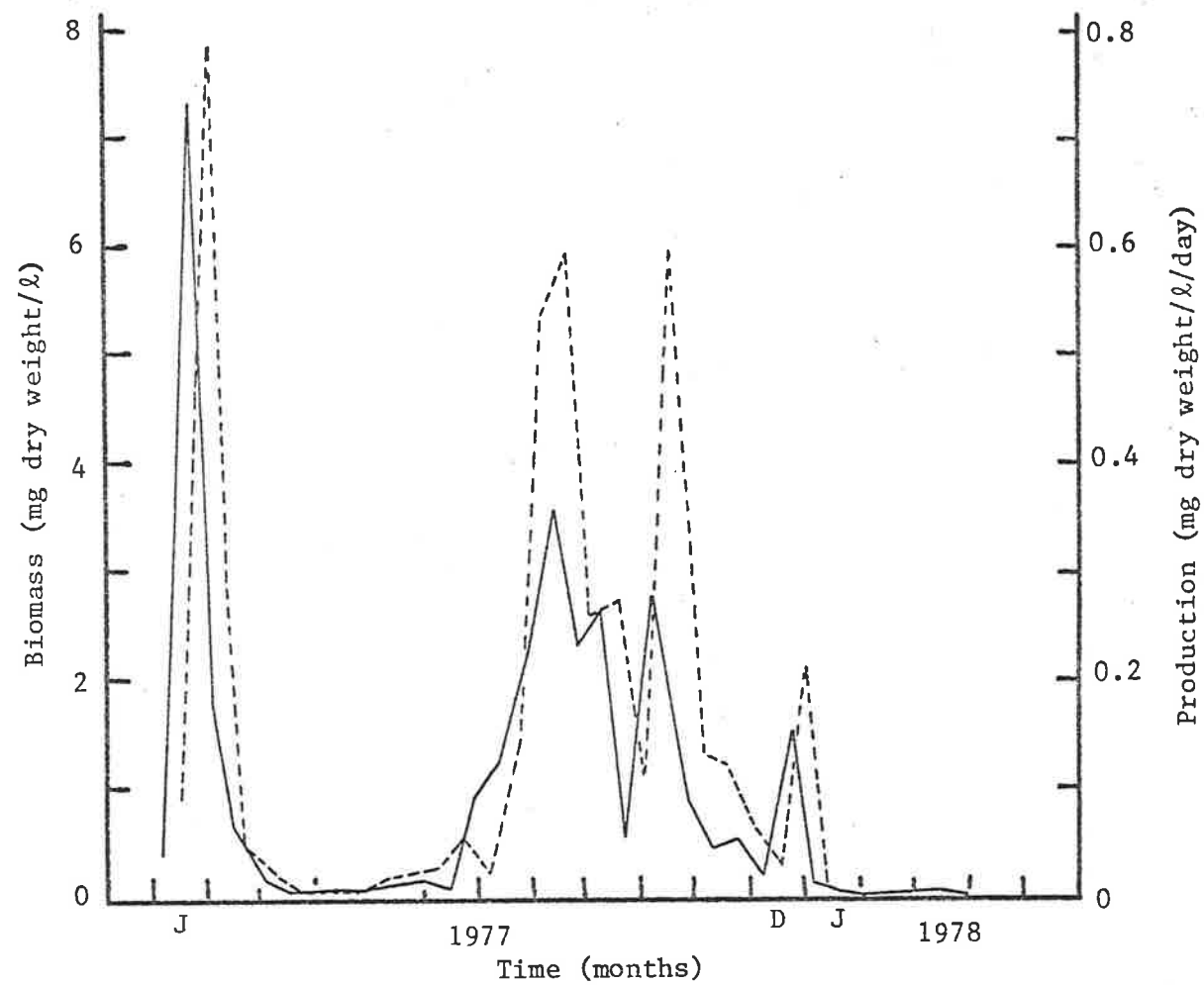


FIGURE 4.49 Standing crop biomass and daily production of *S. exspinosus* (population turnover-time method) in pond 1. Biomass (—), production (----).

accounted for only 3% of the variance in daily P/B ratio. It was shown above that temperature accounted for only a small proportion of the variance in the daily P/B ratio of *D. carinata*. These results contrasted with the findings of Janicki and Da Costa (1977) and Duncan (1975) that daily P/B ratios of *Bosmina* and *Daphnia* showed a strong positive relationship with temperature.

Total monthly and annual net production of *S. exspinosus* was determined by planimetry. Net production was converted to g dry weight/m² of pond surface area, and the results, together with weighted mean monthly biomass (g dry weight/m²) and monthly and annual P/B ratios, are presented in Table 4.12. Monthly net production was highest in January, August and October, 1977. Total annual net production of *S. exspinosus* in pond 1 during 1977 was only 20% of total annual net production of *D. carinata*. Annual P/B ratio for *S. exspinosus* was higher than for *D. carinata* but monthly P/B ratios were higher for *D. carinata*.

As was the case for *D. carinata*, peaks in daily net production rate of *S. exspinosus* occurred during periods of high egg mortality and departure from a stable age distribution. The application of the population turnover-time method for the calculation of production in *S. exspinosus* was subject to the same sorts of error as for *D. carinata*. Total annual net production of *S. exspinosus* was, therefore, overestimated due to failure to take increased egg mortality into account. The population turnover-time method overestimated total annual net production of *D. carinata* by 1.6 to 2.8 times. Therefore, total annual net production of *S. exspinosus* in 1977 was probably closer to 30 g dry weight/m². Total annual net production in pond 1 during 1977 would, therefore, have been 43 kg dry weight. The nutrient content of *S. exspinosus* was not determined during the present study, and was assumed to be similar to *D. carinata*. The nitrogen and phosphorus

Table 4.12

Total monthly and annual net production (P, g dry weight/m²) based on population turnover-time method, mean monthly and annual biomass (B, g dry weight/m²), and P/B ratios for *S. exspinosus* in pond 1 during 1977

	P		B		P/B	
	1977	1978	1977	1978	1977	1978
Jan.	10.0	1.3	4.1	0.2	2.4	6.5
Feb.	8.4	-	1.0	-	8.4	-
March	0.4	-	0.1	-	4.0	-
April	0.1	-	0.02	-	5.0	-
May	0.5	-	0.1	-	5.0	-
June	1.2	-	0.4	-	3.0	-
July	5.1	-	1.9	-	2.7	-
Aug.	16.2	-	3.2	-	5.1	-
Sept.	7.9	-	2.0	-	4.0	-
Oct.	12.7	-	2.0	-	6.4	-
Nov.	3.8	-	0.6	-	6.3	-
Dec.	3.1	-	0.9	-	3.4	-
Annual	69.4 ¹	1.3	1.4 ²		49.6 ³	

¹ Total annual production (ΣP)

² Mean annual biomass ($\bar{B}$)

³ $\frac{\Sigma P}{\bar{B}}$

content (as percentage of dry weight) of *D. carinata* (see 4.3.2.7) was used in the following calculations. Total annual net production of *S. exspinosus* in pond 1 during 1977 represented a nutrient store equivalent to 1.14% of total $\text{PO}_4\text{-P}$, 0.54% of TKN, and 0.32% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained in the pond during 1977. Harvest of *S. exspinosus* did not represent a significant pathway for nutrient removal from the Gumeracha ponds. Harvest of the total annual net production of *D. carinata* and *S. exspinosus* from pond 1 in 1977 would have removed 5.77% of total $\text{PO}_4\text{-P}$, 2.74% of TKN, and 1.64% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) retained in the pond during 1977. Thus, production of herbivorous zooplankton did not represent a significant nutrient store in the Gumeracha ponds, and harvest of this group would not have provided a useful pathway for nutrient removal from the ponds.

Total annual net production of *S. exspinosus* in pond 1 during 1977 was equivalent to 1% of total annual net primary production and 105% of total annual net phytoplankton production. The latter would suggest that *S. exspinosus* was not an obligate suspension feeder. Total annual net production of *D. carinata* and *S. exspinosus* in pond 1 during 1977 was of the order of 216 kg dry weight. The ecological efficiency of the pond, or the efficiency of energy transfer between the primary and secondary trophic levels, as expressed by the ratio of net zooplankton production to net primary production, was equivalent to 0.064.

4.4.3 Discussion

Although *S. exspinosus* and *D. carinata* both reproduced continuously at Gumeracha, some synchronization was apparent in *S. exspinosus* and reflected in periodic bursts of recruitment. Population cycles of the two zooplankters were similar during the early part of 1977. The rapid decline in the percentage of ovigerous females of *S. exspinosus* following the population peak in January, 1977,

suggested that food-limitation was responsible for the decline in population density. Food-limitation may have arisen as a result of competition with *D. carinata*, although this was not reflected in population parameters. Although it has been suggested that *Simocephalus* is an obligate suspension feeder (Horten *et al.*, 1979), observations by Pacaud (in Hutchinson, 1967) and the population increase of *S. exspinosus* in July and August, 1977, suggest that this species may also be a facultative browser to some extent. Thus, *S. exspinosus* and *D. carinata* may have competed for access to the sediments. The decrease in mean brood size of *S. exspinosus* during the latter part of 1977 also suggested food-limitation or, at least, some degree of food-restriction. *S. exspinosus* may not have been able to utilize the sediments as effectively as *D. carinata*. An alternative explanation for the population decline of *S. exspinosus* in January and February, 1977, is the oversaturation of some specialized niche. This could explain why population density was lower from July to November than in January, 1977.

The outcome of competitive interactions is determined by size-selective predation and reproductive rate (Lynch, 1979, 1977; Kerfoot, 1977a). In the absence of vertebrate predation, intense invertebrate predation can result in the replacement of a smaller by a larger species (Lynch, 1979; Dodson, 1974b); larger body size confers protection from invertebrate predators (Dodson, 1974a). Although the death rate of small cladocerans may increase in the presence of copepod predators (Kerfoot, 1977), d' values for *S. exspinosus* and population density of *M. leuckarti* were not correlated at Gumeracha. However, as discussed in 4.3.3, total population density of *M. leuckarti* need not reflect the predation pressure exerted by the species. Although mean brood size of *S. exspinosus* and *D. carinata* were not significantly different in pond 1 during 1977, the birth rate (b') of *D. carinata* was significantly higher than for *S. exspinosus*. An increase in b' may be

achieved by increasing the number of eggs in the population (E) (independently of increasing No), or decreasing egg development time (D). Egg development times of *D. carinata* and *S. exspinosus* are probably very similar (c.f. Bottrell et al., 1976). The percentage of ovigerous females in the population of *D. carinata* in pond 1 during 1977 (mean = 69%) was significantly greater than the percentage in the population of *S. exspinosus* (mean = 36%) (Mann-Whitney U test, $p < 0.01$). Thus, the number of eggs (E) in the population of *D. carinata* exceeded that in *S. exspinosus* for any given population density; this explained the higher birth rate of *D. carinata*. A higher birth rate may have given *D. carinata* a competitive advantage with respect to *S. exspinosus*. This was not reflected in increased r' values for *D. carinata* as might have been expected had the larger species been at a competitive advantage (e.g. Goulden et al., 1978). Competitive interactions are exceedingly complex and although conditions may be favourable for the adults of a given species, survival of earlier stages may be reduced. Such a situation can result in a larger species becoming extinct in the presence of a smaller one (Lynch, 1978). Obviously, a more involved experimental study would be required to elucidate the nature of competitive and predatory interactions amongst the zooplankton community of the Gumeracha ponds. Principally, these would involve determining the age structure of *M. leuckarti* populations, prey selection experiments involving juveniles of *S. exspinosus* and *D. carinata*, and mixed and single species cultures of *S. exspinosus* and *D. carinata* under abundant food and food-limited conditions.

Comparative data on the population dynamics and production of littoral cladocerans are scarce. Food-limitation and predation have been shown to be important in limiting *S. serrulatus* in meso- and eutrophic ponds in Canada (Ang and Fernando, 1973). Mean birth rate (b') of *S. exspinosus* at Gumeracha was much lower than for *S. serrulatus*. As

mean brood size of *S. exspinosus* (9.6/female) exceeded that for *S. serrulatus* (3.7/female) in the Canadian ponds (calculated from Ang and Fernando, 1973), higher birth rate in *S. serrulatus* may have resulted from shorter egg development times for that species (c.f. Ang and Fernando, 1973). Although brood size in *S. exspinosus* at Gumeracha was similar to brood size in *S. acutirostris* (from a small Indian pond) up to a body length of 2.5 mm, above this length brood size in *S. exspinosus* was higher (c.f. Murugan and Sivaramakrishnan, 1973). This also appeared to hold with respect to *S. vetulus* from some habitats (Green, 1956) but not from others (Green, 1966). Brood size in *S. exspinosus* at Gumeracha was similar to that recorded for the same species at some sites in a polluted stream in the Middle East, but lower than recorded from other sites (Mohammad, 1979). Thus, food availability in the Gumeracha ponds did not appear to be exceptionally high.

Ang and Fernando (1973) did not indicate the method used to calculate the production of *S. serrulatus*, and although they referred to "gross" production, included no information on respiration. Total annual net production of *S. exspinosus* in pond 1, calculated using the population turnover-time method, was much lower than total production of *S. serrulatus* during the growing season in the eutrophic Columbia Lake, but similar to total annual production of *S. serrulatus* in the mesotrophic Miller's Lake.

4.5 General Discussion

The zooplankton community of the Gumeracha ponds exhibited low diversity in terms of species number, but contained representatives of all the major ecological groupings of zooplankters. Although the ponds were dominated numerically by a single species (*D. carinata*), the dynamics of the community as a whole were complex. This has important implications for the use of zooplankton in pond management. The

findings of the present study do not support the conclusion of Loedolff (1965) that temperature is the major factor determining the occurrence and abundance of zooplankton in WSPs. While temperature may be important in determining the occurrence of some species, abundance (population density) is influenced by food level, competition, and predation. Thus, zooplankton populations in WSPs would require careful management to maintain an optimal standing crop of a desired species.

Perhaps most surprising was the finding that, even in WSPs with high organic inputs, zooplankton populations could, at times, become food-limited. Food-limitation of *Daphnia* in aerated oxidation ponds has been reported elsewhere (Daborn et al., 1978). In a management context, this problem could, perhaps, be overcome by repeated cropping at critical times during the population cycle. The population would be maintained in a vigorous growth phase (i.e. as at the commencement of population cycles) with a high percentage of ovigerous females and high brood sizes. Annual production would thus be increased, although standing crop biomass at any given time would be reduced. Periodic cropping would, of course, be essential for nutrient removal.

The *D. carinata* populations at Gumeracha terminated phytoplankton blooms but the species was prevented from controlling phytoplankton standing crops during summer by high temperatures. Intensive culture of *D. carinata* for algal removal would require the maintenance of temperatures around 15°C. Obviously, this would inhibit the development of phytoplankton blooms which were triggered at about 18°C at Gumeracha. As with filamentous algae and submerged macrophytes, the major impediment to the use of zooplankton for algal control and effluent polishing at Gumeracha appeared to be the inability to maintain constant standing crops of the major herbivore throughout the year. At Gumeracha, supraoptimal, rather than suboptimal, water temperatures

inhibited the growth of *Cladophora*, *P. ochreatus* and *D. carinata* during the period of phytoplankton blooms. The reduction of organic material in the Gumeracha ponds was highest during spring-winter-autumn when standing crops of *P. ochreatus*, *Cladophora* and *D. carinata* were high. Phytoplankton had a significant detrimental effect on effluent quality. Accordingly, it might be expected that algal problems in Australian WSPs would be exacerbated in areas of higher temperature and that WSP function on an annual basis might be more effective in cooler areas. This conflicts with the widespread view that WSPs are more effective in climates with high temperatures and incident solar radiation. A more extensive seasonal survey of WSPs along a climatic gradient in southern Australia would prove interesting in this regard.

Although *D. carinata* played a major role in the reduction of phytoplankton standing crops and made substantial contributions to the improvement of effluent quality during periods of intensive grazing, the direct importance of zooplankton in pond function throughout the rest of the year was not great. Removal of organic material during periods of high standing crops of *D. carinata* appeared to be effected largely by submerged macrophytes. However, herbivorous zooplankton, such as *D. carinata*, may contribute indirectly to the improvement of effluent quality. By terminating phytoplankton blooms in aerobic WSPs, *Daphnia* can reduce biogenic turbidity and improve light penetration in ponds. This may permit the germination and establishment of submerged macrophytes that could not occur in the absence of *Daphnia*. McNabb (1976) concluded that *Daphnia* was essential for the maintenance of a suitable light regime which allowed submerged macrophytes to develop in fully aerobic maturation ponds in Michigan.

Annual net production of *D. carinata* and *S. exspinosus* represented a combined nutrient store equivalent to less than 6% of total PO_4 -P and less than 2% of total nitrogen retained in the

Gumeracha ponds during 1977. Harvest of herbivorous zooplankton would not have provided a useful pathway for nutrient removal from the Gumeracha ponds. Due to high population turnover rates, zooplankton harvest would need to be conducted every few days. This would increase the operational costs of treatment plants to some extent but would probably be a low-technology process. The incorporation of nitrogen and phosphorus into unicellular algae appeared to be the most effective nutrient removal pathway in the Gumeracha ponds. Effluent NO_3^- and soluble $\text{PO}_4 - \text{P}$ concentrations were lowest during periods of high phytoplankton standing crop. Therefore, a system incorporating zooplankton culture ponds for algal control as a final treatment stage might be expected to exhibit poor performance with respect to nutrient removal. The rate of nitrogen and phosphorus recycling by zooplankton is such that a large proportion of the nutrients ingested is rapidly regenerated in the soluble form or lost to the sediments via incorporation into faecal pellets (Ganf and Blazka, 1974; Peters and Rigler, 1973; Peters and Lean, 1973). Depending upon the relative magnitude of the soluble and particulate components, net movement of nitrogen and phosphorus to the sediments may occur. Nitrogen and phosphorus release from the sediments in fully aerobic WSPs would be expected to be low (see 2.2.3). In such a situation, the most effective means of nutrient removal might be via periodic emptying of the pond and mechanical removal of the sediments. This operational procedure would, of course, increase the areal requirements of the treatment plant as extra ponds would be necessary to allow periodic bypassing.

Future research in this area might involve field-scale experiments upon the effects of moderate grazing pressure on phytoplankton populations in WSPs. Up to a certain grazer density, net primary production may be enhanced by the presence of herbivores (Porter, 1976; Cooper, 1973). Self-shading by phytoplankton is thus

prevented; the efficiency of photosynthesis and the intensity of the decomposition of organic material may be increased (Gliwicz, 1975). Cropping of zooplankton would be required to reduce the intensity of grazing pressure and, as discussed above, this would be expected to increase the production of the group. As a result, a new steady-state with respect to nutrient cycling and partitioning amongst the components of the WSP ecosystem might be established. There is an urgent need for more intensive study of nutrient cycling and partitioning within WSPs during different phases of the annual pond cycle. Via this type of manipulation it may be possible to obtain the beneficial effects of unicellular algae in WSPs at lower standing crops, thereby reducing operational problems.

Studies of the productivity of different trophic levels in the hypereutrophic environment of WSPs allow comment upon relationships between productivity and lake trophic state. Patalas (in Makarewicz and Likens, 1979) has suggested that there is a tendency for the daily P/B ratio of the zooplankton community to increase in proportion to the productivity of the lake. That is, high P/B ratios are expected in eutrophic lakes. Pedersen *et al.* (1979) were unable to support this hypothesis. Mean daily P/B ratio for *S. exspinosus* during 1977 was 0.176 and for *D. carinata* during 1977 and 1978 ranged from 0.068-0.282. These ratios were characteristic of zooplankton in meso- to eutrophic lakes (c.f. Pedersen *et al.*, 1976, Table 8) with the highest mean P/B for *D. carinata* exceeding that for the most eutrophic lake. As year to year fluctuation may be considerable a generalisation of the type suggested by Patalas is difficult to substantiate. It may be said, however, that if Patalas' hypothesis was correct, all P/B ratios from Gumeracha might have been expected to be considerably higher than previously recorded. This did not appear to be the case.

It has been postulated (Hillbricht-Ilkowska, in Pedersen *et al.*,

1976) that energy transfer efficiency between the primary and secondary trophic levels (ecological efficiency) would decrease with increasing lake trophic state. While the data of Pedersen *et al.* (1976) and Hall *et al.* (1970) supported this postulate, Makarewicz and Likens (1979) arrived at the opposite conclusion. Ecological efficiency in pond 1 at Gumeracha during 1977 was 0.064. This was generally lower than recorded for oligo- and mesotrophic lakes (c.f. Pedersen *et al.*, 1976, Table 9). That is, WSPs do not appear to be highly efficient ecologically. On this basis alone, it would not be expected that a high proportion of the nutrients stored in phytoplankton biomass would be incorporated into the zooplankton in WSPs. The present study appeared to support the postulate of Hillbricht-Ilkowska.

Apart from periods of intensive phytoplankton grazing, the direct contribution of zooplankton to the improvement of effluent quality at Gumeracha was small. Harvest of herbivorous zooplankton did not represent a significant pathway for nutrient removal from the Gumeracha ponds. Rapid nutrient regeneration and high rates of population turnover provide problems for the use of zooplankton in WSP management. Organisms which are long-lived (and therefore store nutrients) and which are easily harvested would be more useful for pond management. In this context, the effects of fish upon effluent quality and the importance of fish as a nutrient store are examined in the subsequent chapter. The usefulness of fish as a tool for the management of maturation WSPs is thus examined.

Chapter 5. Fish

5.1 Introduction

The concept of utilizing domestic sewage for fish culture is not new, nor is the observation that fish may grow rapidly in sewage fertilized ponds. The practice of fish culture in ponds connected with latrines and animal pens is widespread and long-standing in Asian countries (Hickling, 1968). Fish culture in ponds to which livestock manure and human sewage are added has been practiced for some time in Israel (e.g. Schroeder and Hepher, 1976). It is only comparatively recently, however, that the direct culture of fish in operational WSPs has been attempted. The only notable exception is the culture of *Cyprinus carpio* in large ponds that are part of the system treating domestic sewage from Munich (Hickling, 1968).

Several species of fish, of widely differing feeding ecology, may occur naturally in WSPs. These include detritivores: *C. carpio* and *Ictalurus melas*; carnivores: *Mugil cephalus*, *Gambusia affinis*, *Perca fluviatilis*, *Leuciscus cephalus*, *Salmo trutta*, and *Lepomis cyanellus*; and herbivores: *Rutilus rutilus*, and several indigenous Asian cyprinids (after Carpenter et al., 1976; Goulden, 1976; Slack, 1974; Chatterjee et al., 1967). Additionally, many species have been deliberately introduced and successfully maintained in WSPs. These include *R. rutilus*, *P. fluviatilis*, *S. trutta*, and *Gasterosteus* *L. cephalus* and Williams, *aculeatus*, (White, 1978), *Tilapia nilotica*, *Ictalurus punctatus*, *Notemigonus crysoleucos*, and *Pimephales promelas* (Carpenter et al., 1976), *C. carpio* (Noble, 1975), *C. carpio* and *Labeo rohita* (Krishnamoorthi et al., 1975), *Retropinna retropinna*, *Carassius auratus*, and *Salmo gairdneri* (Slack, 1974; Teoh, 1974), grass carp (presumably *Ctenopharyngodon idella*) (Ponyi et al., 1973), salmon (Anon., 1972), *L. rohita* and *Catla catla* (Chatterjee et al., 1967), *Micropterus salmoides*, *Tilapia mossambica*, *Tilapia sparmani*, and *Lepomis macrochirus*

(Hey, 1953). These studies have shown that, given suitable physico-chemical conditions, fish will survive, grow rapidly, and may attain spawning condition in WSPs. Fish production in WSPs is very high compared with natural waters and unfertilized fish ponds, and may even exceed production in fertilized fish ponds (White ^{and Williams,} 1978; Gutteridge, Haskins and Davey, 1976).

Despite this widespread interest, the effects of fish upon pond function have rarely been tested under controlled conditions. The detrimental effects of algae upon effluent quality and the problems associated with algal removal have been discussed. The removal of algae via trophic interactions incorporating fish would provide a simple, inexpensive means of improving effluent quality and provide a utilizable, easily harvested by-product. Sewage grown fish are consumed in many countries and need not, as a matter of course, contain pathogens (Carpenter *et al.*, 1976). In any event, many non-consumptive alternatives for the use of sewage grown fish may be envisaged, e.g. in recreation, as fertilizer. Thus, aquaculture systems may provide low cost alternatives to conventional treatment plants (Henderson *et al.*, 1976).

It has been reported that the introduction of fish into a WSP can stabilize and increase dissolved oxygen concentration and pH (Schroeder, 1975; Slack, 1974; Teoh, 1974). The exact process effecting this change is not made clear in these papers. Schroeder (1975) reported that phytoplankton and zooplankton standing crops decreased in the presence of fish, while Teoh (1974) reported increased zooplankton abundance and reduced phytoplankton abundance. Schroeder (1975) suggested that increased oxygen concentrations would allow the pond to satisfy the waste BOD more readily, and that high pH would improve nutrient removal due to loss of NH_3 to the atmosphere and the precipitation of $\text{PO}_4 - \text{P}$. However, no data were presented to substantiate

these predictions. Removal of BOD, SS, total nitrogen and total phosphorus in a WSP has been reported as higher when fish were present than during a similar period in the absence of fish (Carpenter *et al.*, 1976). However, the control was not run concurrently in this study and the effects of other organisms in the pond was not taken into account. Although these studies suggest that the presence of fish is beneficial for pond function, White (1975) has demonstrated that size-selective predation upon zooplankton by fish can limit the ability of the zooplankton as a whole to control the phytoplankton. Increased phytoplankton abundance may result from the introduction of fish to a WSP. This would obviously be detrimental to pond function and reduce effluent quality.

