School of Chemical and Biological Sciences
Department of Environmental Biology

Interactions Between Zooplankton Grazers and Phytoplankton as Part of the Energy and Nutrient Dynamics in the Swan River Estuary, Western Australia.

Sandra Lenore Griffin

This Thesis is presented for the Degree of
Doctor of Philosophy
of
Curtin University of Technology

June 2003

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

Signature: .....

Date: .....

Contents

List of Tables

List of Figures

Acknowledgements

Although a Doctorate is considered to be a study undertaken by a single person, in reality, many people often do contribute and this study is no exception.

The Western Australian Research Foundation and the Department of Environmental Biology, Curtin University of Technology, provided the research funds for this study, for which I am grateful. Field equipment and facilities were provided by CSIRO, the Swan River Trust, the Western Australian Water and Rivers Commission, the Centre for Water Research (The University of Western Australia) and the Department of Environmental Biology, Curtin University of Technology.

I am indebted to my principle supervisor, Rob Rippingale, for his trust and patience, knowledge, guidance and stimulating discussion. Tom Rose and Peter Thompson are also acknowledged for their interest and guidance early on in the process. David Hamilton and Michael Herzfeld are also acknowledged for their lessons in modelling and the support provided. Statistical advice was gratefully received from Ritu Gupta and the late Ernest Hodgkin provided unpublished historical data. The Swan River Trust provided access to their water quality monitoring data for the entire study and allowed me to accompany them on their water quality monitoring runs every fortnight, for which I am very thankful.

Rod Jacobson, Rob Rippingale, Stuart Helleren, Jane Rosser and all of the water quality monitoring staff from the Swan River Trust are thanked for their company, good humour and assistance during many hours of field work. Laboratory experiments were made easier through the expert advice and assistance provided by Rob Rippingale, Michael Payne, Charles La Coste, Ian Abercrombie, Ted Cockett, Claire Williams and Joanne Cooper.

For the friendship, encouragement, entertainment and support, I thank my fellow students, Linda Broadhurst, Reinier Mann, Rachel Meissner, Jane Rosser, Stuart Helleren, Florentine Singarayer and Phil Groom. The support staff of the Department of Environmental Biology are acknowledged for their support and unswerving cheerfulness in the face of my many and varied 'crises'.

Last, but not least, I thank my partner Rod, for his labour, humour, never-ending patience and love.

Abstract

Most Australian studies on estuarine plankton have examined distribution and abundance in relation to hydrological changes, primary productivity and associated nutrient dynamics. Relatively few have examined the complex interactions between zooplankton grazers and the type and quality of food available, or the role of zooplankton grazers in structuring phytoplankton communities, or their contribution to the nutrient pool. The ecological role of zooplankton grazers in the Swan River estuary, Perth, Western Australia, was examined as part of a collaborative research project directed by the Western Australian Estuarine Research Foundation, which was established in response to concern about increasing intensity and persistence of algal blooms. The present study focussed on one component of the zooplankton, the Copepoda, as model zooplankton grazers.

A regular zooplankton monitoring programme, undertaken over a two year period, provided data on seasonal patterns of abundance and distribution of zooplankton over a broad spectrum of physical conditions. Relationships were identified between habitat variables, such as algal biomass, dissolved oxygen, salinity and suspended solids and zooplankton distribution, relative abundance and species composition.

Prior to the inception of this study, it was assumed that copepod species composition, abundance and richness in the Swan River estuary may have changed over time, in response to long-term declines in water quality. Comparison of historical copepod monitoring data with current data did not detect any such change and it was concluded that there was greater variation in copepod species composition, abundance and richness within years than between years and that no significant change had occurred between 1966 and 1997. However, an absence or reduction in abundance of copepods in areas of very high algal biomass (>80 µg chlorophyll *a*.L^{-1}) suggests that local loss of water quality may have an impact on copepods over a small spatial scale within the estuary.

Different aspects of the interactions between zooplankton grazers and phytoplankton were studied. Zooplankton grazing rates were measured *in situ* during algal blooms and in the laboratory under controlled conditions to determine the potential for zooplankton grazers to reduce algal biomass. Field and laboratory experiments supported the hypothesis that copepods and other zooplankton can exert 'top-down control' over phytoplankton biomass, but that the type and biomass of phytoplankton present affected their ability to exert this control.

The results of the field and laboratory grazing experiments, along with literature data, were used to provide input data for a model of zooplankton and phytoplankton dynamics during a dinoflagellate bloom in the Swan River estuary. The model was tested against biomass measurements of zooplankton and phytoplankton to determine how well it predicted actual changes in the plankton community. The simulated output closely followed the measured

field data and fitted regression curves and provided information about diurnal patterns of phytoplankton production, respiration and migration and hydrodynamic transport, which was not available from field data. It was shown that zooplankton grazing, particularly grazing by microzooplankton, was the process contributing most to the observed decline in dinoflagellate biomass.