The latter result is not surprising in view of the profound effects of fish predation upon aquatic communities in natural water bodies. Intense fish predation generally eliminates larger species or size classes of zooplankton, thereby favouring smaller animals (e.g. Archibald, 1975; De Bernardi and Guissani, 1975; Hillbricht-Ilkowska and Weglenska, 1973; Galbraith, 1967; Grygierek *et al.*, 1966; Straskraba, 1965; Brooks and Dodson, 1965; Hrbacek *et al.*, 1961). The abundance, biomass, fecundity, and production of smaller species may increase in the presence of fish (Archibald, 1975; Hillbricht-Ilkowska and Weglenska, 1973). Although Brooks and Dodson (1965) originally suggested that the absence of smaller species of zooplankton in the presence of larger species was the result of competitive displacement (that is, the size-efficiency hypothesis), competitive advantage is determined by many factors (see Chapter 4). Both vertebrate and invertebrate predation are important in structuring zooplankton communities (Lynch, 1979; O'Brien *et al.*, 1979; Zaret, 1975). Nevertheless, the effect of planktivorous fish upon phytoplankton populations observed by White (1975) has been described elsewhere

(Anderson *et al.*, 1978; Hurlbert *et al.*, 1972). Benthivorous fish may also increase phytoplankton populations due to regeneration of phosphorus from the sediments (Lamarra, 1975). Thus, the benefits of fish for WSP function seem far from clear.

Fish may represent a significant nutrient pool in some natural waters. Kitchell *et al.* (1975) have shown that over half the total epilimnetic standing crop of phosphorus may be contained in fish biomass under some circumstances. This phosphorus store is remineralized slowly compared to invertebrate consumers, and consequently, fish may maintain a large reservoir of nutrients throughout an annual cycle (Kitchell *et al.*, 1979, 1975). A large part of the phosphorus contained in fish biomass is bound in bones and scales and is, thus, resistant to rapid degradation (Kitchell *et al.*, 1975). The harvest of fish may represent a potentially useful pathway for nutrient removal from WSPs.

The effects of fish introduction upon pond function and effluent quality were studied at Gumeracha. The influence of an omnivore, *Carassius auratus*, on planktonic communities and water chemistry were monitored. The nutrient pool represented by the annual net production of *C. auratus* was compared with annual pond nutrient retention to determine the usefulness of fish harvest for nutrient removal. In this manner, an attempt was made to evaluate the value of fish as a tool for the management of WSPs. The advantages of using fish for pond management, should this prove effective, are obvious. Fish are long-lived and relatively easily harvested. Ponds can be restocked with fish of any size at any desired density immediately following harvest. Thus, pond efficiency would not decline, as after macrophyte or zooplankton harvest, and extra ponds to allow for bypassing would not be required.

5.2 Methods

5.2.1 Enclosures and Experimental Design. The effects of *C. auratus* on pond function and effluent quality were investigated using an enclosure technique. That is, fish were introduced into enclosures constructed within the ponds at Gumeracha, and the effects upon the chemistry and biology of water within the enclosures were monitored.

Enclosures had to be large enough to take a reasonable number of fish, but within the limits of the project's resources. Optimal stocking rate for the rapid growth of fingerlings (approx. 20-100 g live weight, approx. 5-15 cm standard length) of many species, including *C. auratus*, in shallow ponds under intensive culture conditions is about 1 fish/m² pond surface (after Krishnamoorthi et al., 1975; Noble, 1975; Reich, 1975; Bardach et al., 1972; Nambiar, 1970; Hickling, 1968, 1962; Swingle, 1968; Vaas-Van Oven, 1957; Lin, 1955). It was decided that a diameter of 4.5 m would give a sufficient surface area (16 m²). Enclosures (Fig. 5.1) were circular to avoid corner effects, and constructed of heavy (010) black plastic sheeting. The ends of 14.5 m lengths of plastic were overlapped and heat-welded; the top and bottom of the plastic sheeting were folded over about 15 cm and heat-welded to form envelopes. When finally constructed this gave a wide, shallow cylinder (approx. 4.5 m diameter) 1.3 m tall, open at the top and bottom. Fish thus had access to the sediments. A nylon rope was run around the circumference of each enclosure in the top envelope and attached to 1.8 m wooden stakes driven into the pond bottom. 1 m lengths of 1 cm diameter steel reinforcing rod were placed around the circumference of each enclosure in the bottom envelope to sink enclosures firmly into the sediments.

Significant qualitative and quantitative changes in planktonic communities and water chemistry may occur when standing water is

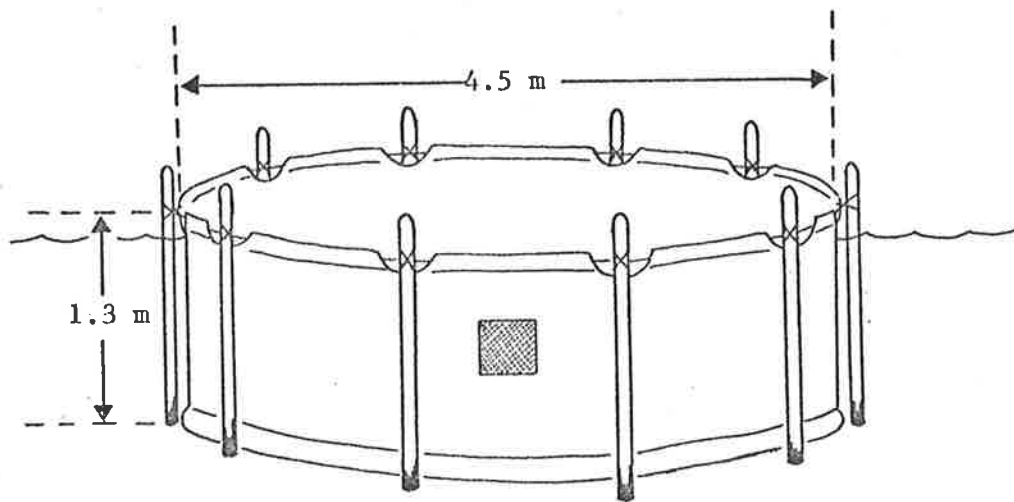


FIGURE 5.1 Experimental fish enclosure design

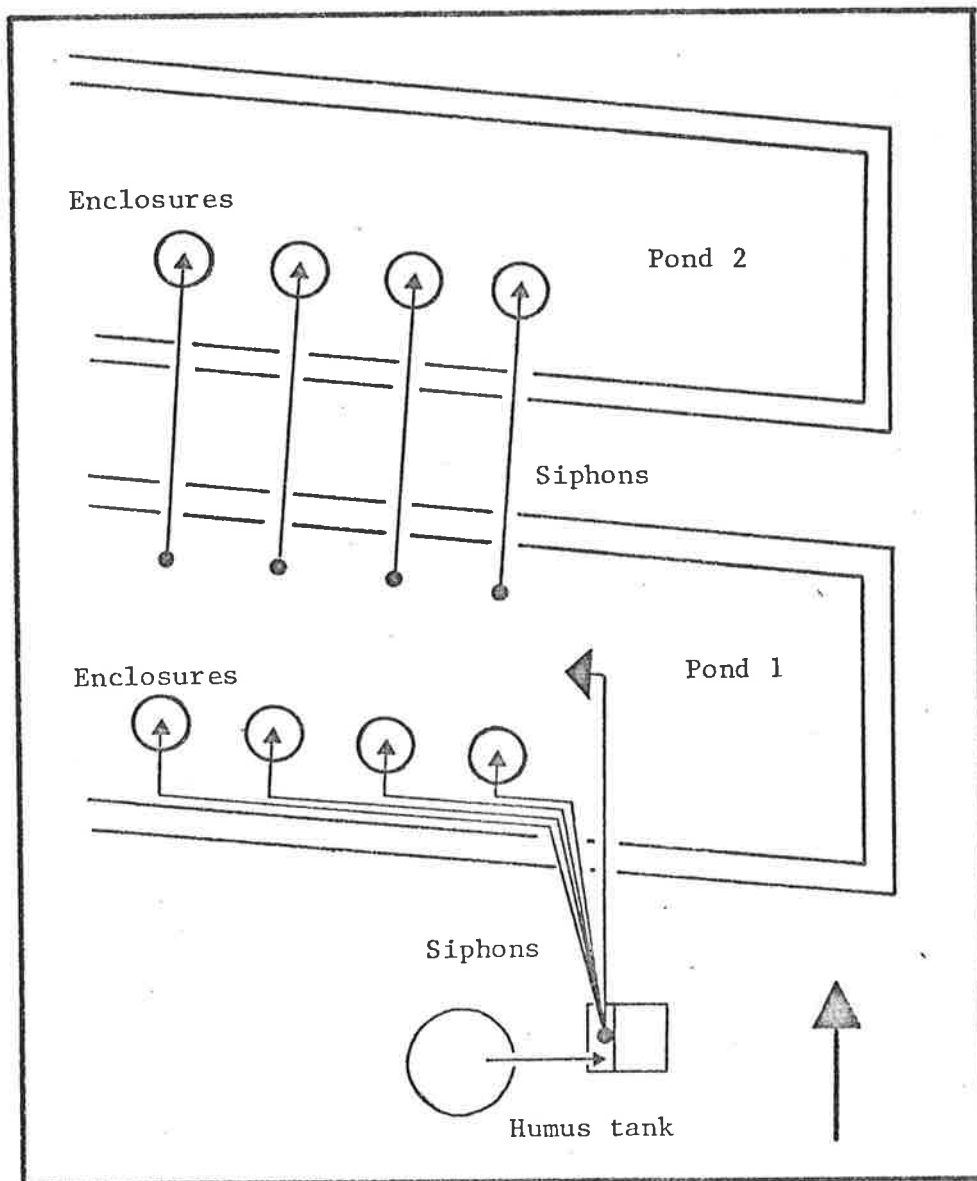


FIGURE 5.2 Experimental design

enclosed (Smyly, 1976; Lack and Lund, 1974; Lund, 1972). These changes arise as a result of the prevention of nutrient renewal. To avoid these effects and to make the situation within enclosures comparable to a functional WSP, a flow-through situation was produced in each enclosure. A 16 cm square window was cut into the side of each enclosure (just below the water level) and covered with 1 cm plastic mesh. The Gumeracha ponds are gravity fed; siphons (1 cm diameter plastic hose) were run from the pond 1 influent sump into each enclosure in pond 1 and from pond 1 into each enclosure in pond 2. The rate of flow through the siphons gave a retention time within enclosures that was similar to retention time of the ponds. Retention times in pond 2 enclosures were slightly lower than in pond 1 due to a greater head of water from pond 1 to pond 2.

Four enclosures were constructed in each pond: 3 experimental (plus fish) and 1 control (no fish). To examine the effect of fish density, and therefore to determine optimal stocking rate, experimental enclosures were stocked at rates of 0.5 fish/m^2 (8/enclosure), 1 fish/m^2 (16/enclosure), and 2 fish/m^2 (32/enclosure). The overall experimental design is shown in Figure 5.2.

To prevent the access of predatory water birds into enclosures, floating covers were constructed of 2.5 cm stretched mesh fish netting saddle-stitched to circular frames of plastic hose and bouyed by polystyrene floats. Dense growths of *Stigeoclonium* sp. and *Ulothrix* sp. formed on some of the floating covers in July, 1978. These growths had significant effects upon water temperature and dissolved oxygen concentration in enclosures (see 2.2.2). Enclosure covers were raised clear of the water surface after July, 1978, and algal growth died off.

5.2.2 Experimental Fish. Several wild populations of *C. auratus* were sampled to find a source of large numbers of suitable and similar sized fish (6-10 cm). All fish used in the experiment were collected

from the same population. This population was from a small (approx. 300 m²), deep (approx. 3 m) farm dam near Uraidla, Mount Lofty Ranges (138° 30'50" E, 34° 48' S). The bore-fed dam has clear water which is underlain by a gravel and clay substrate. At the time of fish collection (February, 1978) the entire pond bottom was covered by a dense, submerged stand of *Vallisneria spiralis*. Fish were captured using a cylindrical trap (12 cm aperture, 1 mm mesh). Fish were returned to the laboratory and anaesthetized in 50 ppm MS 222. Each fish was then weighed, measured (standard length), and tagged. Tagging was carried out using 5 cm lengths of nichrome wire passed through the dorsal musculature between the proximal part of the pterygiophores at the base of the posterior portion of the dorsal fin. A numbered plastic sleeve was slipped onto one protruding end of the wire and the two ends then interlocked. Fish were then placed into an outdoor holding tank (2.2 × 0.5 × 0.7 m) and fed "Aqua-Lab Supreme" fish pellets. Fish were left in the tank for several days to determine whether severe handling effects or tag loss occurred. All fish recovered from handling and only 2 of the 112 tagged fish dropped tags.

At the termination of the field experiment, recaptured fish showed no ill effects from tagging. No wounds or fungal infections were observed around the point of wire entry. Animals that had dropped tags showed only minor, localised scale damage. 22% of recaptured fish had dropped tags. Tag loss varies with tag type, fish species, and tag attachment site, and may be as high as 90% in some cases (Laird and Scott, 1978). The system of tagging employed during the present study was reasonably effective.

5.2.3 Experimental Procedure. The stocking density and biomass of *C. auratus* in each enclosure is shown in Table 5.1. A concerted effort was made to ensure that a similar size range of fish was introduced to each enclosure. Fish were introduced to pond 1 enclosures

Table 5.1

Stocking density and biomass (g) of *C. auratus*
in enclosures at Gumeracha

Enclosure	Stocking density	POND 1					POND 2				Stocking biomass (g)
		Standard length(cm)		Weight (g)		Stocking biomass (g)	Standard length (cm)		Weight (g)		
		Mean	Range	Mean	Range		Mean	Range	Mean	Range	
E ₁	8	10.7	8.5-14.3	44.8	22-84	268	8.6	6.4-12.5	24.2	10-64	193
E ₂	16	9.2	7.6-12.2	25.2	13-49	403	7.4	6.0-12.0	16.1	10-50	242
E ₃	32	8.3	6.7-13.1	20.3	9-63	668	7.3	5.5-12.4	16.2	8-59	519
E ₄ *	No fish	-	-	-	-	-	-	-	-	-	-

* Control

on 6 March, 1978, and to pond 2 enclosures on 13 March, 1978. The experiment was terminated on 27 September, 1978. Fortnightly measurements of water temperature and dissolved oxygen concentration were made (as in 2.2.1) at the surface and successive 10 cm depth intervals in each enclosure. A 1200 ml water sample was also taken from the surface of each enclosure and the following parameters determined as in 2.2.1: pH, SS, total (unfiltered) BOD, soluble $\text{PO}_4 - \text{P}$, total oxidized nitrogen ($\text{NO}_3^- + \text{NO}_2^-$), TC, TOC and TIC.

600 ml surface water samples were taken fortnightly (after filtration through 150 μm zooplankton mesh). Chlorophyll a was determined as in 3.2.1, and algal cell density determined as in 3.2.2.

A single sample of the zooplankton of each enclosure was taken fortnightly with the tube sampler (see 4.2.1). An attempt was made to homogenize the zooplankton within each enclosure, prior to taking the sample, by moving the sides of the enclosure back and forth at various points around its circumference. The major zooplankter in all enclosures was *D. carinata*. The numerical density of that species in enclosures was determined as in 4.2.1. The percentage of adult female *D. carinata* in reproductive condition, and the length-frequency distribution (plus mean length of adults) in enclosures was determined as in 4.3.1.1 and 4.3.1.2.

The original experimental design called for monthly recapture of fish to determine growth rates. Several methods were employed during the course of the experiment in an attempt to recapture fish. These included electro-shocking, fish traps, and seine netting. No fish were recaptured from any enclosure using these methods. It was later discovered that the wave-form generated by the electro-shocker (a Cybertronic Mark 12 S) was entirely inappropriate for the conditions at Gumeracha (still, fairly turbid water of moderate TDS). Half-pulsed direct current (or half-wave rectified alternating current) would have

been most suitable under those conditions (after Helawell, 1978; Vincent, 1971). The experiment was terminated on 27 September, 1978, by applying "Pro-Noxfish" (active constituent rotenone, 2.5% W/V) to each enclosure at a rate of 10 ppm (dose strength from F. Reynolds, N.S.W. State Fisheries, pers. comm., 1978). Potassium permanganate was added to each enclosure at the same rate (10 ppm) approximately 1 hour after treatment to neutralise the rotenone. Fish returns from the enclosures are shown in Table 5.2. Additionally, dead fish were retrieved from some enclosures on 11 October, 1978, as follows: pond 1 enclosure 2: 1 fish, enclosure 3: 10 fish; pond 2, enclosure 2: 1 fish, enclosure 3: 1 fish. It was concluded that fish not recaptured either died during the experiment or escaped from the bottom of enclosures due to an imperfect seal with the sediments.

Recaptured fish were treated as follows. Standard length (cm) was measured on all fish, and 6 large, symmetrical scales removed from the left side of the body between the lateral line and the anterior half of the dorsal fin (after Tesch, 1968). Scales were cleaned and examined microscopically using transmitted light; annuli were determined after Tesch (1968). Live weight (g) was measured on fish collected on 27 September. The digestive tracts of those animals were removed and representative samples of material from the fore and hind gut examined microscopically. This material was analysed semi-quantitatively using the points method (after Hynes, 1950).

5.3 Results

Due to the death or escape of fish from some enclosures the effect of varying fish density on pond function could not be determined. The effects of *C. auratus* could, in some measure, be gauged from a comparison of physico-chemical and biological conditions in enclosure 2 with conditions in the control enclosure in pond 1. In the following sections "control" refers only to the control enclosure in pond 1 and

Table 5.2

Returns of *C. auratus* from experimental enclosures in
the Gumeracha ponds on 27 September, 1978, after
treatment with rotenone

Enclosure	Stocking density	POND 1		POND 2	
		Recaptured		Recaptured	
		Tagged	Untagged	Tagged	Untagged
E ₁	8	1	-	1	-
E ₂	16	10	4	-	1
E ₃	32	-	-	-	1

"fish" refers only to enclosure 2 in pond 1.

5.3.1 Physico-Chemical Characteristics in Enclosures. Depth-averaged water temperature ($^{\circ}\text{C}$) and dissolved oxygen concentration (mg/ℓ) in fish and control enclosures are shown in Figure 5.3. Variation in both parameters was similar to that in the pond proper during the same period (Fig. 2.6). Dissolved oxygen concentration was high at the start of the experiment ($> 15 \text{ mg}/\ell$) but declined markedly in both enclosures during April, 1978. Dissolved oxygen concentration was low ($< 2 \text{ mg}/\ell$) in May, increased steadily from June to mid-September, and then increased markedly in early October. There was no significant difference between depth-averaged temperature or dissolved oxygen concentration in fish and control enclosures (Mann-Whitney U test, $p > 0.05$).

Variation in pH, total BOD, and SS in fish and control enclosures is shown in Figures 5.4, 5.5 and 5.6 respectively. pH was high in both enclosures (> 10.5) at the start of the experiment but declined during April. Thereafter pH in both enclosures was fairly constant (approx. 7-7.5). Total BOD was high in both enclosures ($20\text{-}30 \text{ mg}/\ell$) at the start of the experiment, declined markedly during late April, and remained at low, fairly constant concentrations thereafter ($< 5 \text{ mg}/\ell$). SS in both enclosures followed a similar pattern to total BOD: SS was high at the start of the experiment ($> 80 \text{ mg}/\ell$), declined during April, and remained low thereafter (approx. $5\text{-}10 \text{ mg}/\ell$). Variation in pH, BOD and SS in both enclosures was similar to variation in those parameters in the pond proper during the same period (Figs. 2.15-2.17). There was no significant difference between pH, BOD or SS in fish and control enclosures (Mann-Whitney U test, $p > 0.05$).

Variation in soluble $\text{PO}_4\text{-P}$ and total oxidized nitrogen in fish and control enclosures is shown in Figure 5.7. Soluble $\text{PO}_4\text{-P}$ was low in both enclosures at the start of the experiment ($< 2 \text{ mg}/\ell$),

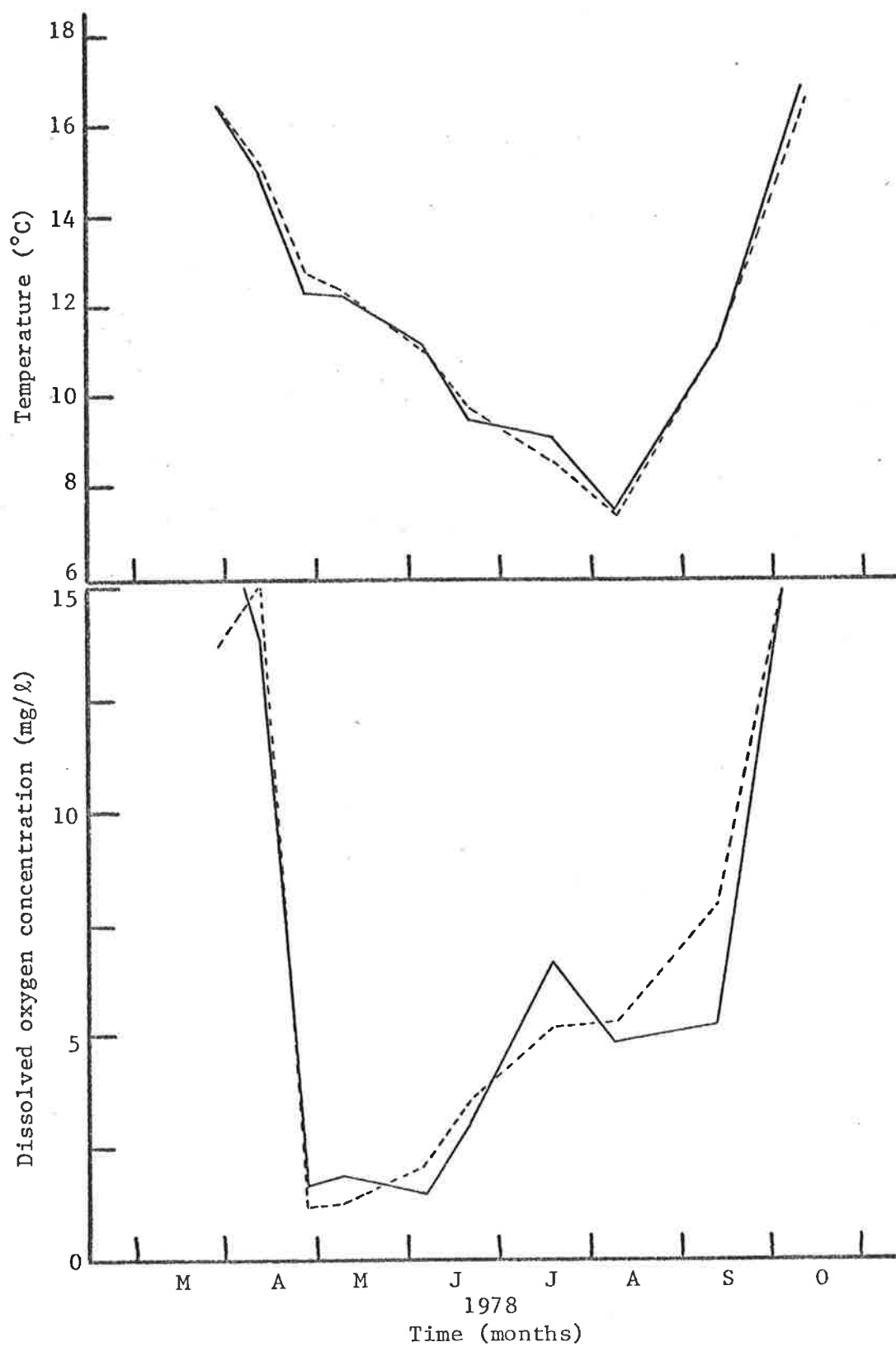


FIGURE 5.3 Depth-averaged water temperature and dissolved oxygen concentration in fish (—) and control (---) enclosures.

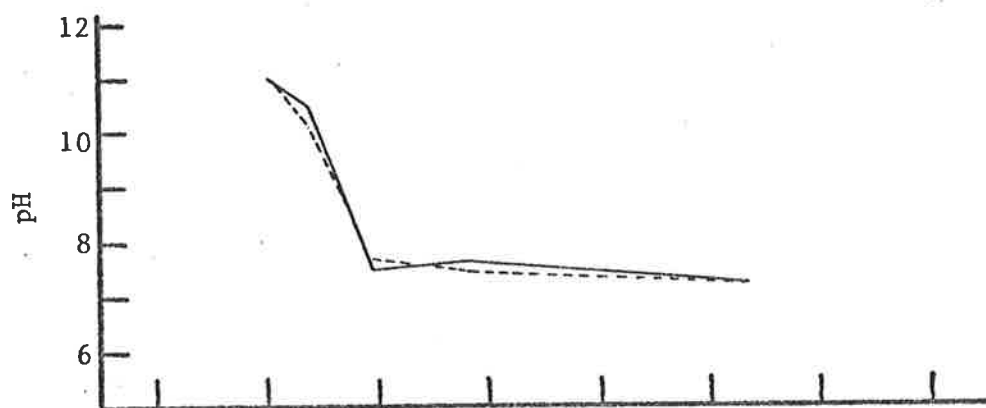


FIGURE 5.4 pH of water in fish (—) and control (---) enclosures.

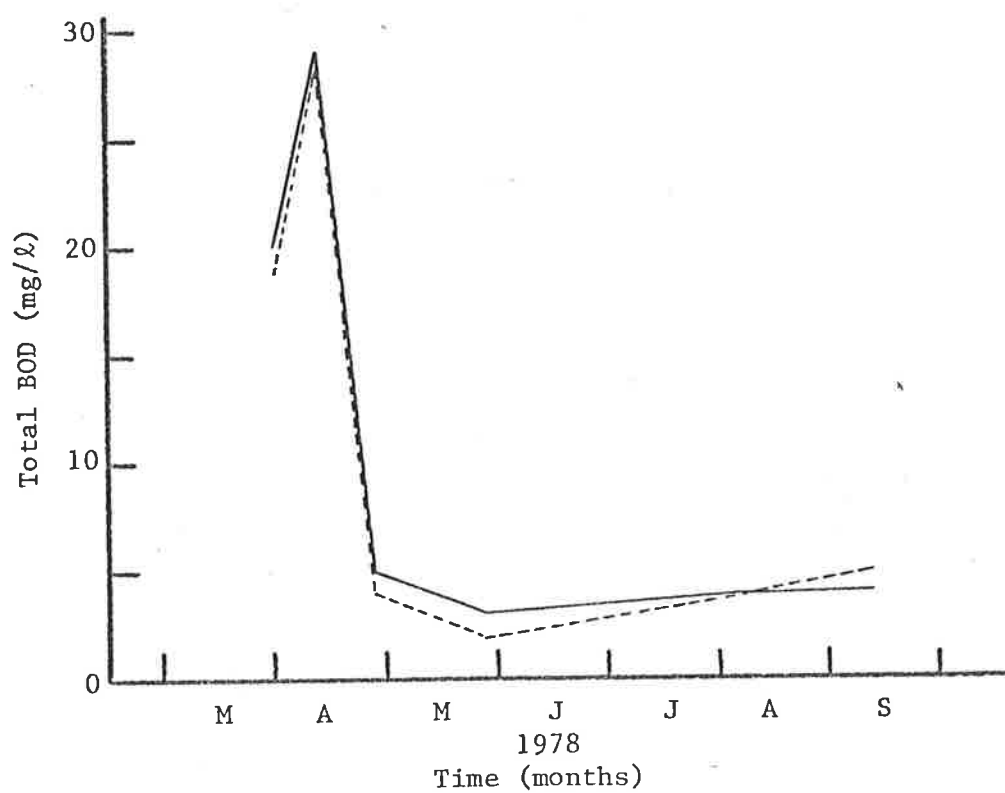


FIGURE 5.5 Total BOD of water in fish (—) and control (---) enclosures.

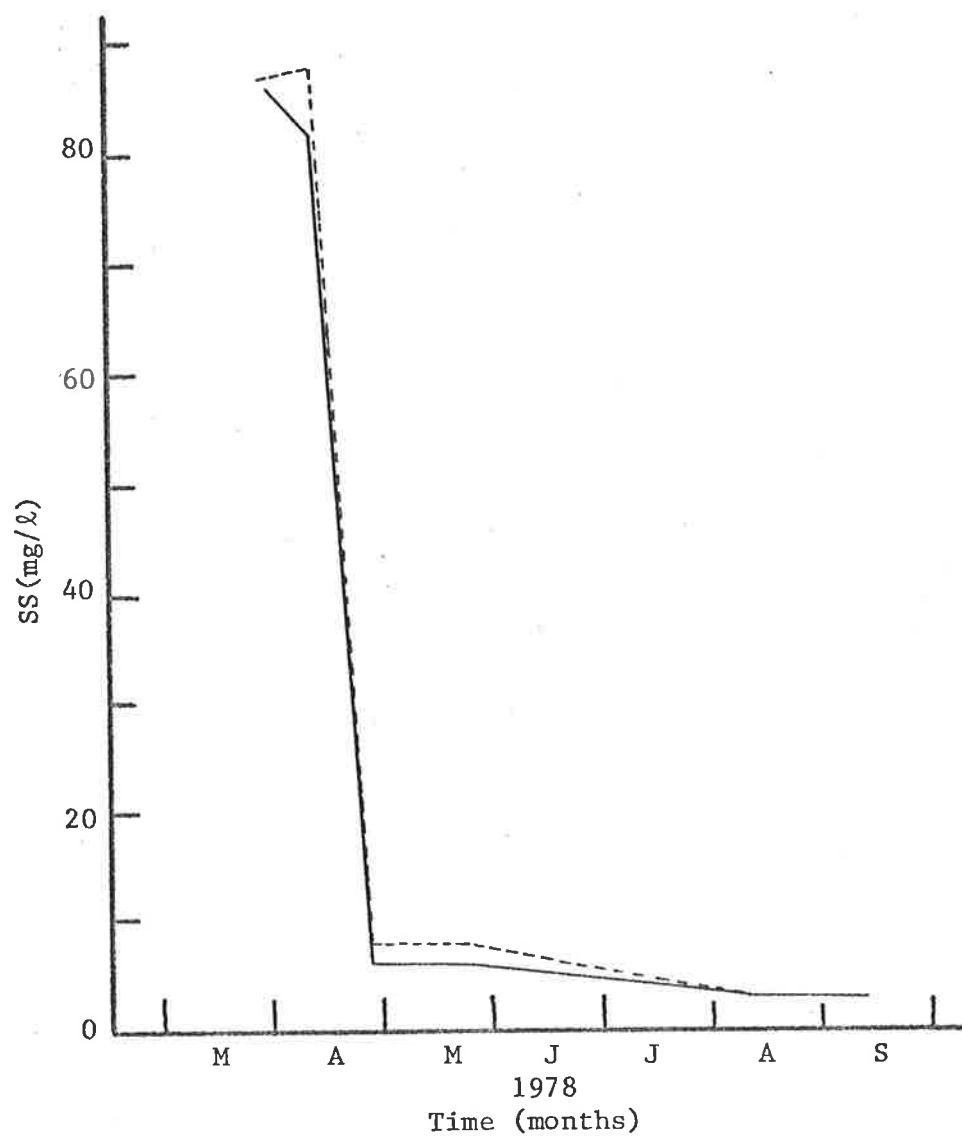


FIGURE 5.6 SS concentration in fish (—) and control (---) enclosures.

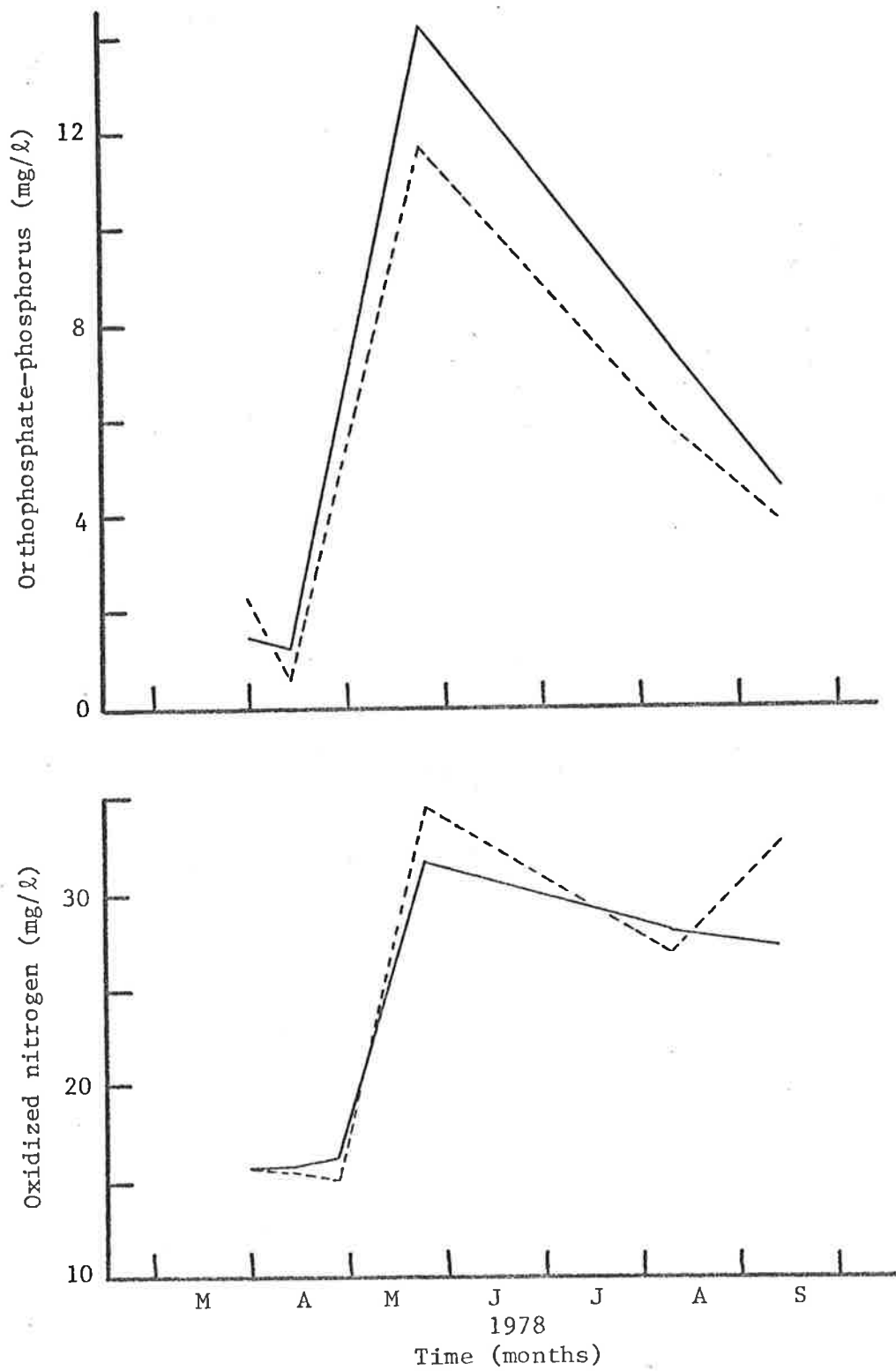


FIGURE 5.7 Total orthophosphate-phosphorus and oxidized nitrogen concentration in fish (—) and control (---) enclosures.

increased markedly during April and May (reaching a peak of 11-14 mg/ℓ in late May), but declined steadily thereafter. There was no significant difference between soluble $\text{PO}_4\text{-P}$ concentration in fish and control enclosures (Mann-Whitney U test, $p > 0.05$). Total oxidized nitrogen in both enclosures was also low at the start of the experiment and increased during May. Total oxidized nitrogen in both enclosures reached a peak in late May (30-35 mg/ℓ) but decreased somewhat thereafter. There was no significant difference between total oxidized nitrogen concentration in fish and control enclosures (Mann-Whitney U test, $p > 0.05$).

Variation in TOC and TIC in fish and control enclosures is shown in Figure 5.8. TOC was fairly high in both enclosures (approx. 50 mg/ℓ) at the start of the experiment but decreased markedly in April. TIC was low in both enclosures (< 5 mg/ℓ) at the start of the experiment, increased to a peak in late April (approx. 38-40 mg/ℓ), but declined thereafter. There was no significant difference between TOC or TIC in fish and control enclosures (Mann-Whitney U test, $p > 0.05$).

That is, physico-chemical conditions in enclosures were similar to those in pond 1 proper and enclosures therefore replicated the pond situation fairly accurately. At a stocking rate of 1 fish/m², *C. auratus* had no significant effect upon physico-chemical conditions within enclosures.

5.3.2 Phytoplankton in Enclosures. Variation in the concentration of active chlorophyll a (mg/m³) in fish and control enclosures is shown in Figure 5.9. The experiment commenced during a phytoplankton bloom in pond 1 and, consequently, chlorophyll a concentration was high (> 700 mg/m³) in both enclosures. Chlorophyll a concentration declined markedly to very low levels (< 10 mg/m³) in late April, and remained low until termination of the experiment. There was no significant difference between Chlorophyll a concentrations in fish and control enclosures

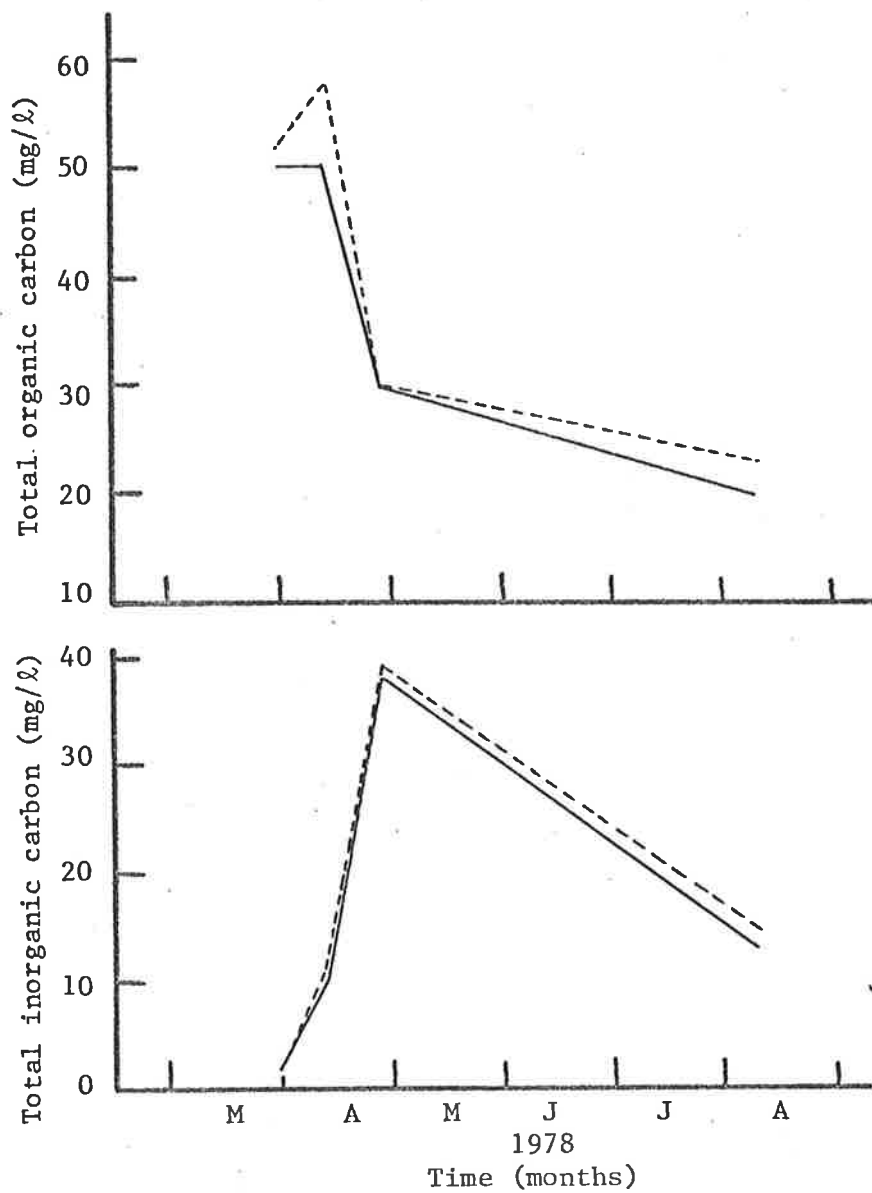


FIGURE 5.8 Total organic carbon and total inorganic carbon concentration in fish (—) and control (---) enclosures.

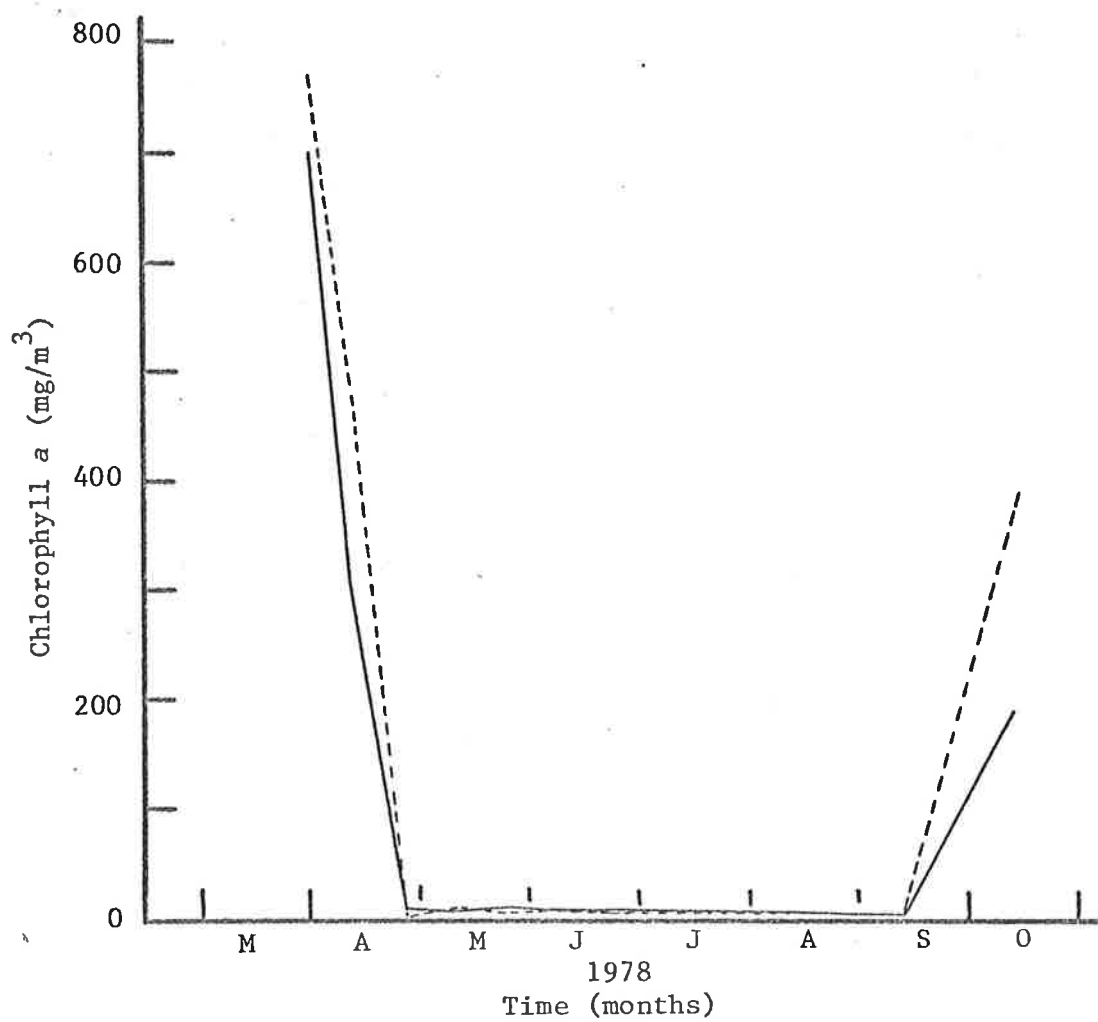


FIGURE 5.9 Active chlorophyll a concentration in fish (—) and control (---) enclosures.

(Mann-Whitney U test, $p > 0.05$). Variation in chlorophyll a concentrations in enclosures was very similar to variation in chlorophyll a in the pond proper during the same period (Fig. 3.2).

The composition of the phytoplankton within enclosures was similar to that in the pond proper during the same period. The bloom at the start of the experiment was composed mainly of *S. opoliensis*, *S. quadricanda*, *S. acutiformis* and *S. acuminatus*. During periods of lower temperatures and low chlorophyll a concentrations diatoms, mainly *Nitzschia* sp., *Navicula* sp., *Cymbella* sp. and *Diatoma* sp., predominated.

Variation in total cell density in fish and control enclosures is shown in Figure 5.10. Total cell density was high in both enclosures at the start of the experiment (when chlorophyll a concentration was high) but decreased during April as the phytoplankton bloom declined. Although some variation occurred between cell densities in enclosures in May, total density was not significantly different in the fish and control enclosure (Mann-Whitney U test, $p > 0.05$). Variation in *Scenedesmus* species composition in fish and control enclosures is shown in Figure 5.11. Species succession in both enclosures was similar, and the same as that observed in the pond proper during the same period (Fig. 3.5).

C. auratus had no significant effect upon chlorophyll a concentration or phytoplankton species composition in the experimental enclosure. The variation in chemistry of enclosures was the result of variation in the standing crop of phytoplankton. The decrease in dissolved oxygen concentration, pH, BOD and SS during the course of the experiment was due to the decline of phytoplankton standing crop in April. Soluble $PO_4 - P$ and total oxidized nitrogen were low at the start of the experiment due to incorporation into algal cells. Nutrient removal decreased as the phytoplankton standing crop declined.

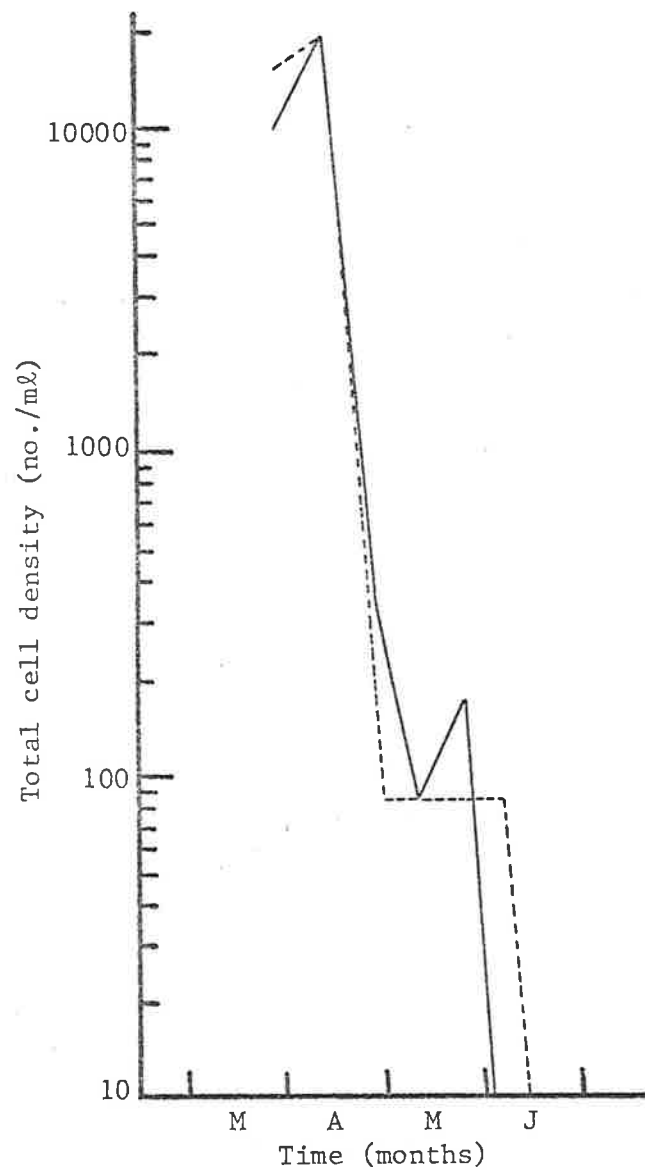


FIGURE 5.10 Total algal cell density in fish (—) and control (---) enclosures.

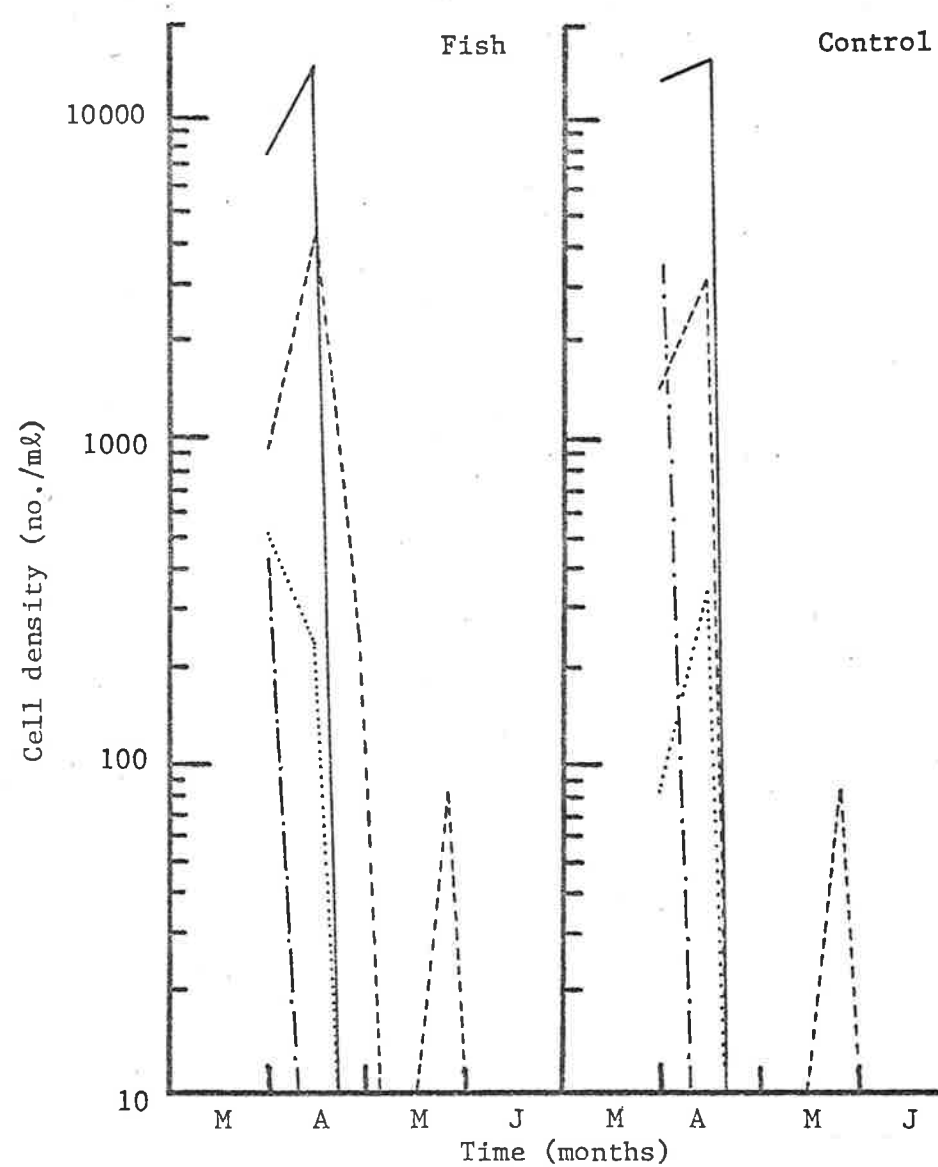


FIGURE 5.11 Succession of *Scenedesmus* species in fish and control enclosures. *S. opoliensis* (—), *S. quadricaudra* (---), *S. acutiformis* (.....), *S. acuminatus* (-.-).

Qualitatively and quantitatively, the phytoplankton population within the enclosures resembled that in the pond proper. That is, no significant alteration of the phytoplankton occurred due to enclosure effects.

5.3.3 Zooplankton in Enclosures. Variation in the density of *D. carinata* in the fish and control enclosures is shown in Figure 5.12. In both enclosures, *D. carinata* populations developed from the hatching of ephippial eggs in early April. Population density increased markedly during late April. The *D. carinata* population in the fish enclosure showed two density peaks, one in late April (298/ℓ) and one in early June (625/ℓ) after a marked population decline. Population density in the control enclosure increased more rapidly than in the fish enclosure but showed only a single peak (428/ℓ) in May. Population density in both enclosures declined steadily from June until mid-September. Thereafter, populations rapidly disappeared from both enclosures. There was no significant difference between the density of *D. carinata* in the fish and control enclosures (Mann-Whitney U test, $p > 0.05$).

Non-significant

correlations were found between the density of *D. carinata* and chlorophyll a concentration in the fish (Spearman's $\rho = -0.43$, $p > 0.05$) and control (Spearman's $\rho = -0.22$, $p > 0.05$) enclosures.

The length-frequency distribution of *D. carinata* in both enclosures is shown in Figure 5.13. The proportion of post-embryonic individuals in different size classes varied throughout the experiment. However, no consistent trend emerged with respect to size distribution in the fish enclosure. That is, the population length distribution was not skewed towards smaller individuals, and *D. carinata* greater than 2 mm in body length were recorded in the presence of *C. auratus* throughout the experiment. Variation in the mean body length of

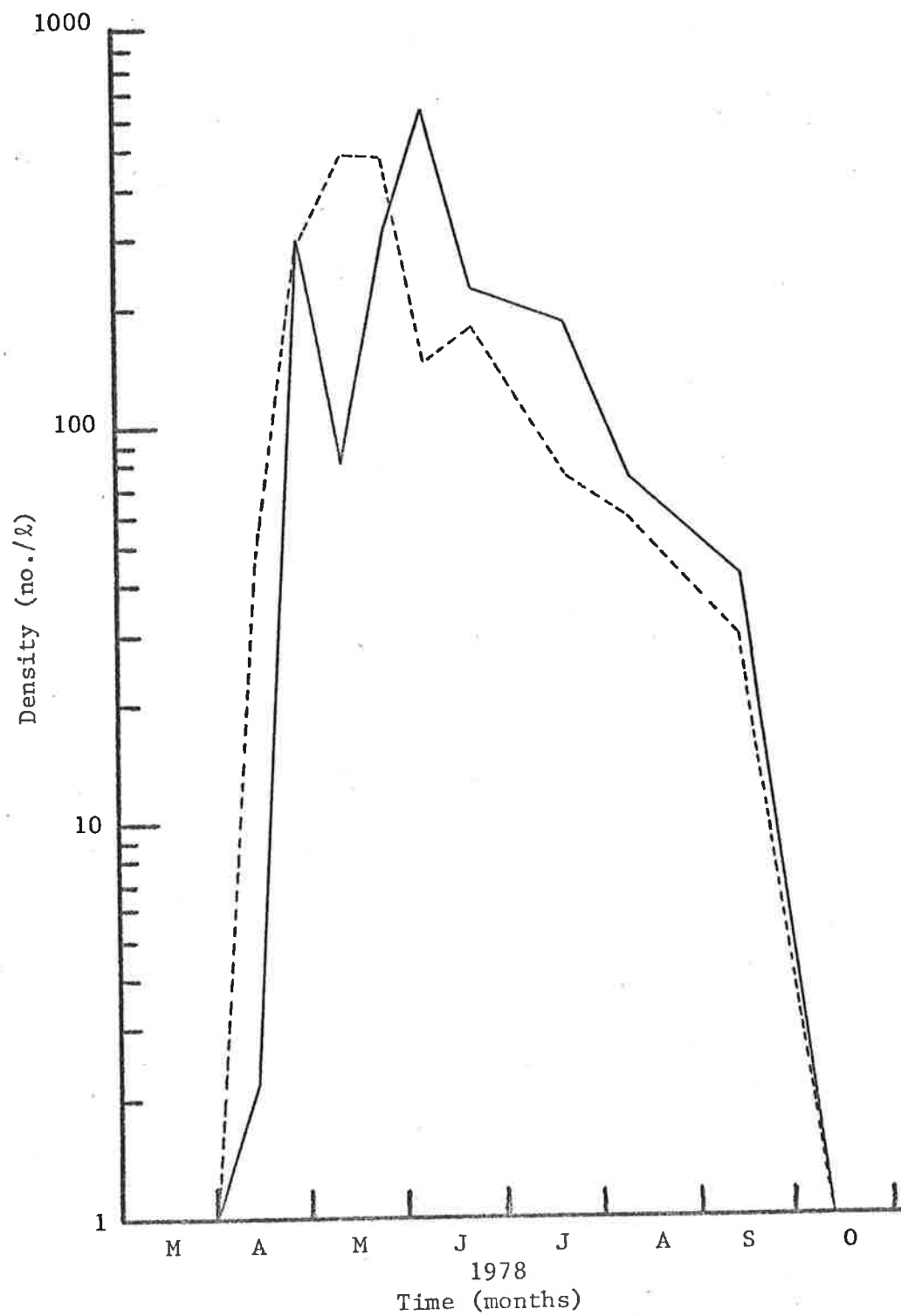


FIGURE 5.12 Density of *D. carinata* in fish (—) and control (---) enclosures.

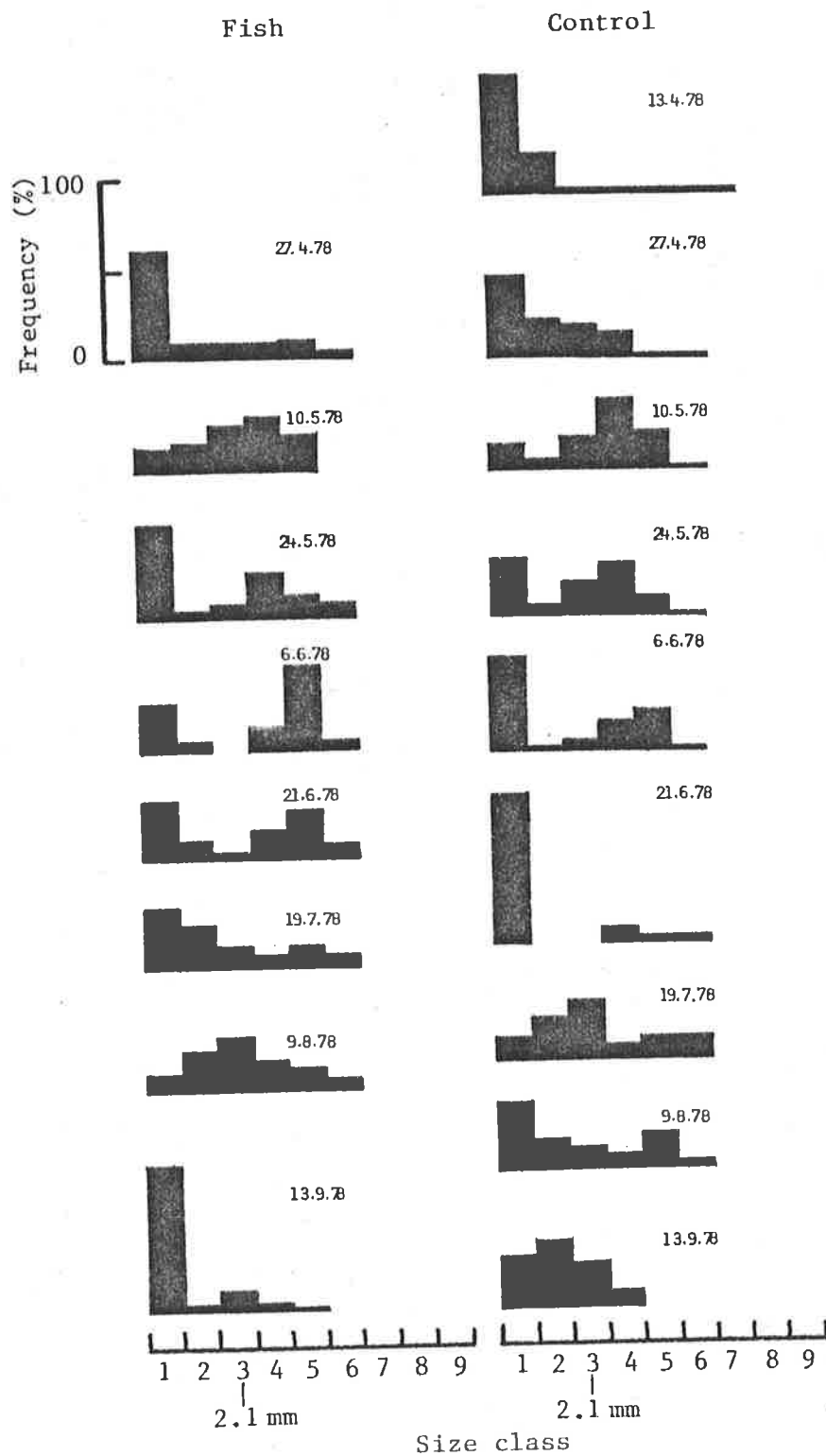


FIGURE 5.13 Length-frequency distribution of *D. carinata* in fish and control enclosures.

D. carinata in both enclosures is shown in Figure 5.14. Apart from an initial peak in body length in the control enclosure, the range and pattern of variation in mean body length was similar in both enclosures. There was no significant difference between mean body length in the fish and control enclosures (Mann-Whitney U test, $p > 0.05$). Thus, predation by *C. auratus* upon *D. carinata* did not appear to be intense, and, if it occurred at all, was not size-selective.

Variation in the percentage of ovigerous and ephippial adult female *D. carinata* in both enclosures is shown in Figure 5.15. Although there was no significant difference between the percentage of ovigerous females in the fish and control enclosures (Mann-Whitney U test, $p > 0.05$), the percentage was often lower in the fish enclosure. There was no significant difference between the percentage of ephippial females in both enclosures (Mann-Whitney U test, $p > 0.05$), although the percentage was often higher in the fish enclosure. This suggests that the presence of fish may have made conditions unfavourable for *D. carinata*, but indicates that *C. auratus* did not prey selectively upon the darker ephippial females. Although not studied intensively, the presence of fish appeared to have no major effect upon the external morphology of *D. carinata*. That is, no marked formation of helmets or other carapace protuberances was observed.

Thus, *C. auratus* did not exert significant trophic effects upon the zooplankton or phytoplanktonic communities in the experimental enclosure. At a stocking rate of 1 fish/m², *C. auratus* had no significant effect upon pond function and, therefore, upon effluent quality.

5.3.4 Fish Growth and Production in Enclosures. All fish recaptured on 27 September, 1978, were in reproductive condition. Testes of male fish were large, pinkish in colour, and equivalent to (on average) 5.9% of total live weight ($\pm$ standard error equivalent to

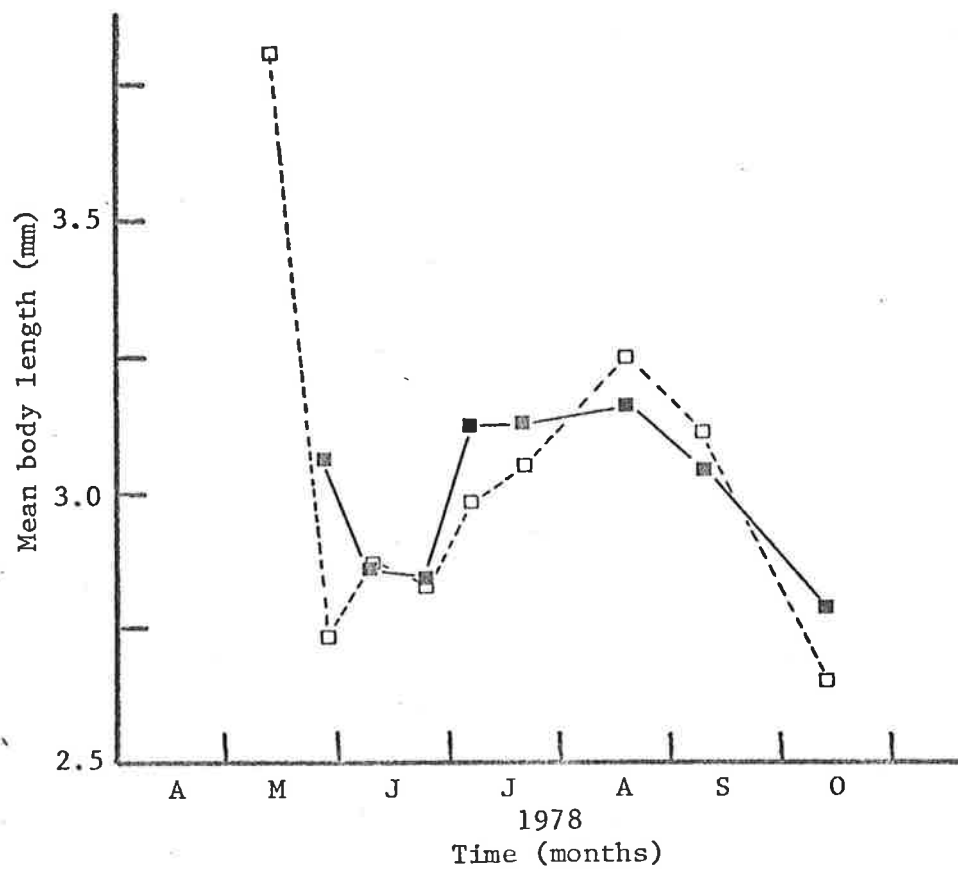


FIGURE 5.14 Mean body length of *D. carinata* in fish (■—■) and control (□--□) enclosures.

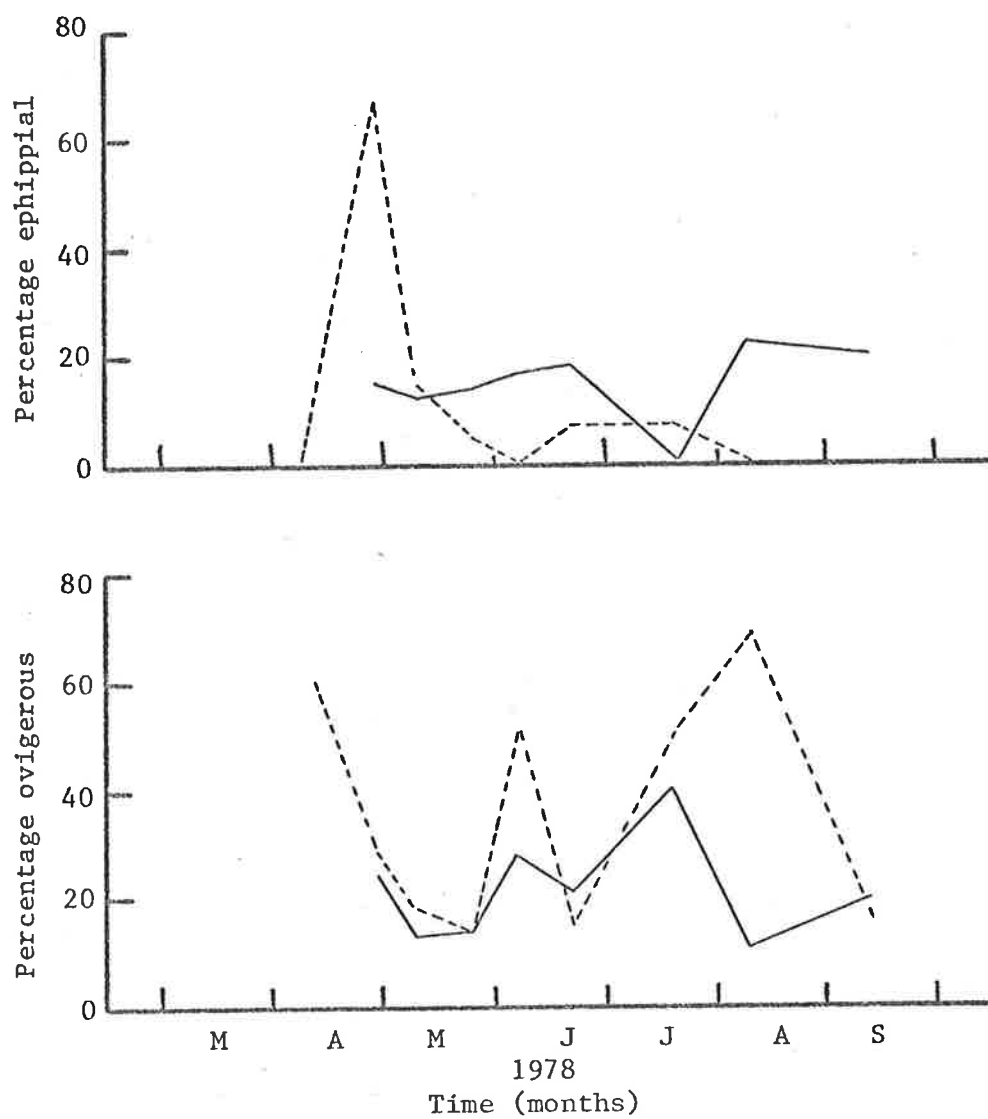


FIGURE 5.15 Percentage of adult *D. carinata* carrying eggs or ephippia in fish (—) and control (---) enclosures.

11% of the mean). Ovaries of female fish distended the body cavity (eggs were orange in colouration and clearly visible) and were (on average) equivalent to 21.9% of total live weight ($\pm$ standard error equivalent to 12% of the mean). Although the gonads of cyprinids may develop gradually during winter, final ripening occurs 10 to 15 days prior to spawning (Nikolsky, 1963). Mean depth-averaged temperature during the fortnight prior to the recapture of *C. auratus* at Gumeracha was 12.5°C. Thus, physico-chemical conditions and food levels in pond 1 were apparently suitable for the survival and reproduction of *C. auratus*.

Recaptured fish exhibited marked weight gains and increases in length. The mean length of fish recaptured from pond 1 - enclosure 2 was 11.7 cm (range 10.5 to 14.2 cm), and the mean weight of fish was 66.4 g (range 43-128 g). Total recaptured biomass was 929 g (including weight of gonads). The mean length of fish recaptured from pond 1 - enclosure 3 was 11.9 cm (range 10.9 to 13.7 cm). The mean weight and mean length of fish recaptured from pond 1 - enclosure 2 were significantly greater than mean weight and length when introduced (Mann-Whitney U test, $p < 0.05$). The mean length of fish recaptured from pond 1 - enclosure 3 was significantly greater than when introduced (Mann-Whitney U test, $p < 0.05$).

Examination of the scales of recaptured fish revealed an apparent change in the spacing of circuli after introduction to the pond at Gumeracha. Two growth patterns were evident. In the first, a transition occurred from a region of more closely spaced circuli to a region of more widely spaced circuli with no cutting over. That is, a change in growth had occurred but this was not the same as an annual growth check. In the second pattern, a transition occurred from a region of widely spaced circuli to another region of widely spaced circuli with a growth check. Fish were introduced at Gumeracha just prior to a decrease in water temperature. Thus, a transition from a

summer growth pattern (widely spaced circuli) to a slower, winter growth pattern (closely spaced circuli) after a growth check would have been expected. Transition from rapid summer growth to another period of rapid growth, despite reduced water temperature, appeared to have occurred after the introduction of *C. auratus* at Gumeracha.

For comparative purposes the growth of *C. auratus* was studied in the Uraidla population and in populations from Millbrook Reservoir, and a shallow backwater of the River Murray at Cobdogla (see Mitchell, 1979*). Age was determined from scale readings and growth determined from the back-calculation of length at the time of formation of successive annuli using the modified direct proportionality formula (Chugunova, 1970; Tesch, 1968). Significant differences in length-weight relationships and growth rates occurred between populations. Fish from Uraidla grew at the slowest rate of all populations studied. The time of recapture of *C. auratus* from Gumeracha would have corresponded to the period of annulus formation. The length and weight of recaptured fish was assumed to represent size at the end of the year's growth. The mean length (plus 95% confidence limits) of recaptured *C. auratus* has been plotted against age, and compared with back-calculated growth history of other populations (including that at Uraidla) from South Australia in Figure 5.16. The growth rate of *C. auratus* in the Gumeracha pond increased appreciably above that of the Uraidla population, that is, the population from which animals were originally collected. Mean live weight (minus gonad weight) of recaptured fish has been plotted against age and compared with weight versus age data for the Uraidla and Cobdogla populations (calculated from growth curves and length-weight relationships in Mitchell, 1979) in

*This paper is presented in Appendix 3.

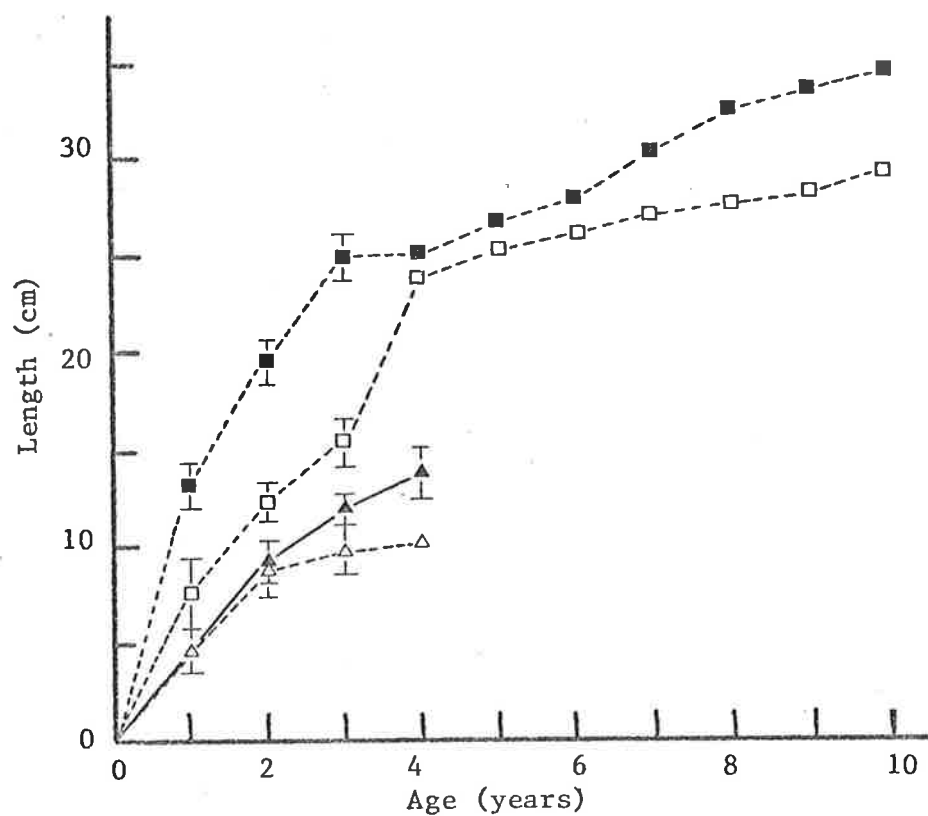


FIGURE 5.16 Growth of *C. auratus* in the Gumeracha pond (▲) compared with growth at Uraidla (△), Cobdogla (□), and in Millbrook Reservoir (■).

Figure 5.17. Live weight of *C. auratus* at a given age (above the second year of life) increased markedly after introduction to the Gumeracha pond.

The daily net production of *C. auratus* (g live weight/m²/day) in pond 1 - enclosure 2 during the course of the experiment was calculated from

$$\frac{\text{Recovered Biomass (g)} - \text{Initial (Stocking) Biomass (g)}}{\text{Area (m}^2\text{)} \cdot \text{Time (days)}}$$

The weight of gonads was included in recovered biomass as suggested by Chapman (1967). The duration of the experiment was 204 days. Daily net production of *C. auratus* during the experiment was 0.16 g live weight/m²/day. If this rate of production had been maintained throughout the year, annual net production would have been 58.4 g live weight/m²/year. Fish growth is directly proportional to food intake and assimilation above maintenance requirements (Nikolsky, 1963; Brown, 1957). Oxygen consumption (a measure of standard metabolism) of *C. auratus* increases by a factor of 2 for each 10°C increase in water temperature up to 30°C (Beamish and Mookherjee, 1964; Fry and Hart, 1948). Thus, food intake and growth rate of *C. auratus* would have increased as maintenance requirements increased in response to higher temperatures. Annual production of *C. auratus*, including periods of summer growth, would probably have been slightly higher than the above figure, provided food levels were adequate to meet and exceed maintenance requirements.

Had the annual rate of net production of *C. auratus* in pond 1 - enclosure 2 been maintained in the pond proper, total annual net production in pond 1 would have been 84 kg live weight. The nutrient content of *C. auratus* tissue was not determined during the present study. The nutrient content of freshwater fishes varies with food quality and quantity (Papoutsoglou and Papapararskeua-Papoutsoglou, 1978);

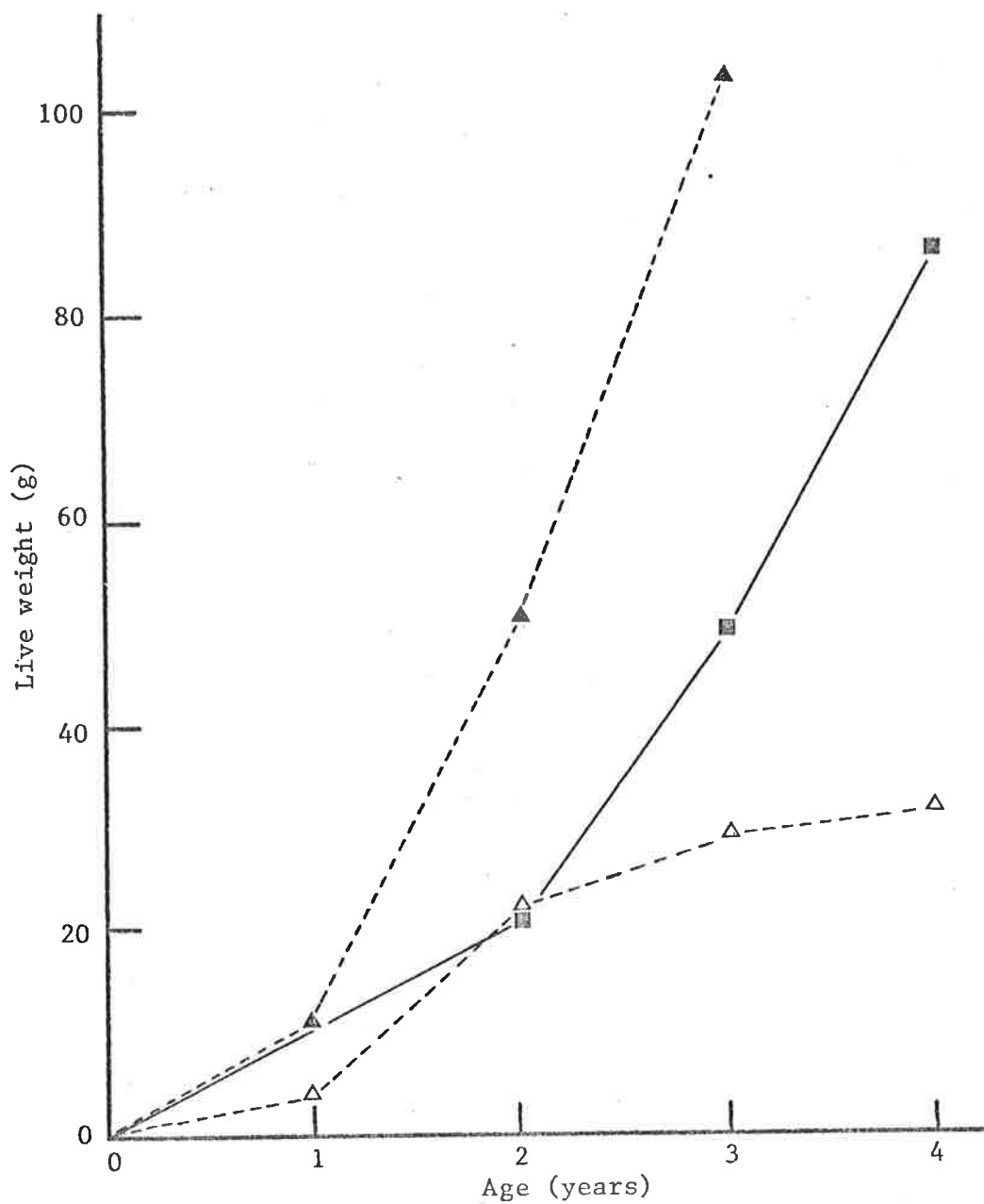


FIGURE 5.17 Live weight versus age for *C. auratus* from the Gumeracha pond (■) compared with *C. auratus* from Uraidla (Δ) and Cobdogla (▲).

total nitrogen content of freshwater fishes ranges from 2.2 to 3.6% of live weight and total phosphorus content from 0.3 to 0.8% live weight (calculated from Papoutsoglou and Papapararskeua-Papoutsoglou, 1978, assuming that protein content is equivalent to $\text{TKN} \times 6.25$: same authors; Bull and Mackay, 1976; calculated from Goodyear and Boyd, 1972, assuming that dry weight is equivalent to 20% of live weight: Lagler *et al.*, 1962, p. 170). The studies quoted analysed whole fish, and therefore included bones and scales in nutrient determinations. In the following calculation the total nitrogen content of *C. auratus* has been assumed to be 2.9% of live weight and the total phosphorus content assumed to be 0.6% of live weight. Actual nutrient content of *C. auratus* may have been slightly higher than these values. Total annual net production of *C. auratus* in pond 1 (as determined above) represented a nutrient store equivalent to 0.27% of total nitrogen ($\text{TKN} + \text{NO}_3^-$) and 1.02% of total $\text{PO}_4 - \text{P}$ retained in pond 1 during 1977. Harvest of *C. auratus* would not have removed a significant proportion of the nutrients retained in the pond annually. At the production rate exhibited in enclosure 2, fish harvest did not represent a useful pathway for nutrient removal from the Gumeracha pond.

Food items found in the intestines of *C. auratus* recaptured on 27 September, 1978, included *D. carinata*, *Alonella* sp., *M. leuckarti*, *C. assimilis*, larval and adult chironomids, fragments of *Scenedesmus* cells and filamentous algae, diatoms (*Navicula* sp., *Nitzschia* sp., *Cymbella* sp., *Cyclotella* sp., *Amphora* sp.) and detritus. The mean percentage of estimated volume of major food items in recaptured fish is shown in Figure 5.18. The dominant food items were *D. carinata* and detritus. Benthic organisms, that is ostracods and chydorids, were the next most abundant food items. *C. auratus* in the experimental enclosure appeared to have been ingesting the sediments. Although *D. carinata* formed a large proportion of the food in *C. auratus*,

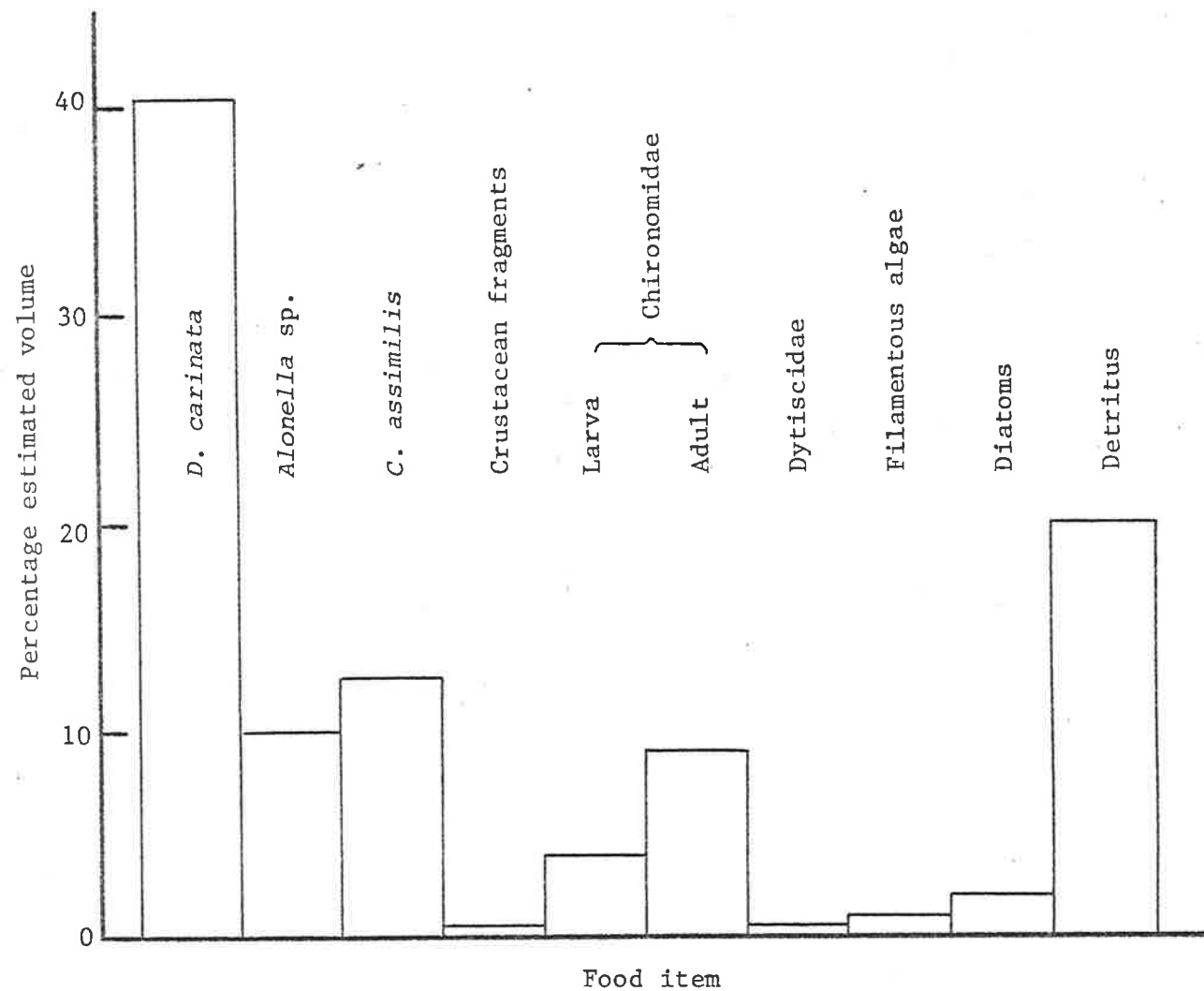


FIGURE 5.18 Composition of gut contents of *C. auratus* (percentage estimated volume) from the Gumeracha pond.

ingestion was not size-selective. As *D. carinata* foraged amongst the sediments when phytoplankton standing crops were low, it is likely that the *D. carinata* in the intestines of *C. auratus* were ingested incidentally with the sediments. That is, *C. auratus* did not actively prey upon *D. carinata*.

5.4 Discussion

C. auratus was able to survive, make appreciable weight gains, and reach spawning condition in pond 1 at Gumeracha. The success of spawning would have been determined by the availability of suitable spawning sites and the occurrence of favourable physico-chemical conditions for egg development. *C. auratus* is a phytophil and deposits its eggs on submerged aquatic vegetation or on recently inundated terrestrial vegetation (Balon, 1975; Kukuradze and Mariyash, 1975). The species never lays its egg on the bottom. Spawning success at Gumeracha would, therefore, have depended upon the presence of *P. ochreatus*. The provision of spawning sites is an indirect benefit of the presence of submerged macrophytes in WSPs. Water temperature and dissolved oxygen concentration are important factors affecting the development of fish eggs (Bagenal and Braum, 1978). Although phytophils are generally adapted to low oxygen concentrations (Balon, 1975), oxygen levels at Gumeracha after the decline of phytoplankton blooms could have been detrimental to egg survival or development.

Growth and production of *C. auratus* in pond 1 were determined from small sample sizes ($n = 31$ and $n = 14$ respectively) and must be regarded as tentative. However, growth rate of *C. auratus* from Uraidla increased after introduction to the Gumeracha pond. The Uraidla population exhibited the lowest growth rate of the natural populations studied (Mitchell, 1979). This appeared not to be due to temperature differences but may have reflected genetically determined varietal differences (c.f. Kukuradze and Mariyash, 1975). Growth rates of

C. auratus at Gumeracha may have been more pronounced had fish from other populations been introduced. Tagging may affect the growth rate of fish (Jones, 1977) and ideally, growth rates of tagged and untagged fish should be compared. It is possible that the tagging procedure may have retarded the growth of *C. auratus* at Gumeracha to some degree.

Study of the scales of *C. auratus* from Gumeracha indicated that growth had increased after introduction to pond 1. A typical winter growth pattern was not apparent. Although seasonal changes in growth of fish correlate with temperature variation and temperature influences maintenance requirements and appetite (Brown, 1957), growth rate is also significantly influenced by food level. Variation in the width of scale circuli spacing appears to depend primarily on food availability (Bilton and Robins, 1971; Wingfield, 1940; Bhatia, 1931) and, if food is superabundant, seasonal periodicity in the spacing of scale circuli need not occur (Gray and Senta, 1931). Increased food availability in the Gumeracha pond (compared to the dam at Uraidla) gave rise to a period of rapid growth despite decreasing water temperature. All fish recaptured from Gumeracha were deep-bodied in appearance and resembled Balon's (1977) "obese" forms. These forms only arise under conditions of extreme food abundance. *C. auratus* from Millbrook Reservoir, the population with the highest growth rate (Mitchell, 1979), were also deep-bodied in appearance.

The annual production of *C. auratus* at Gumeracha was much higher than generally recorded for freshwater fish from natural water bodies (approx. 5 to 10 g live weight/m²/year) (see reviews by Waters, 1977; Gutteridge, Haskins and Davey, 1976; Le Cren, 1972; Chapman, 1967; Brown, 1957). The major exception to this was the production of *Tilapia* and carp in tropical ponds (40 to 200 g live weight/m²/year) (Brown, 1957). The annual production of *C. auratus* at Gumeracha was generally greater than for fish in unfertilized fish ponds (10 to 20 g

live weight/m²/year) but similar to that in fertilized ponds (20 to 40 g live weight/m²/year) (c.f. Gutteridge, Haskins and Davey, 1976; Brown, 1957). The major exception to this was the production of cyprinids in fertilized ponds in Israel and the tropics (> 200 g live weight/m²/year). The annual production of *C. auratus* at Gumeracha was similar to the production of freshwater fish in some WSPs (c.f. White and Williams, 1978; Noble, 1975), but lower than reported for others (60 to > 200 g live weight/m²/year) (c.f. Gutteridge, Haskins and Davey, 1976). The results of the present study confirm the conclusions of White and Williams (1978) and Noble (1975) that high fish production can be obtained in WSPs without intensive management or supplement feeding. Operating costs of WSP aquaculture schemes would, therefore, be considerably lower than for conventional fish culture systems.

It appeared that *C. auratus*, at a stocking rate of 1 fish/m², had no significant influence upon pond function. That is, *C. auratus* could be cultured in WSPs without significant detrimental effects on effluent quality. However, the presence of *C. auratus* would not improve effluent quality. *C. auratus* did not reduce the grazing pressure of the zooplankton upon the phytoplankton and so increase algal standing crops as reported for planktivores in WSPs by White (1975). *C. auratus* had no significant effect on the density or size distribution of *D. carinata* at Gumeracha. This contrasted with the findings of Archibald (1975) who reported intense selective predation of larger *D. pulex* by *C. auratus* of a similar size to that used in the present study. *C. auratus* does not possess a true stomach and relative gut length is high (Shuljak, 1968; Suyehiro, 1942). These features suggest that *C. auratus* characteristically has a diet containing large amounts of indigestible material (Kapoor et al., 1975; Nikolsky, 1963). The gut contents of *C. auratus* from Uraidla (Mitchell, 1979) and Gumeracha indicated that the species was detritivorous and ingested the sediments.

D. carinata appeared to be ingested incidentally and this would explain the lack of size-selectivity and cyclomorphic effects. Archibald's (1975) experimental design prevented the access of *C. auratus* to the sediments and may have induced some switching in feeding behaviour.

C. carpio, also a detritivore, may increase the phytoplankton standing crop by regenerating phosphorus from the sediments and excreting $\text{PO}_4 - \text{P}$ (Andersson et al., 1978; Lamarra Jr., 1975). The mode of feeding of *C. carpio* increases the amount of organic material in suspension (Spodniewska, 1962) and would be expected to increase BOD and SS. *C. auratus* appeared not to exert these effects at Gumeracha. Although *C. auratus* may increase turbidity in some situations (Lake, 1966) this did not appear to be pronounced at Gumeracha. *C. auratus* may ingest more of the sediments than *C. carpio* which resuspends much sedimental material in the water column. Thus, *C. auratus* appeared to be a more suitable species for culture in WSPs than *C. carpio* which could have a detrimental effect on effluent quality. Although several stocking densities were incorporated into the experimental design, data have been obtained for only one stocking rate (1 fish/m^2). The effects of *C. auratus* on effluent quality may vary at higher densities.

The harvest of *C. auratus* from the Gumeracha pond did not represent a significant pathway for nutrient removal. In this respect, the results of the present study agreed with the finding of Bull and Mackay (1976) that the harvest of the total maximal fish yield from eutrophic and oligotrophic lakes in Canada would have removed less than 1% of phosphorus and nitrogen entering the lake annually. Bull and Mackay compared the nutrient store represented by fish production with annual nutrient load and not, as in the present study, with annual nutrient retention. The nutrient store contained in fish production in the Canadian lakes would, therefore, have represented a somewhat higher percentage of annual nutrient retention.

The usefulness of planktivorous and some detritivorous fish for the management of WSPs appears to be doubtful. Some species, such as *C. auratus*, may be cultured in WSPs without significant effects upon effluent quality. However, of the species of fish tested in WSPs to date, none have been shown conclusively to improve pond function and increase effluent quality. One group of fishes that have, as yet, been unstudied in WSPs are the phytoplankton filtering cyprinids (e.g. *Hypophthalmichthys molitrix*). However, such species are restricted to the tropics and may be unsuitable for use in temperate climates. In any event, their introduction and use in non-endemic areas would engender many environmental and legal problems.

Chapter 6. Concluding Discussion

The present study set out to provide basic information on the ecological interactions between organisms in maturation WSPs, and, in so doing, to establish a firmer basis for biological principles of pond management. The dynamics of organisms from different trophic levels were related to effluent quality, and therefore the efficiency of pond function, and the usefulness of those organisms as management tools evaluated. Previous studies on biological aspects of pond function have been based upon *a priori* judgements as to the likely importance of a species or trophic group in the treatment process. Moreover, organisms have been studied in isolation from the rest of the pond ecosystem. Such studies have failed to take into account the effects of other organisms present with the object of major interest. The present study attempted to investigate the overall pond ecosystem and to relate the role of the major ecological groupings to the overall functioning of the system. The relative usefulness of various organisms for pond management can only be evaluated in the light of this type of investigation. Obviously, such a study was ambitious and some groups were studied less intensively than others. To some extent, this reflected the bias of the investigator. However, a concerted attempt has been made to provide a model of the functioning of the overall pond ecosystem.

Conventional solutions to WSP operating problems generally involve altering the areal requirements of the treatment plant, or the introduction of biochemical or mechanical processes. Both these approaches increase the financial and energetic costs of waste treatment and detract from the fundamental advantages of WSPs as simple, economical systems for waste treatment. The major impetus for the present study was the possibility of providing WSP management principles based upon the fundamental ecological interactions within ponds. Biological management of WSPs would not increase operating costs greatly

(provided that any technology involved was relatively simple) and could have the added advantage of producing utilizable by-products.

The major operating problem of WSPs has been the presence of algae in effluents and the concomitant effects of effluent discharge upon receiving waters. Algal control was therefore a primary consideration in studying the ecology of WSPs with a view to biological management. The stabilization of organic matter is not usually a primary requirement of maturation ponds. However, the present study has shown that, during phytoplankton blooms, effluent BOD, SS and TOC may increase substantially above influent concentrations, thereby exceeding present water quality criteria. The removal of organic material was, therefore, also a consideration during the present study. The major functional requirement of maturation ponds is effluent polishing, in particular nutrient removal; this was also of primary concern during the present study. Although nutrient removal is the prime function of maturation ponds, nutrient partitioning, removal pathways, and removal efficiency have been virtually unstudied in this type of WSP.

The major ecological interactions influencing phytoplankton populations in the Gumeracha ponds are summarized in Figure 6.1. This scheme may be used as a predictive model for the management of maturation ponds to reduce phytoplankton standing crops. Phytoplankton blooms in the Gumeracha ponds were triggered by increasing temperature but were terminated by zooplankton (*D. carinata*) grazing. *D. carinata*, a cold water species, was prevented from controlling phytoplankton abundance during summer by high water temperatures. Greater than 50% pond surface coverage by filamentous algal mats (*Cladophora*) during the critical period for the onset of phytoplankton blooms and the presence of substantial stands of submerged macrophyte (*P. ochreatus*) inhibited the development of a summer phytoplankton bloom. Thus, phytoplankton in WSPs may be controlled by encouraging the development of populations of

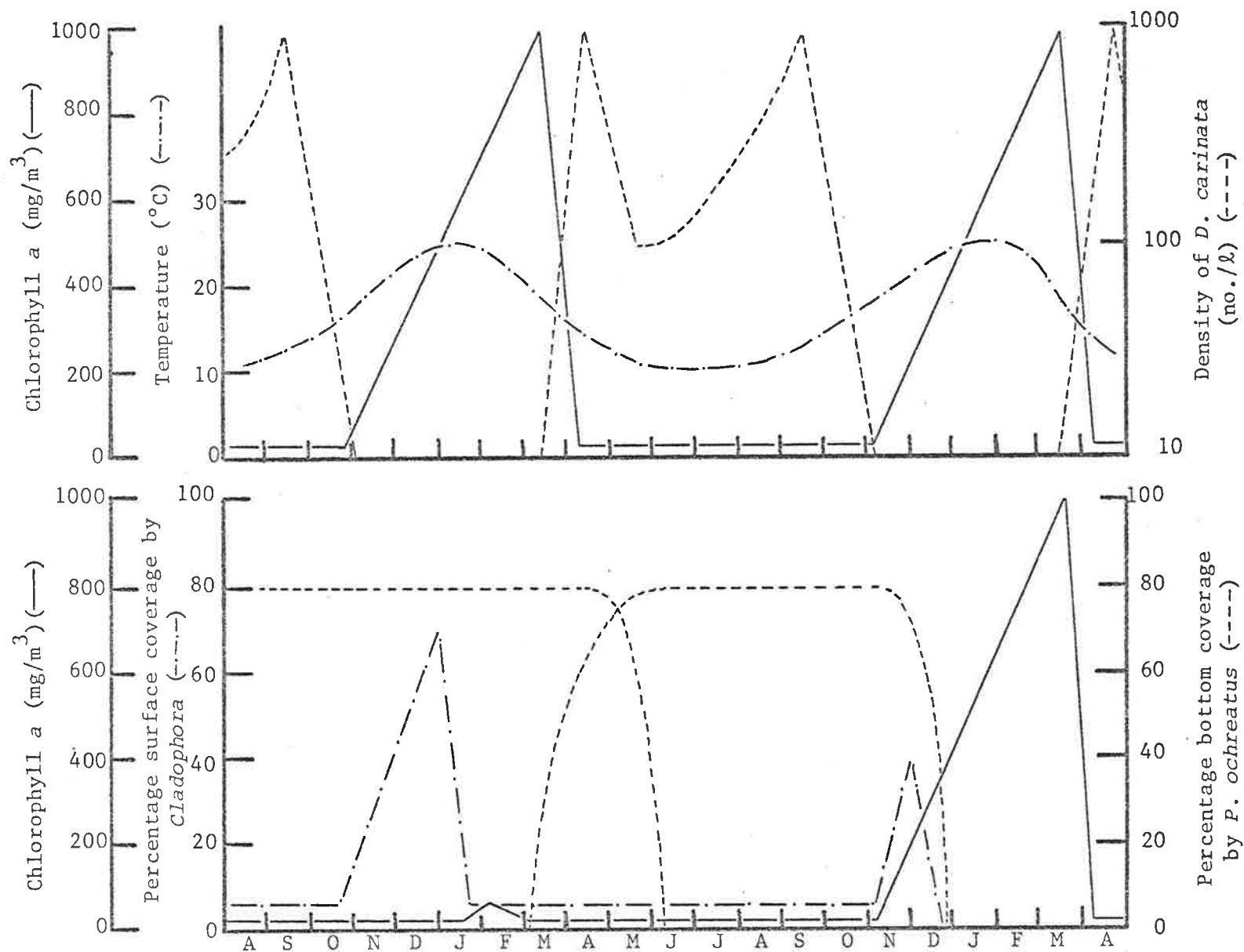


FIGURE 6.1 Model of major ecological interactions in the Gumeracha ponds.

filamentous algae, submerged macrophytes, and zooplankton in the ponds. Management of these populations would be required to maintain optimal standing crops and would probably chiefly involve periodic cropping. This would be essential to prevent food limitation of zooplankton. Some problems could be encountered in attempting to culture filamentous algae and submerged macrophytes simultaneously. It would be essential for algal mats to remain on the pond surface during November and December, even if the filaments were in a senescent phase. The culture of *Cladophora* and *P. ochreatus* has been discussed in Chapter 3, and problems encountered in the management of *D. carinata* discussed in Chapter 4.

Removal of BOD, SS, TOC and organic nitrogen at Gumeracha was highest during periods of dominance of *P. ochreatus* and *D. carinata*; BOD and SS concentrations of the final effluent satisfied present quality criteria only during those periods. Effluent quality deteriorated substantially during phytoplankton blooms. In this regard, the Gumeracha ponds functioned more efficiently at lower water temperatures and in the absence of phytoplankton. Unicellular algae were unnecessary for the stabilization of organic material which appeared to be effected largely by *P. ochreatus*. Management of maturation ponds for the effective stabilization of organic material would involve the encouragement of submerged macrophytes, and zooplankton (to a lesser degree). Such a management strategy would be compatible with, and in fact would be directly dependent upon, the control of unicellular algae.

Partitioning of the total nitrogen ($\text{TKN} + \text{NO}_3^-$) and total $\text{PO}_4\text{-P}$ retained in the Gumeracha ponds during 1977 is shown in Figures 6.2 and 6.3. The relative share (as a percentage) of total nitrogen and phosphorus for any species is equivalent to the nutrient store represented by the total annual net production of that species. In pond 1, when phytoplankton standing crops were low, the greatest share

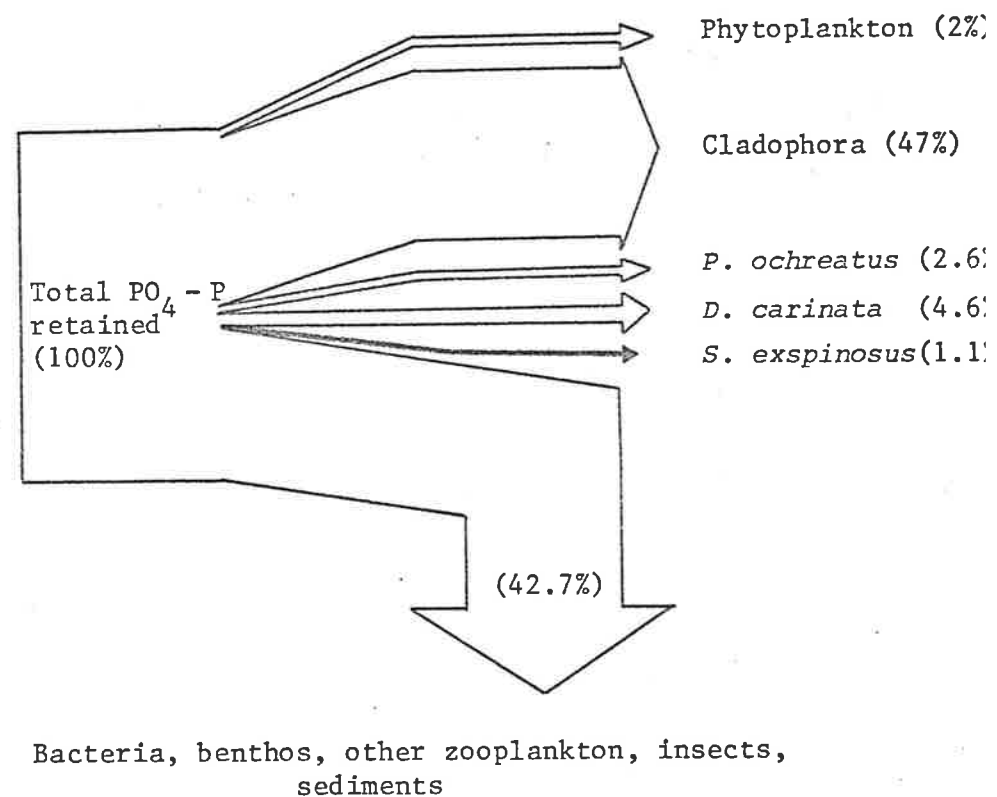
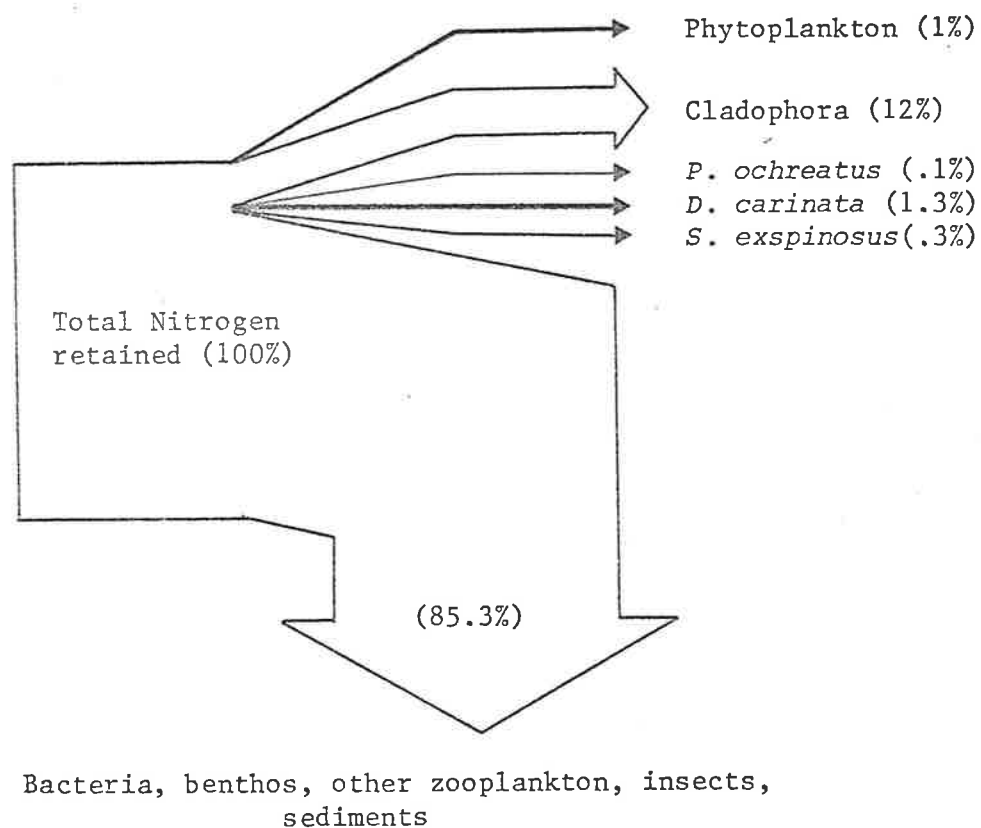


FIGURE 6.2 Nutrient partitioning in pond 1 during 1977.

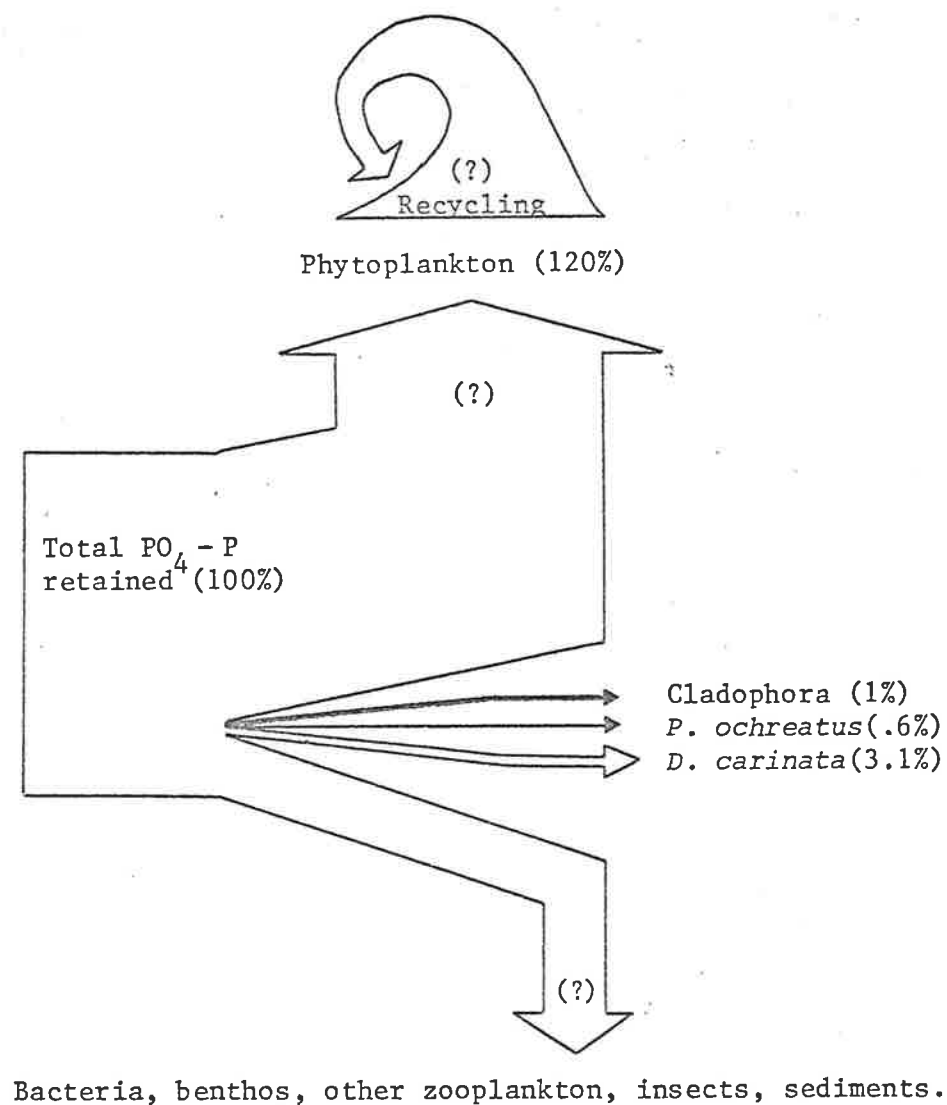
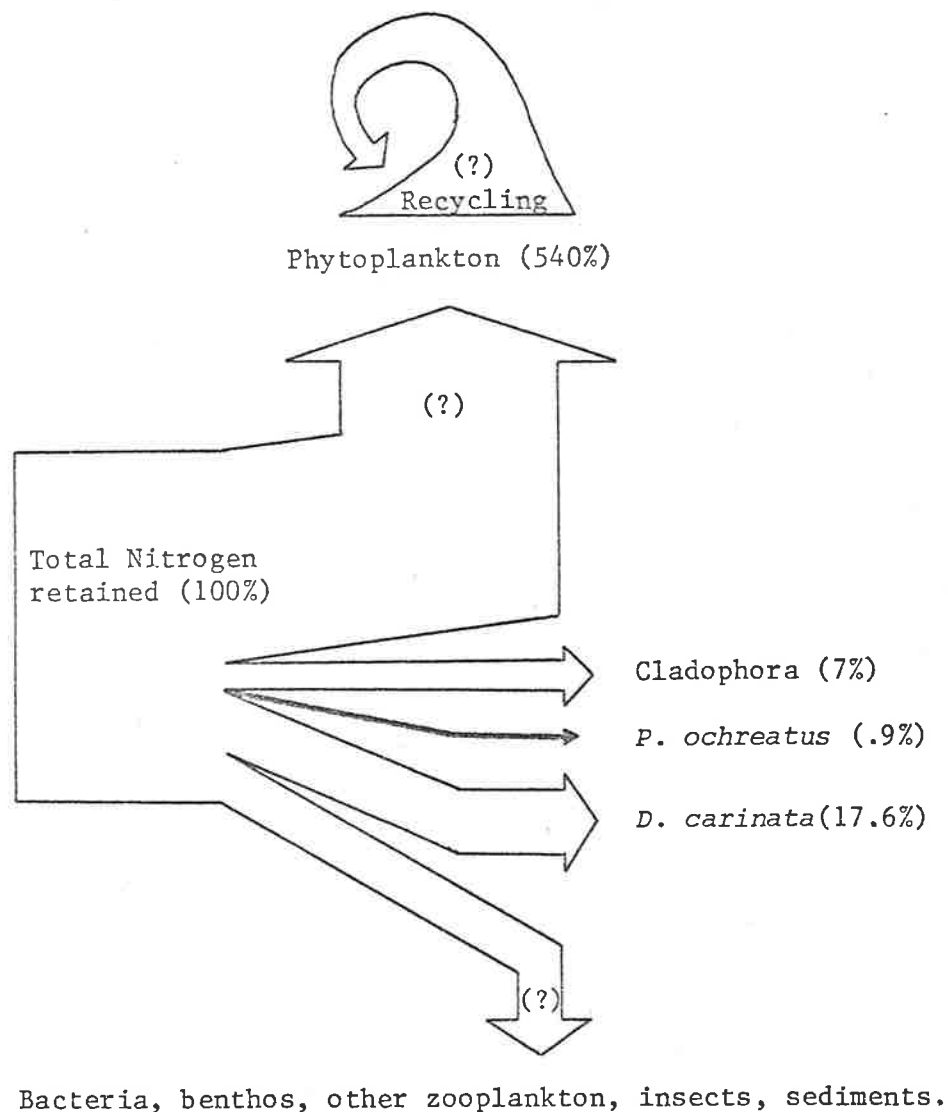


FIGURE 6.3 Nutrient partitioning in pond 2 during 1977.

of nitrogen and phosphorus retained in the pond was channelled into organisms not studied during the present investigation (i.e. bacteria, benthos, insects) and to the sediments. After this, the major nutrient store, particularly for phosphorus, was represented by the production of *Cladophora*. Although the production estimate for *Cladophora* was tentative, it was probably an underestimate. An increase in the production of *Cladophora*, for example by cropping, could have provided a major nutrient store in the Gumeracha ponds and, therefore, a useful pathway for nutrient removal. As filamentous algae is also important for the control of phytoplankton, the culture of species such as *Cladophora* appears to represent a useful tool for WSP management. Despite high annual net production of *D. carinata* and *C. auratus*, harvest of these organisms and *P. ochreatus* appeared to be of little potential value for nutrient removal.

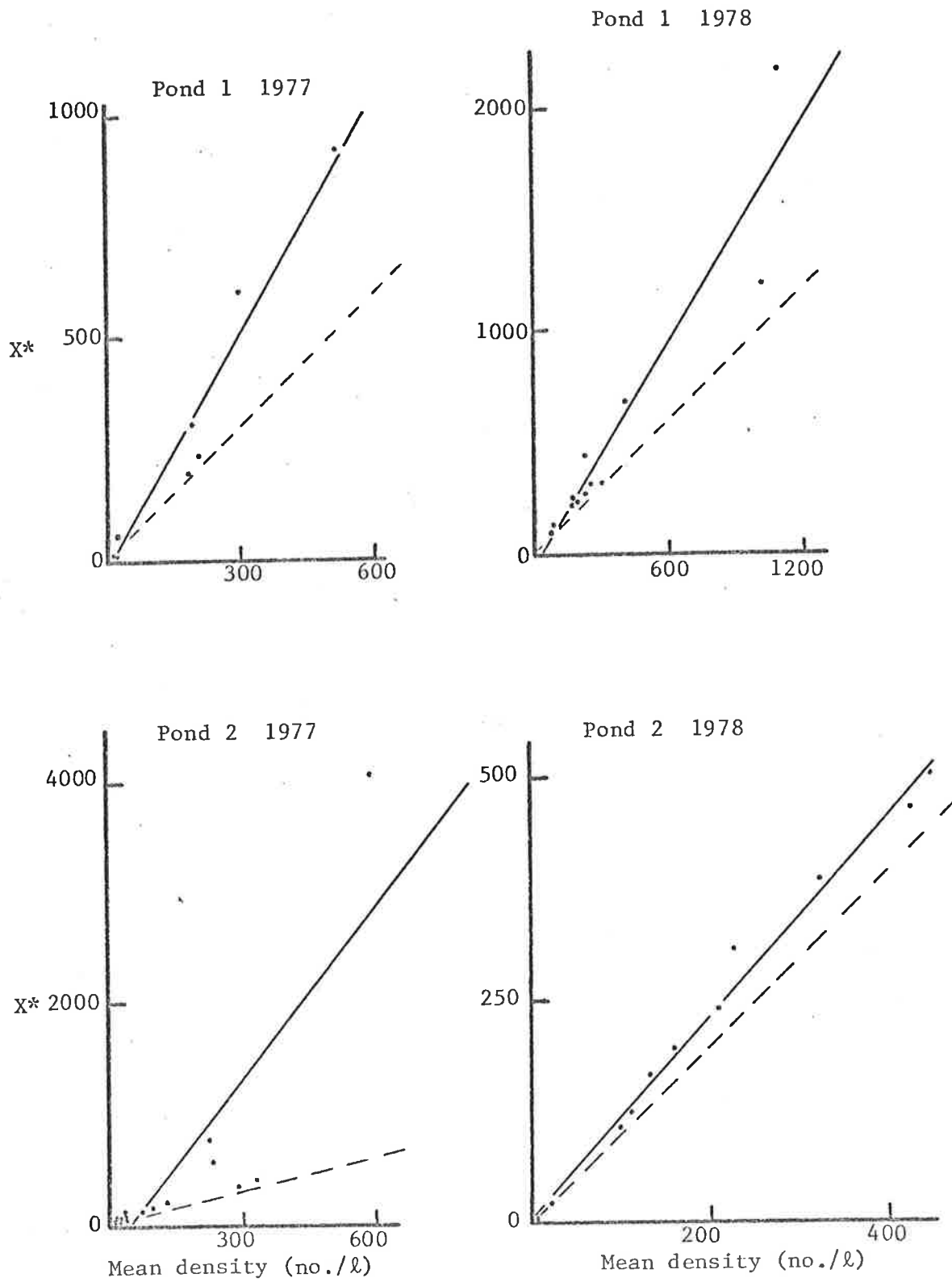
The harvest of *D. carinata*, *P. ochreatus*, and *Cladophora* from pond 2 also appeared to be of little value for nutrient removal. Phytoplankton production estimates were tentative but were of such magnitude as to suggest that a major proportion of the nutrients retained in the pond were incorporated into unicellular algae. This was consistent with the finding of Kimerle and Anderson (1971) that phytoplankton were a dominant energetic component of WSP ecosystems. The proportion of nutrients incorporated into phytoplankton in pond 2 appeared to greatly exceed that incorporated into *Cladophora* in pond 1. The harvest of unicellular algae appeared to be the most effective means of nutrient removal from the Gumeracha ponds. This was reflected in low effluent concentrations of soluble $\text{PO}_4 - \text{P}$ and NO_3^- during phytoplankton blooms. However, nutrient uptake by algal cells does not constitute removal from effluents unless the algae are harvested continuously prior to discharge. If algal harvest is not practiced, the nutrient load of the influent sewage is exported (bound into algal

cells) to the receiving water body.

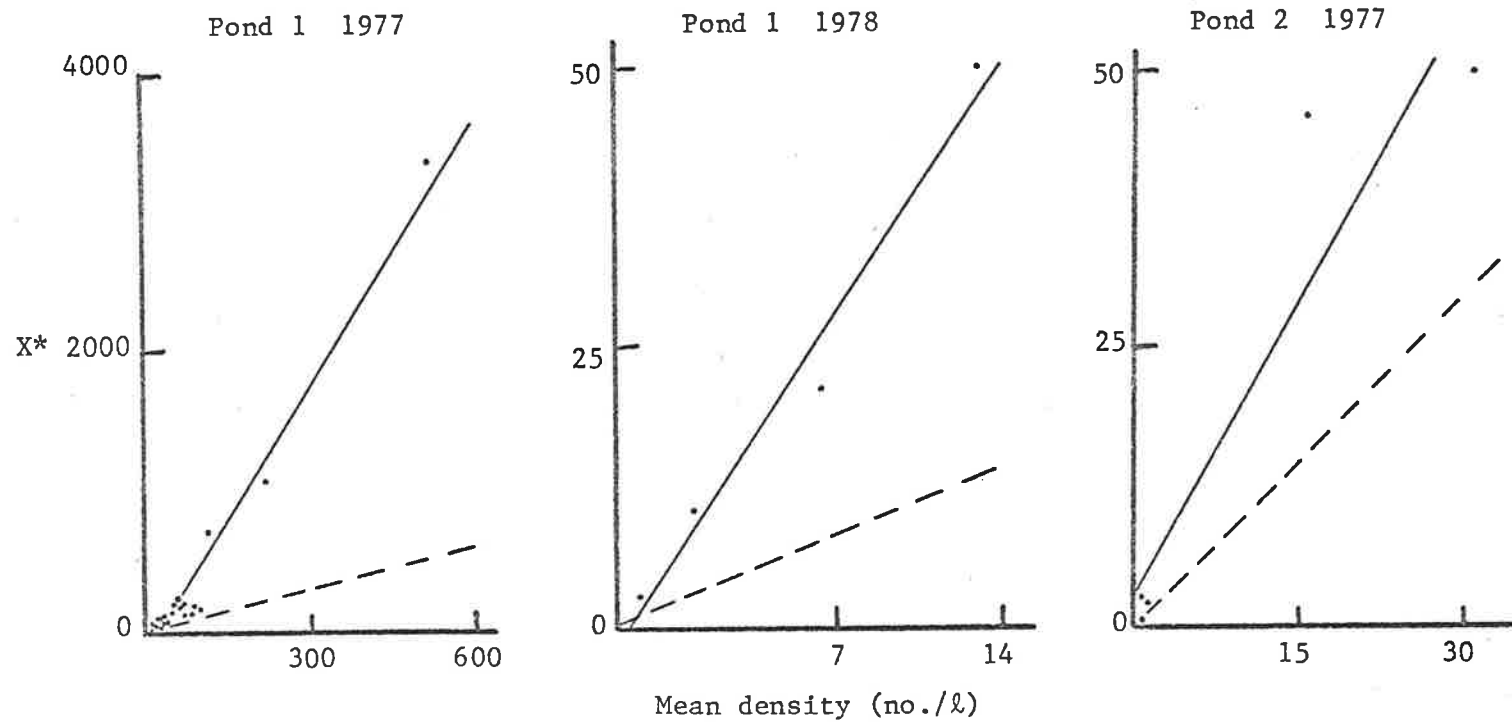
Suitable technology currently exists for the mechanical removal of algae from effluents. However, the financial and energetic investments required for mechanical harvest substantially increase WSP operating costs. Biological alternatives for algal control involve filamentous algae, submerged macrophytes, and zooplankton. However, if algal control, via inhibition or consumption, rather than algal harvest is practiced, the capacity for nutrient removal from the pond system is reduced. Thus, algal control (as opposed to algal harvest) and high nutrient removal appear to be incompatible. The decision to introduce mechanical harvest into a given treatment system must, therefore, be based upon both economic and treatment requirement considerations. If unicellular algal harvest is not desirable, a pond ecosystem based upon filamentous algae, submerged macrophytes, and zooplankton is likely to prove more efficient with respect to overall waste treatment. With careful, effective management and harvest of filamentous algal populations, reasonable nutrient removal could be achieved.

The present study has examined the relative merits of various, naturally occurring groups of organisms for the management of WSPs on biological rather than engineering principles. Those groups offering the most promise as pond management tools have been highlighted. It now remains for the management principles outlined in the present study to be developed and applied by those bodies responsible for the treatment of waste, on an operational day-to-day basis.

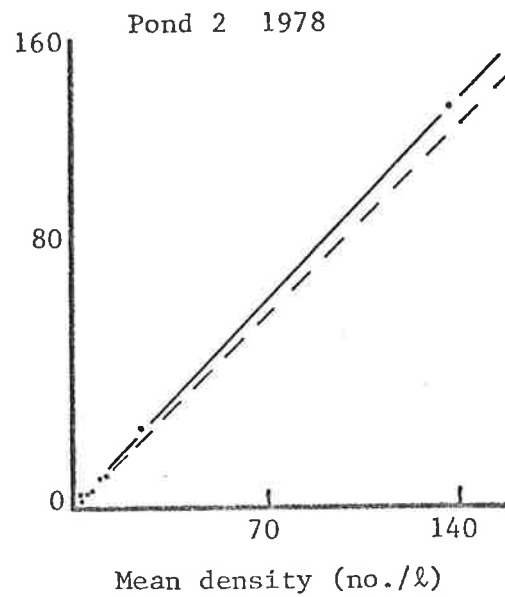
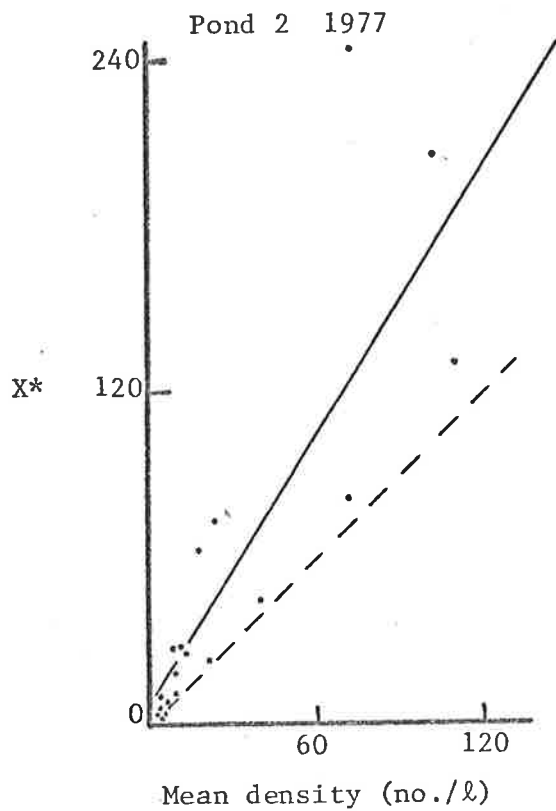
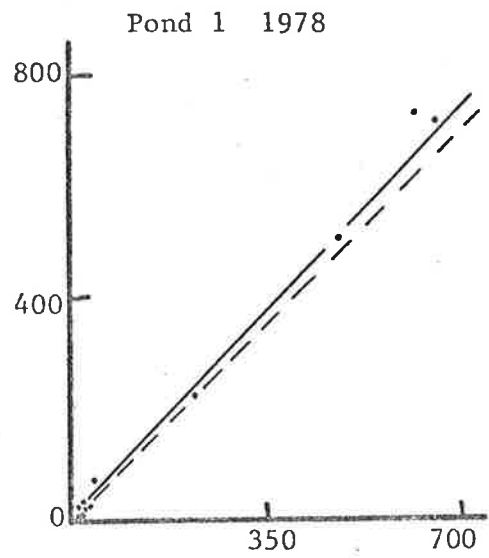
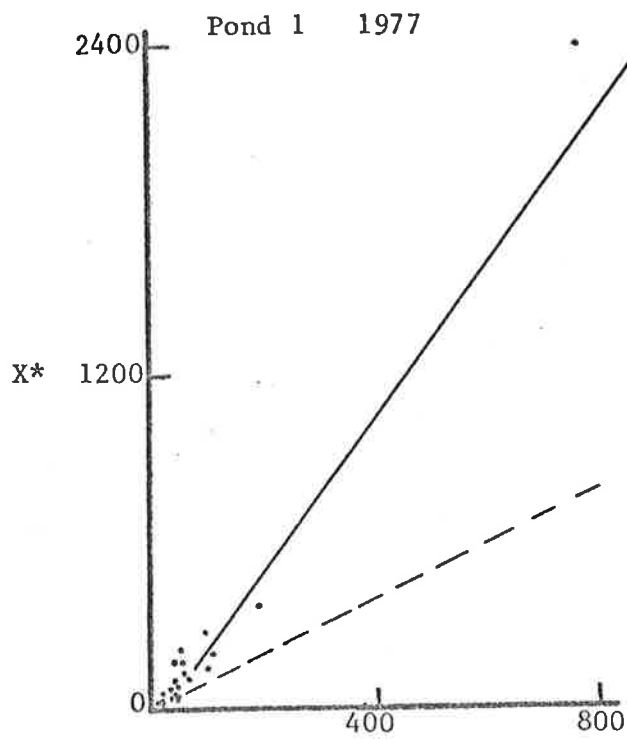
Appendix 1



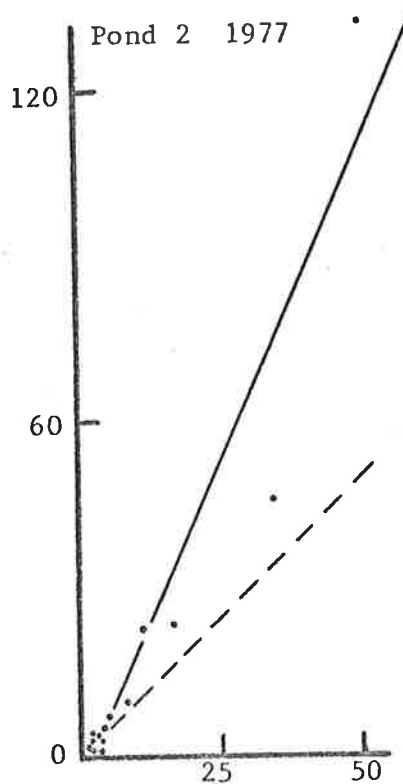
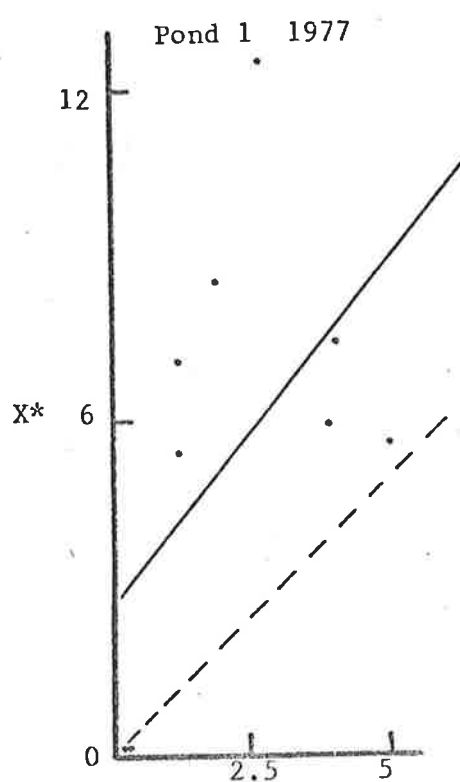
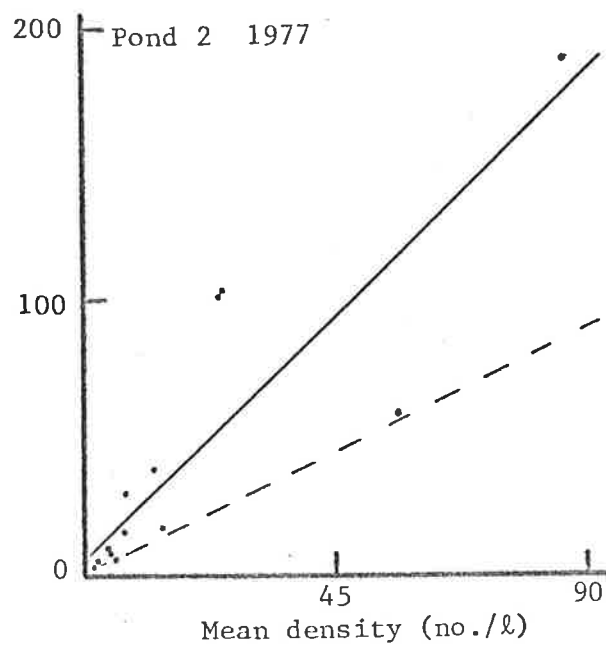
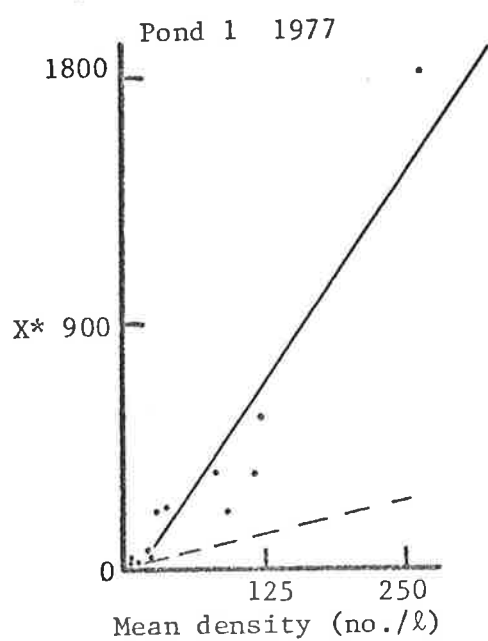
Mean crowding (X^*) versus mean density for *D. carinata* in the Gumeracha ponds (---, random expectation).



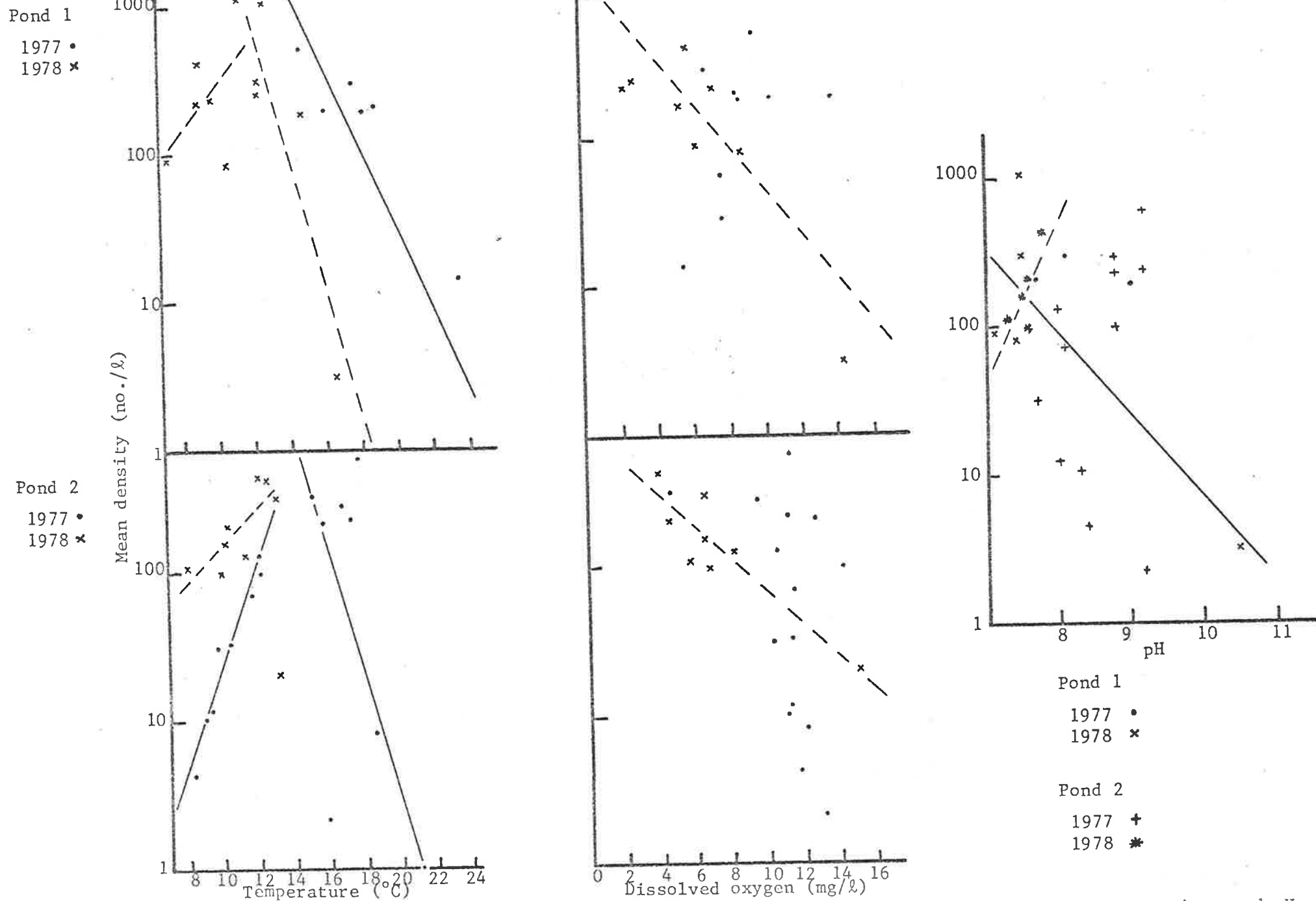
Mean crowding (X^*) versus mean density for *S. exspinosus* in the Gumeracha ponds (---, random expectation).

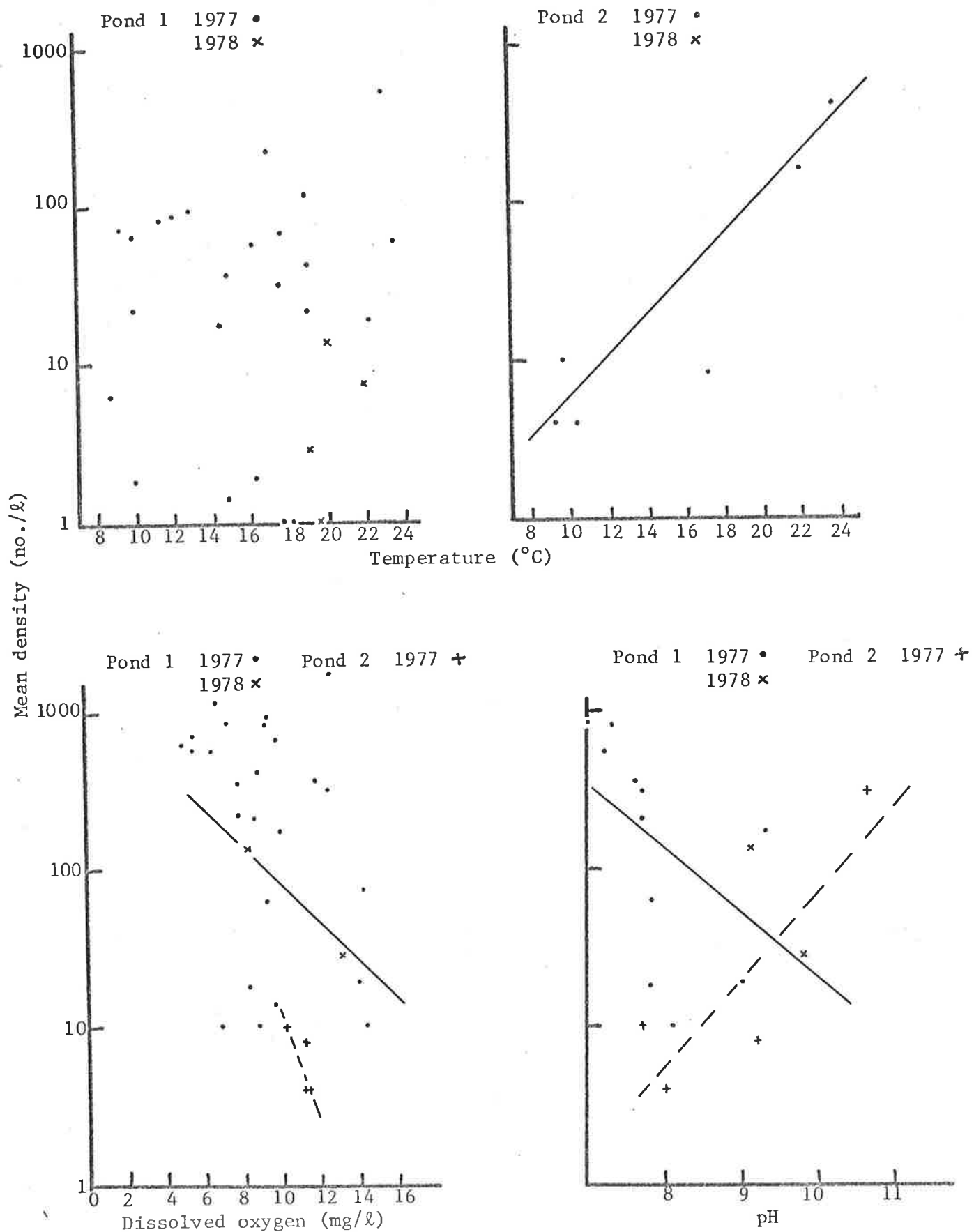


Mean crowding (X^*) versus mean density for *M. leuckarti* in the Gumeracha ponds (---, random expectation).

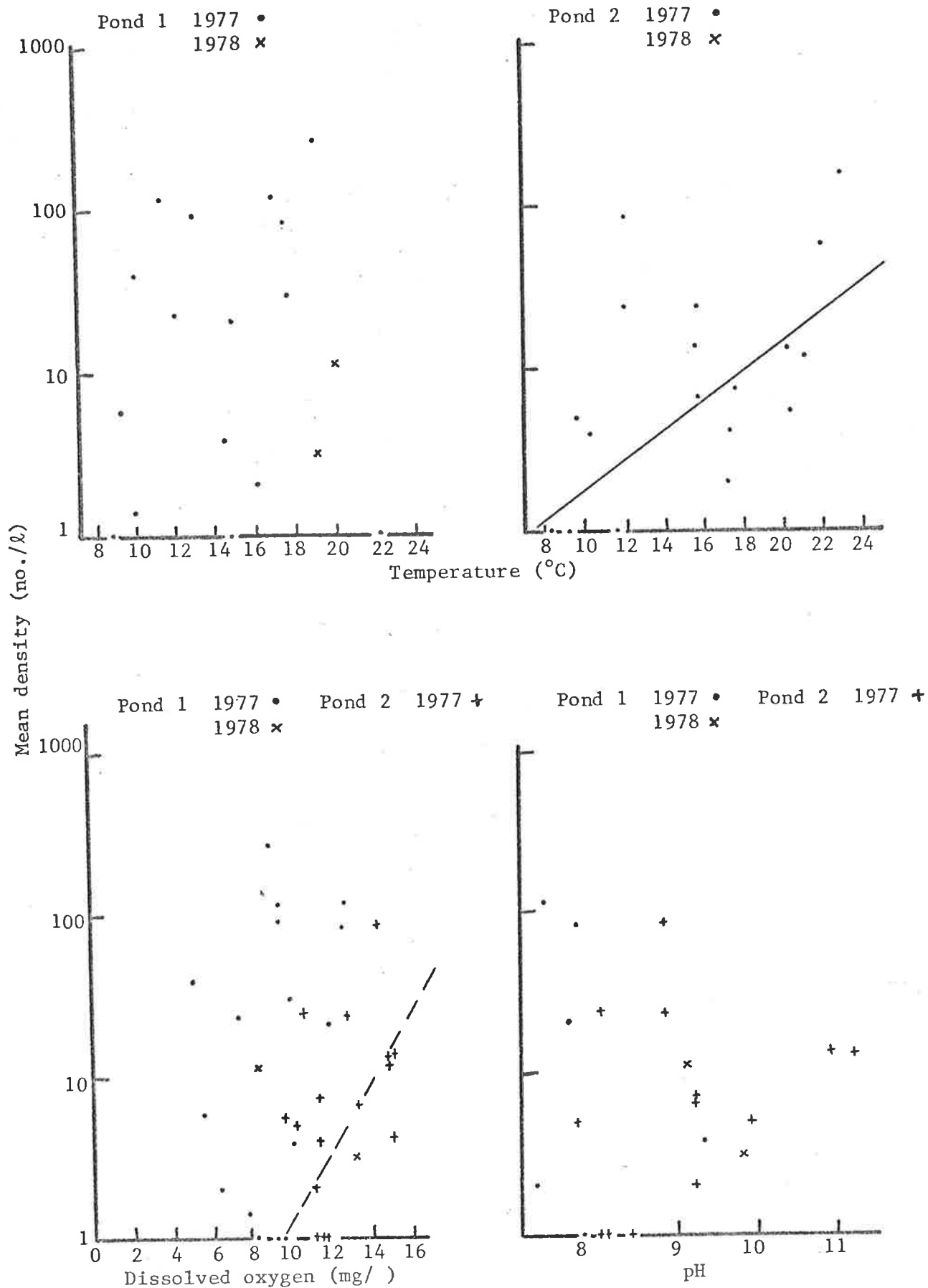
B. triarticulata*M. hirsuticornis*

Mean crowding (X^*) versus mean density for *B. triarticulata* and *M. hirsuticornis* in the Gumeracha ponds (---, random expectation).

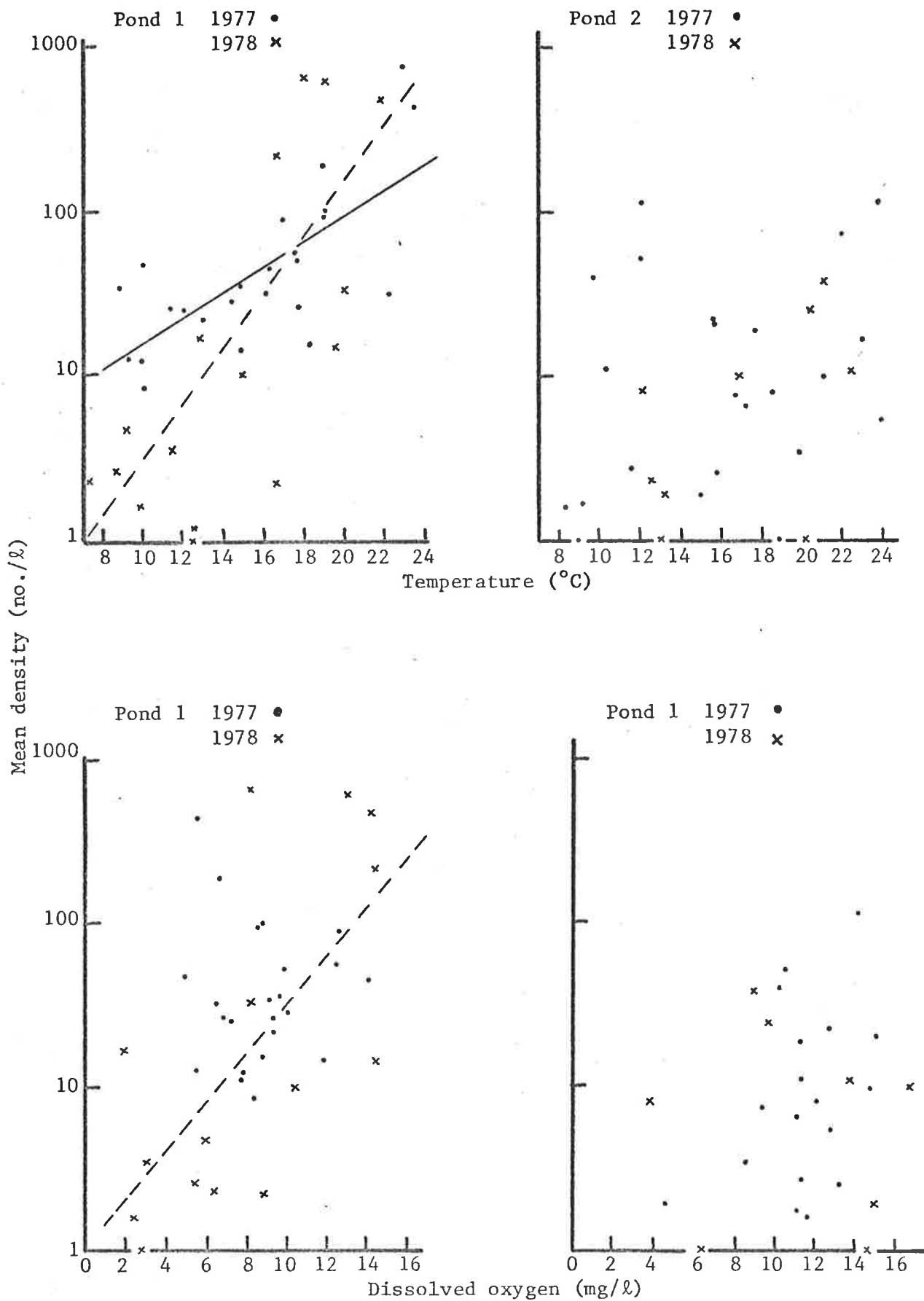




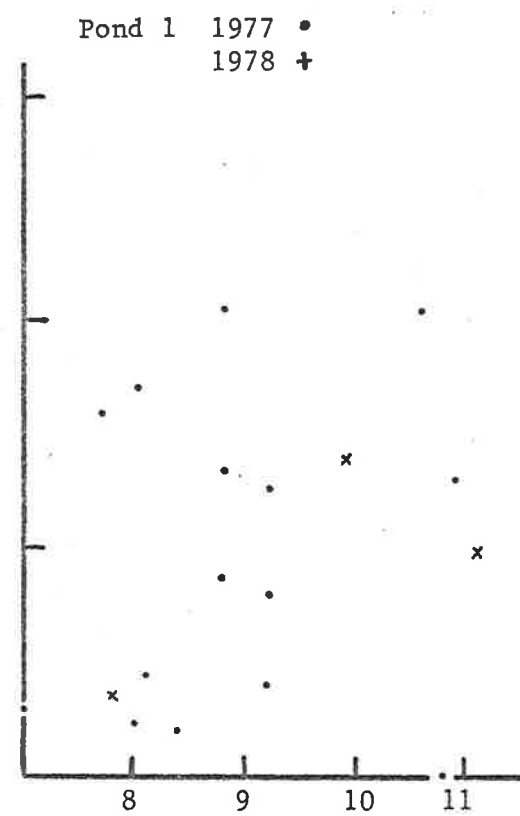
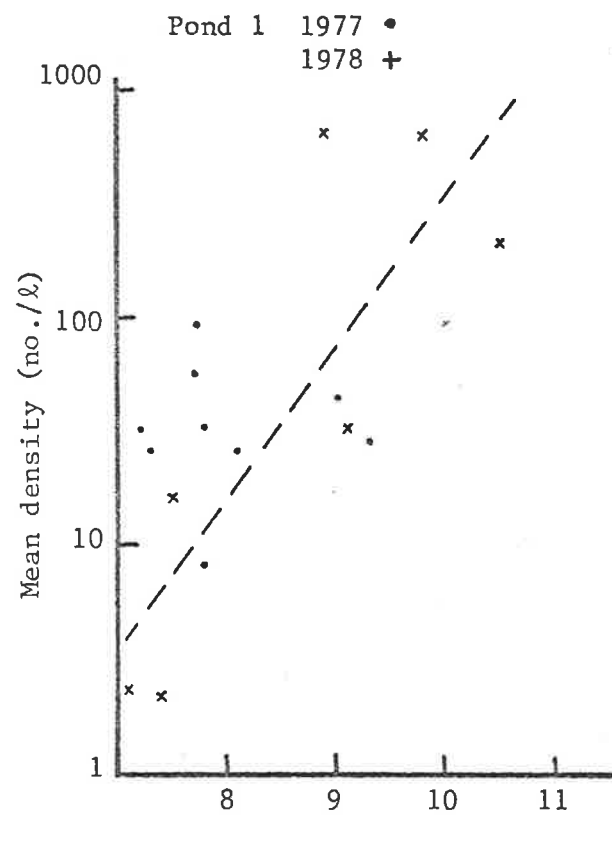
Mean density of *S. exspinosus* versus depth-averaged water temperature and dissolved oxygen concentration, and pH.



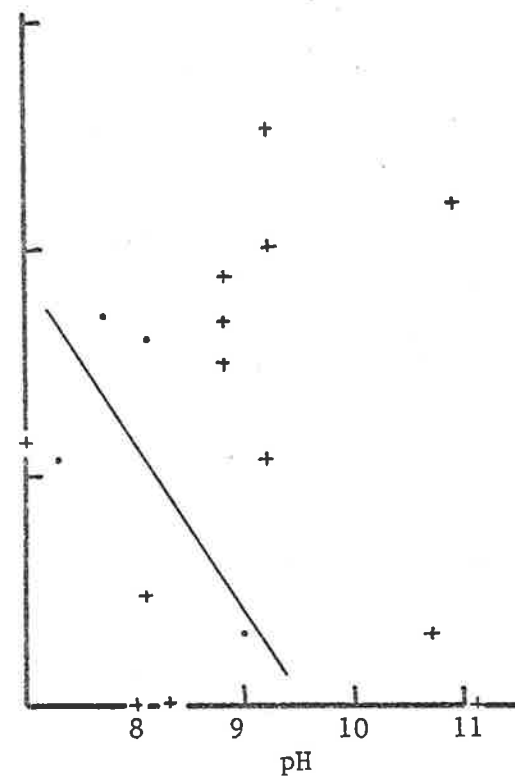
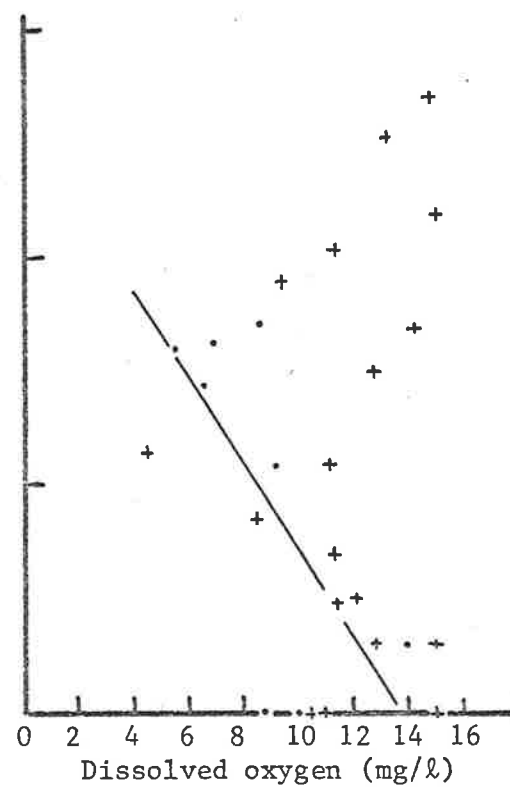
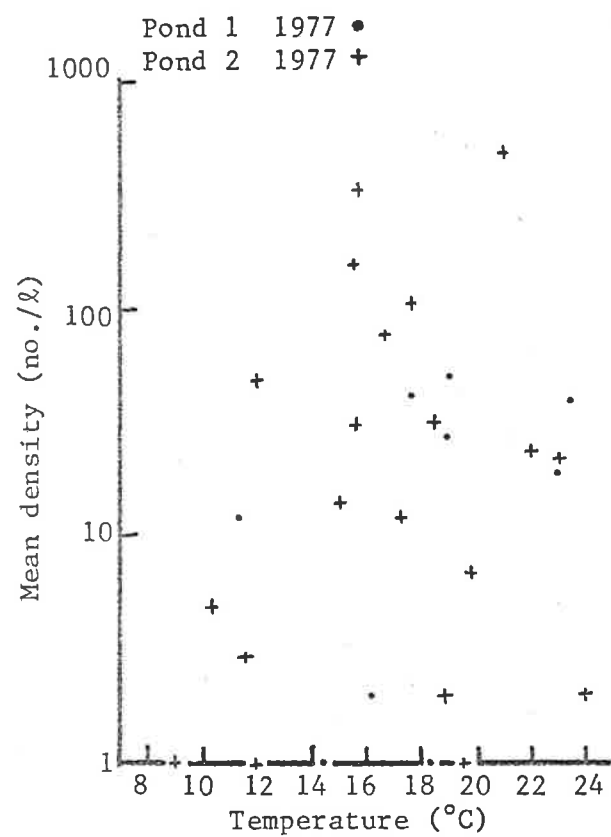
Mean density of *M. hirsuticornis* versus depth-averaged water temperature and dissolved oxygen, and pH.



Mean density of *M. leuckarti* versus depth-averaged water temperature and dissolved oxygen concentration.



Mean density of *M. Leuckarti* versus pH



Mean density of *B. triarticulata* versus depth-averaged water temperature and dissolved oxygen concentration, and pH.

APPENDIX 3

Papers presented in support
of the thesis

Mitchell, B.D., (1980) Waste stabilisation ponds. In W.D. Williams (ed.) *An Ecological Basis for Water Resources Management* (pp. 360-375.
Canberra, Australia: Australian National University Press.

NOTE:

This publication is included in the print copy of the thesis held
in the University of Adelaide Library.

Mitchell, B.D., (1978) Cyclomorphosis in *Daphnia carinata* king (Crustacea : Cladocera) from two adjacent sewage lagoons in South Australia.
Australian Journal of Marine and Freshwater Research, v. 29 (5), pp. 565-576.

NOTE:

This publication is included in the print copy of the thesis held
in the University of Adelaide Library.

It is also available online to authorised users at:

<http://dx.doi.org/10.1071/MF9780565>

Mitchell, B.D., (1979) Aspects of growth and feeding in golden carp, *Carassius auratus*, from South Australia.

Transactions of the Royal Society of South Australia, v. 103 (6), pp. 137-144.

NOTE:

This publication is included in the print copy of the thesis held
in the University of Adelaide Library.

Appendix 4. Production of *Daphnia carinata* (Pond 1) calculated using the population turnover-time model

Date	Depth-averaged temperature (°C)	Mean temperature	(E)	(D)	(No)	B	b'	Time (days)	r'	d'	D	T	Biomass (ug/l)	Mean biomass (mg/l)	Production (mg/l/day)
2. 2.77	18.9		0		0								0		
16. 2.77	23.5	21.2	63.4	2.62	13.7	0.382	0.3235	14	0.1870	0.1365	0.1276	7.84	507	0.254	0.032
2. 3.77	19.0	21.3	190.7	2.61	204.0	1.773	0.7781	14	0.1929	0.5852	0.4430	2.26	3487	1.997	0.884
16. 3.77	17.7	18.4	151.9	3.15	297.2	0.297	0.2601	14	0.0269	0.2332	0.2080	4.81	4961	4.220	0.877
30. 3.77	18.3	18.0	218.4	3.25	185.7	0.157	0.1458	14	-0.0336	0.1794	0.1642	6.09	4603	4.782	0.785
13. 4.77	16.2	17.3	316.0	3.42	191.4	0.344	0.2957	14	-0.0022	0.2979	0.2576	3.88	7669	6.136	1.581
27. 4.77	14.8	15.5	1132.3	3.97	518.2	0.416	0.3478	14	0.0711	0.2767	0.2417	4.14	29529	18.599	4.493
1. 6.77	8.7	11.8	0	5.80	0	0.377	0.3199	34	-0.4465	0.7664	0.5353	1.87	0	14.765	7.896
15. 3.78	21.9		0		0								0		
29. 3.78	16.6	19.3	5.0	2.96	3.1	0.338	0.2912	14	0.0808	0.2104	0.1897	5.27	16	0.008	0.002
13. 4.78	14.9	15.8	175.3	3.88	181.5	0.416	0.3475	15	0.2713	0.0763	0.0735	13.61	4557	2.287	0.168
27. 4.78	12.8	13.9	194.9	4.62	1025.7	0.209	0.1898	14	0.1237	0.0661	0.0640	15.63	15894	10.226	0.654
10. 5.78	12.4	12.6	21.6	5.30	255.0	0.036	0.0354	13	-0.1071	0.1425	0.1328	7.53	5997	10.946	1.454
24. 5.78	12.5	12.5	353.4	5.36	304.0	0.016	0.0157	14	0.0126	0.0031	0.0031	322.58	10674	8.335	0.026
6. 6.78	11.4	12.0	203.7	5.70	1106.9	0.204	0.1856	13	0.0994	0.0862	0.0826	12.11	29106	19.890	1.642
21. 6.78	9.8	10.6	198.8	6.70	231.2	0.027	0.0266	15	-0.1044	0.1310	0.1228	8.14	10595	19.851	2.439
5. 7.78	9.0	9.4	45.0	7.94	225.1	0.108	0.1026	14	-0.0019	0.1045	0.0992	10.08	8982	9.789	0.971
19. 7.78	8.6	8.8	139.9	8.70	172.3	0.023	0.0227	14	-0.0191	0.0418	0.0409	24.44	6638	7.810	0.320
9. 8.78	7.2	7.9	76.8	9.93	90.7	0.082	0.0788	21	-0.0306	0.1094	0.1036	9.65	3982	5.310	0.550
30. 8.78	9.1	8.2	52.5	9.50	416.7	0.089	0.0853	21	0.0726	0.0127	0.0126	79.37	11470	7.726	0.097
13. 9.78	10.6	9.9	24.3	7.37	82.5	0.017	0.0169	14	-0.1157	0.1326	0.1242	8.05	2764	7.117	0.884
11.10.78	16.6	10.6	0	6.70	0	0.044	0.0431	28	-0.1576	0.2007	0.1818	5.50	0	1.382	0.251

Appendix 4. (Cont.) Production of *D. carinata* (Pond 2)

Date	Depth-averaged temperature (°C)	Mean temperature	(E)	(D)	(No)	B	b'	Time (days)	r'	d'	D	T	Biomass (µg/ℓ)	Mean biomass (mg/ℓ)	Production (mg/ℓ/day)
16. 3.77	18.8		0		0								0		
30. 3.77	18.5	18.7	10.0	3.10	8.4	0.323	0.2799	14	0.1520	0.1279	0.1201	8.34	116	0.058	0.007
13. 4.77	16.7	17.6	145.3	3.60	286.0	0.331	0.2857	14	0.2520	0.0337	0.0331	30.18	7375	3.745	0.124
27. 4.77	15.0	15.9	232.8	3.84	332.6	0.132	0.1240	14	0.0108	0.1132	0.1070	9.34	8928	8.152	0.873
1. 6.77	8.9	12.0	1.2	5.70	10.5	0.123	0.1160	34	-0.1016	0.2176	0.1956	5.11	184	4.556	0.892
15. 6.77	8.3	8.6	3.0	8.94	4.4	0.013	0.0129	14	-0.0621	0.0750	0.0723	13.83	379	0.282	0.020
29. 6.77	9.2	8.8	8.6	8.70	12.0	0.078	0.0757	14	0.0717	0.0040	0.0040	250.00	167	0.273	0.001
12. 7.77	10.3	9.8	37.1	7.48	33.8	0.096	0.0915	13	0.0797	0.0118	0.0117	85.25	930	0.548	0.006
27. 7.77	9.6	10.0	25.2	7.28	31.8	0.151	0.1406	15	-0.0041	0.1365	0.1276	7.84	429	0.679	0.087
10. 8.77	11.5	10.6	138.7	6.70	71.8	0.121	0.1141	14	0.0582	0.0559	0.0544	18.38	3598	2.013	0.110
24. 8.77	12.0	11.8	56.6	5.80	129.5	0.333	0.2874	14	0.0421	0.2453	0.2175	4.60	3465	3.532	0.729
7. 9.77	12.0	12.0	56.0	5.70	100.0	0.077	0.0742	14	-0.0185	0.0927	0.0885	11.30	5276	4.371	0.387
21. 9.77	15.6	13.8	291.6	4.66	222.2	0.120	0.1133	14	0.0570	0.0563	0.0547	18.30	10055	7.666	0.419
5.10.77	17.2	16.4	114.2	3.67	232.2	0.358	0.3060	14	0.0031	0.3029	0.2613	3.83	7680	8.867	2.315
26.10.77	17.6	17.4	141.6	3.40	590.2	0.145	0.1354	21	0.0444	0.0910	0.0870	11.50	10986	9.333	0.812
8.11.77	15.8	16.7	9.0	3.58	2.2	0.067	0.0649	13	-0.4302	0.4951	0.3905	2.56	237	5.612	2.192
23.11.77	21.1	18.5	0	3.14	0.2	1.303	0.8342	15	-0.1599	0.9941	0.6299	1.59	1	0.119	0.075
13. 4.78	15.2		0		0								0		
27. 4.78	13.1	14.2	50.3	4.49	20.8	0.223	0.2013	14	0.2168	-0.0155			462	0.231	
10. 5.78	13.0	13.1	126.7	5.05	322.4	0.236	0.2119	13	0.2108	0.0011	0.0011	909.09	7402	3.932	0.004
24. 5.78	12.5	12.8	196.0	5.20	424.2	0.076	0.0733	14	0.0196	0.0537	0.0523	19.12	9167	8.285	0.433
6. 6.78	12.0	12.3	164.3	5.50	446.6	0.084	0.0807	13	0.0040	0.0767	0.0738	13.54	21106	15.137	1.118
21. 6.78	10.3	11.2	53.5	6.23	207.2	0.059	0.0573	15	-0.0512	0.1085	0.1028	9.73	11576	16.341	1.679
19. 7.78	9.9	9.7	17.0	7.60	97.8	0.034	0.0334	28	-0.0268	0.0602	0.0584	17.12	8065	9.821	0.574
9. 8.78	7.9	8.9	110.2	8.57	110.1	0.020	0.0198	21	0.0056	0.0142	0.0141	70.92	2243	5.154	0.073
30. 8.78	10.1	9.0	33.3	8.45	158.4	0.119	0.1124	21	0.0173	0.0951	0.0907	11.02	5955	4.099	0.372
13. 9.78	11.2	10.7	16.4	6.60	130.5	0.032	0.0315	14	-0.0138	0.0453	0.0443	22.57	3455	4.705	0.209
11.10.78	18.8	15.0	0	4.16	0	0.030	0.0296	28	-0.1664	0.1960	0.1780	5.62	0	1.728	0.308

Appendix 5. Production of *D. carinata* (Pond 1) calculated using the biomass turnover model

Size Class	Initial weight (g)	Final weight (g)	Weight change	16.2.77 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	2.3.77			16.3.77		
Eggs	0.0000	0.0050	0.0050	63.4	2.30	0.1378	190.7	3.05	0.3126	151.9	3.30	0.2302
1	0.0050	0.0088	0.0038	7.7	2.70	0.0108	166.3	3.94	0.1604	168.8	4.33	0.1481
2	0.0088	0.0222	0.0134	2.2	3.61	0.0082	12.2	5.25	0.0311	80.8	5.78	0.1873
3	0.0222	0.0442	0.0220	1.1	4.05	0.0060	13.1	5.91	0.0488	26.5	6.50	0.0897
4	0.0442	0.0768	0.0326	0.6	4.05	0.0048	6.7	5.91	0.0370	12.5	6.50	0.0627
5	0.0768	0.1215	0.0447	1.0	7.21	0.0062	5.5	10.51	0.0234	4.2	11.57	0.0162
6	0.1215	0.1800	0.0585	0.8	9.91	0.0047	2.2	14.44	0.0089	1.5	15.90	0.0055
7	0.1800	0.2539	0.0739	0.2	12.62	0.0012	1.0	18.34	0.0040	2.7	20.24	0.0099
8	0.2539	0.3446	0.0907	0.1	20.28	0.0004	1.0	29.55	0.0031	-	-	-

30.3.77			13.4.77			27.4.77			29.3.78		
218.4	3.18	0.3434	316.0	3.75	0.4213	1132.3	4.23	1.3384	5.0	3.60	0.0069
118.9	4.33	0.1043	87.7	5.16	0.0646	62.2	5.67	0.0417	3.1	4.95	0.0024
17.8	5.78	0.0413	27.9	6.89	0.0543	81.9	7.57	0.1450	-	-	-
16.3	6.50	0.0552	12.1	7.75	0.0599	132.1	8.51	0.3415	-	-	-
22.3	6.50	0.1118	31.0	7.75	0.1304	147.7	8.51	0.5658	-	-	-
7.4	11.57	0.0286	27.9	13.79	0.0904	65.8	15.14	0.1943	-	-	-
-	-	-	3.8	18.95	0.0117	25.4	20.80	0.0714	-	-	-
3.0	20.24	0.0110	1.0	24.12	0.0031	3.1	26.49	0.0085	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. (Cont.)

13.4.78 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	27.4.78			10.5.76			24.5.78		
175.3	4.20	0.2087	194.9	5.20	0.1874	21.6	5.43	0.0199	353.4	5.37	0.3291
112.5	5.67	0.0754	649.3	6.98	0.3535	97.4	7.40	0.0500	139.8	7.40	0.0718
19.8	7.57	0.0350	160.0	9.35	0.2293	83.1	9.88	0.1127	28.0	9.88	0.0380
15.8	8.51	0.0408	141.6	10.52	0.2961	34.4	11.11	0.0681	48.6	11.11	0.0962
27.6	8.51	0.1057	56.4	10.52	0.1748	28.6	11.11	0.0839	55.9	11.11	0.1640
2.0	15.14	0.0059	18.5	18.70	0.0442	11.5	19.76	0.0260	28.0	19.76	0.0633
2.0	20.80	0.0056	-	-	-	-	-	-	3.7	27.16	0.0080
-	-	-	-	-	-	-	-	-	-	-	-
1.8	42.56	0.0038	-	-	-	-	-	-	-	-	-

6.6.78			21.6.78			5.7.78			19.7.78		
203.7	6.10	0.1670	198.8	7.47	0.1331	45.0	8.45	0.0266	139.9	8.95	0.0782
557.9	8.23	0.2576	102.2	9.64	0.0403	68.0	11.01	0.0235	30.5	11.81	0.0098
229.1	10.99	0.2799	29.1	12.87	0.0303	84.0	14.70	0.0766	56.3	15.76	0.0479
119.6	12.36	0.2129	12.5	14.47	0.0190	19.6	16.53	0.0261	40.5	17.72	0.0503
81.9	12.36	0.2160	33.3	14.47	0.0750	10.8	16.53	0.0213	20.3	17.72	0.0373
118.4	21.98	0.2408	45.8	25.74	0.0795	23.2	29.40	0.0353	21.7	31.53	0.0308
-	-	-	8.3	35.38	0.0137	19.6	40.41	0.0284	2.9	43.33	0.0039
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. (Cont.)

9.8.78 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	30.8.78			13.9.78		
76.8	11.0	0.0349	52.5	8.30	0.0316	24.3	6.70	0.0181
26.3	14.37	0.0070	201.7	11.01	0.0696	15.7	9.17	0.0065
19.9	19.18	0.0139	68.3	14.70	0.0623	28.6	12.24	0.0313
12.7	21.57	0.0130	75.0	16.53	0.0998	17.7	13.77	0.0283
16.7	21.57	0.0252	40.8	16.53	0.0805	15.0	13.77	0.0355
12.0	38.37	0.0140	20.4	29.40	0.0310	4.8	24.49	0.0088
3.2	52.74	0.0035	10.4	40.41	0.0151	0.7	33.66	0.0012
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

Production of *D. carinata* (Pond 2)

30.3.77			13.4.77			27.4.77			1.6.77		
-	-	-	145.3	3.57	0.2035	232.8	4.15	0.2805	1.2	8.60	0.0007
4.4	5.99	0.0028	205.9	4.73	0.1654	180.3	5.67	0.1208	6.6	11.01	0.0023
3.3	8.00	0.0055	27.5	6.30	0.0584	63.2	7.57	0.1119	1.7	14.70	0.0015
-	-	-	11.7	7.10	0.0363	30.6	8.51	0.0791	0.7	16.53	0.0009
0.7	9.00	0.0025	12.9	7.10	0.0592	25.9	8.51	0.0992	0.8	16.53	0.0016
-	-	-	10.9	12.63	0.0386	25.9	15.13	0.0765	0.3	29.40	0.0005
-	-	-	13.7	17.36	0.0462	4.3	20.80	0.0121	0.1	40.41	0.0001
-	-	-	1.4	22.10	0.0047	2.3	26.64	0.0064	-	-	-
-	-	-	2.0	35.50	0.0051	-	-	-	-	-	-

Appendix 5. (Cont.)

15.6.77 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	29.6.77			12.7.77			27.7.77		
3.0	9.40	0.0016	8.6	8.20	0.0052	37.1	6.95	0.0267	25.2	7.70	0.0164
-	-	-	10.2	11.01	0.0035	9.2	8.28	0.0042	22.6	10.32	0.0083
-	-	-	0.5	14.70	0.0005	17.2	12.87	0.0179	3.5	13.79	0.0034
1.5	18.86	0.0017	0.4	16.53	0.0005	2.8	14.47	0.0043	3.8	15.50	0.0054
1.5	18.86	0.0026	0.3	16.53	0.0006	1.1	14.47	0.0025	1.6	15.50	0.0034
0.7	33.55	0.0009	0.7	29.40	0.0011	2.1	27.74	0.0036	0.3	27.57	0.0005
0.7	46.11	0.0009	-	-	-	1.1	35.38	0.0018	-	-	-
-	-	-	-	-	-	0.3	45.04	0.0005	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

10.8.77			24.8.77			7.9.77			21.9.77		
138.7	6.00	0.1156	56.6	5.70	0.0496	56.0	5.70	0.0491	291.6	3.94	0.3701
19.2	8.23	0.0089	78.2	7.80	0.0381	19.0	7.80	0.0093	54.4	5.42	0.0381
18.5	10.99	0.0226	10.8	10.41	0.0139	21.0	10.41	0.0270	13.1	7.23	0.0243
5.0	12.36	0.0089	18.9	11.71	0.0355	21.9	11.71	0.0413	50.0	8.13	0.1353
12.1	12.36	0.0319	8.2	11.71	0.0228	13.0	11.71	0.0362	100.2	8.13	0.4018
14.2	21.98	0.0289	10.8	20.82	0.0232	16.0	20.82	0.0344	4.4	14.46	0.0136
2.2	30.21	0.0043	2.7	28.62	0.0055	8.0	28.62	0.0164	-	-	-
0.7	38.46	0.0013	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. (Cont.)

5.10.77 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	26.10.77			8.11.77			27.4.78		
114.2	3.43	0.1665	141.6	3.35	0.2113	9.0	3.87	0.116	50.3	5.05	0.0498
50.0	4.73	0.0402	190.6	4.55	0.1592	-	-	-	11.2	7.00	0.0061
64.0	6.31	0.1359	280.4	6.07	0.6190	-	-	-	3.7	9.35	0.0053
74.0	7.10	0.2293	59.6	6.83	0.1920	0.9	7.75	0.0026	3.0	10.51	0.0063
25.0	7.10	0.1148	47.8	6.83	0.2282	0.9	7.75	0.0038	1.9	10.51	0.0059
6.0	12.63	0.0212	11.8	12.15	0.0434	0.3	13.79	0.0010	1.1	18.70	0.0026
7.0	17.36	0.0236	-	-	-	-	-	-	-	-	-
2.0	22.10	0.0067	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

10.5.78			24.5.78			6.6.78			21.6.78		
126.7	5.08	0.1247	196.0	5.25	0.1867	164.3	5.70	0.1441	53.5	6.95	0.0385
231.5	7.00	0.1257	336.4	7.40	0.1727	179.5	7.80	0.0874	62.2	9.64	0.0245
22.9	9.35	0.0328	23.8	9.88	0.0323	40.2	10.41	0.0517	20.7	12.87	0.0216
19.0	10.51	0.0398	19.5	11.11	0.0386	51.4	11.71	0.0966	24.9	14.47	0.0379
26.4	10.51	0.0818	7.6	11.11	0.0223	84.4	11.71	0.2350	45.6	14.47	0.1027
15.2	18.70	0.0363	19.5	19.76	0.0441	73.2	20.82	0.1572	45.6	25.74	0.0792
3.6	25.71	0.0082	15.3	27.16	0.0330	17.9	28.62	0.0366	8.3	35.38	0.0137
3.9	32.73	0.0088	3.8	34.58	0.0081	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. (Cont.)

19.7.78 Density (No./ℓ)	Duration (days)	Production (mg/ℓ/day)	9.8.78			30.8.78			13.9.78		
17.0	7.37	0.0115	110.2	9.95	0.0554	33.3	7.15	0.0233	16.4	6.23	0.0132
25.9	9.64	0.0102	65.0	12.56	0.0197	46.4	9.64	0.0183	54.3	8.66	0.0238
34.5	12.87	0.0359	17.8	16.77	0.0142	33.8	12.87	0.0352	36.4	11.57	0.0422
18.7	14.47	0.0284	12.2	18.86	0.0142	32.8	14.47	0.0499	16.1	13.01	0.0272
7.2	14.47	0.0162	10.4	18.86	0.0180	25.2	14.47	0.0568	13.6	13.01	0.0341
8.6	25.74	0.0149	4.7	33.55	0.0063	19.3	25.74	0.0335	9.3	23.14	0.0180
2.8	35.38	0.0046	-	-	-	1.0	35.38	0.0017	1.0	31.80	0.0018
-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Production of *Simocephalus exspinosus* (Pond 1) calculated using the population turnover-time model

Date	Depth-averaged temperature (°C)	Mean temperature	(E)	(D)	(No)	B	b'	Time (days)	r'	d'	D	T	Biomass (µg/ℓ)	Mean biomass (mg/ℓ)	Production (mg/ℓ/day)
5. 1.77	22.2		17.2		18.7								393		
19. 1.77	23.0	22.6	151.6	3.08	520.9	0.2983	0.2611	14	0.2376	0.0235	0.0232	43.10	7349	3.871	0.090
2. 2.77	18.9	21.0	133.8	3.51	113.5	0.0829	0.0796	14	-0.1088	0.1884	0.1717	5.82	1788	4.569	0.785
16. 2.77	23.5	21.2	10.9	3.61	57.7	0.3266	0.2826	14	-0.0483	0.3309	0.2817	3.55	675	1.232	0.347
2. 3.77	19.0	21.3	6.0	3.61	21.0	0.0523	0.0510	14	-0.0722	0.1232	0.1159	8.63	141	0.408	0.047
16. 3.77	17.7	18.4	1.8	4.41	0.9	0.0648	0.0628	14	-0.2250	0.2878	0.2501	4.00	21	0.081	0.020
30. 3.77	18.3	18.0	0.8	4.63	0.4	0.4320	0.3590	14	-0.0730	0.4320	0.3508	2.85	5	0.013	0.005
13. 4.77	16.2	17.3	1.1	5.00	1.9	0.4000	0.3365	14	0.1113	0.2252	0.2016	4.96	32	0.019	0.004
27. 4.77	14.8	15.5	3.6	5.82	1.4	0.0995	0.0948	14	-0.0218	0.1166	0.1101	9.08	32	0.032	0.004
1. 6.77	8.7	11.8	20.6	8.46	6.2	0.3040	0.2654	34	0.0438	0.2216	0.1988	5.03	149	0.090	0.018
15. 6.77	10.0	9.4	6.9	11.25	1.8	0.2953	0.2588	14	-0.0883	0.3471	0.2933	3.41	41	0.095	0.028
29. 6.77	9.1	9.6	25.9	11.15	21.8	0.3438	0.2955	14	0.1782	0.1173	0.1107	9.03	932	0.487	0.054
12. 7.77	9.9	9.5	71.6	11.15	62.7	0.1066	0.1013	13	0.0813	0.0200	0.0198	50.50	1209	1.070	0.021
27. 7.77	9.2	9.6	173.0	11.15	71.4	0.1024	0.0975	15	0.0087	0.0888	0.0850	11.76	2265	1.737	0.148
10. 8.77	12.0	10.6	114.8	9.95	87.2	0.2435	0.2179	14	0.0143	0.2036	0.1842	5.43	3507	2.886	0.532
24. 8.77	12.9	12.5	83.2	8.02	93.2	0.2623	0.2329	14	0.0048	0.2281	0.2040	4.90	2296	2.902	0.592
7. 9.77	11.3	12.1	84.3	8.45	82.1	0.1056	0.1004	14	-0.0090	0.1094	0.1036	9.65	2646	2.471	0.256
21. 9.77	14.8	13.1	22.4	7.58	36.2	0.1355	0.1270	14	-0.0585	0.1855	0.1693	5.91	576	1.611	0.273
5. 10.77	16.1	15.5	144.5	5.82	56.2	0.1063	0.1010	14	0.0314	0.0696	0.0672	14.88	2756	1.666	0.112
26. 10.77	17.6	16.9	58.7	5.07	66.8	0.5071	0.4102	21	0.0082	0.4020	0.3310	3.02	875	1.816	0.601
8. 11.77	17.5	17.6	52.4	4.85	30.9	0.1812	0.1665	13	-0.0593	0.2258	0.2021	4.95	446	0.661	0.134
23. 11.77	19.0	18.3	34.5	4.52	41.4	0.3752	0.3186	15	0.0195	0.2991	0.2585	3.87	530	0.488	0.126
7. 12.77	14.4	16.7	24.6	5.21	17.4	0.1599	0.1484	14	-0.0619	0.2103	0.1897	5.27	186	0.358	0.068
22. 12.77	16.9	15.7	72.4	5.82	216.2	0.2430	0.2175	15	0.1800	0.0375	0.0368	27.17	1518	0.852	0.031
4. 1.78	20.0	18.5	1.8	4.41	13.4	0.0759	0.0732	13	-0.2139	0.2871	0.2496	4.01	134	0.826	0.206
18. 1.78	19.1	19.6	0	4.01	2.8	0.0335	0.0330	14	-0.1118	0.1448	0.1348	7.42	58	0.096	0.013

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