Nutrient availability is one of several factors determining productivity of phytoplankton. Nutrients within copepod faecal pellets are relocated by faecal deposition to sediments, where microbial activity leads to the remineralisation of these nutrients. Quantification of metabolic excretion of nutrients by copepods and the rate at which pellets are produced by copepod grazers, the concentration of nutrients within faecal pellets and the rate at which these nutrients are released indicated that copepods may play an important role in nutrient regeneration during summer and autumn when allochthonous nutrients are unavailable. At other times of the year, it is unlikely that copepods play an important role in nutrient regeneration.

The research has provided a more detailed level of understanding of the interactions between zooplankton, phytoplankton and their environment. The data is ideally suited for use in a computer model to predict the effects of management actions on the Swan River estuary. This would allow pre-emptive management strategies to be developed and lessen the focus on reactive management.

Thesis Organisation

The thesis is divided into five chapters. The General Introduction (Chapter 1) introduces the three main areas of research undertaken and provides background information on the study site. Chapters 2, 3 and 4 consist of an introduction to the research topics, paper/s published in peer-reviewed journals[1], manuscripts submitted for publication and unpublished research results. Each paper or manuscript includes a review of the relevant literature, necessitating some degree of repetition.

Table and figure numbers from each paper or manuscript have been altered to ensure consistency within the thesis and a single reference list is provided for all chapters. Chapter 5 is a General Discussion, which draws together the outcomes of each area of study and provides a commentary on how the data collected as part of this research may be used to guide the development of management strategies for the Swan River estuary.

[1] Statements from co-authors, attesting to their relative contributions, are provided in Appendix 4.

Chapter 1 - General Introduction

Introduction

Zooplankton are planktonic animals, typically between 20 and 2000 μm in length, that spend most of their life cycle in the water column (Dussart, 1965; Sieburth *et al.*, 1978). Being small, these animals are unable to make ecologically significant independent movement in the horizontal plane, but move with currents. Zooplankton movement in the vertical plane, however, even of only a few metres, may be ecologically significant. Zooplankton provide a range of ecological functions, being consumers of primary production and both direct and indirect sources of energy for other organisms.

The zooplankton of estuaries are able to survive cyclical fluctuations in water salinity, somewhere within the range of 0.5 (Practical Salinity Scale of 1978; UNESCO, 1981[2]) to 35 (M^{c}Lusky, 1989). This group of zooplankton are able to persist in time through dynamic fluctuations of environmental conditions on both short (minutes, hours) and long (months, years) time frames. Thus an understanding of estuarine zooplankton ecology can assist in our understanding of estuarine ecosystem function and the biological, chemical and physical processes involved. Such information can be used to formulate management frameworks for urban estuaries, to ensure that they continue to function as healthy ecosystems.

Genesis of Research Topic

During the mid 1990s, scientists, managers, government agencies and the general public became increasingly concerned about the state of health of the Swan-Canning Estuary, located close to the city of Perth, southwest Western Australia (Hamilton and Turner, 2001). This concern centred on a growing recognition that without intervention, estuarine health would continue to decline, as evidenced by increasing severity and frequency of nuisance algal blooms in the Swan and Canning Rivers (Hamilton and Turner, 2001).

Management intervention in the Swan and Canning Rivers required detailed understanding of the biological, chemical and physical processes that occur within the estuarine system but it was recognised that there were many gaps in knowledge and understanding (Hamilton and Turner, 2001). As a result, the Western Australian State Government established and funded the Western Australian Estuarine Research Foundation in 1994, in order to initiate a

[2] In this thesis, the Practical Salinity Scale of 1978 (PSS 78) has been adopted. PSS 78 is an internationally preferred method of expressing water salinity (UNESCO, 1981). Salinity is reported in dimensionless values and scales on figures are labelled 'Salinity' without any unit or index. A salinity of 35.39 ‰ becomes 35.395 on the PSS 78 scale.

range of research projects focussing on the gaps in current knowledge. The various research projects were to culminate in the development of a 3-dimensional ecosystem model of the estuarine system called CAEDYM (Computational Aquatic Ecosystem Dynamics Model), which could be used to predict the effect of various processes or events on estuarine health (refer to Figure 1.1).

The ecological role of zooplankton within the Swan-Canning Estuary was identified as an area in which information was lacking. The interactions between phytoplankton and zooplankton in Australian estuaries are less well understood than those of estuaries in the northern hemisphere. The majority of Australian studies have focussed on temporal change in plankton communities (Kott, 1955; Arnott and Hussainy, 1972; Taw and Ritz, 1978; Shiel *et al.*, 1982; Gaughan and Potter, 1995), with fewer studies concentrating on processes (Bhuiyan, 1966; Rippingale and Hodgkin, 1974a; Ikeda *et al.*, 1982a; Boon *et al.*, 1994). In the Swan-Canning Estuary, there had been previous studies of zooplankton species composition, distribution and abundance (Rippingale, 1987; Rippingale, 1994; Rippingale and Hodgkin, 1974a; Rippingale and Hodgkin, 1977), but all had been undertaken prior to the concern of the 1990s about nuisance algal blooms. Previously, there had been no research on the role of zooplankton in nutrient recycling and no detailed field-based studies of zooplankton grazing in relation to algal blooms. Of importance, it was not clear at the inception of this project whether the reported increasing severity and frequency of nuisance algal blooms had an effect on zooplankton populations.

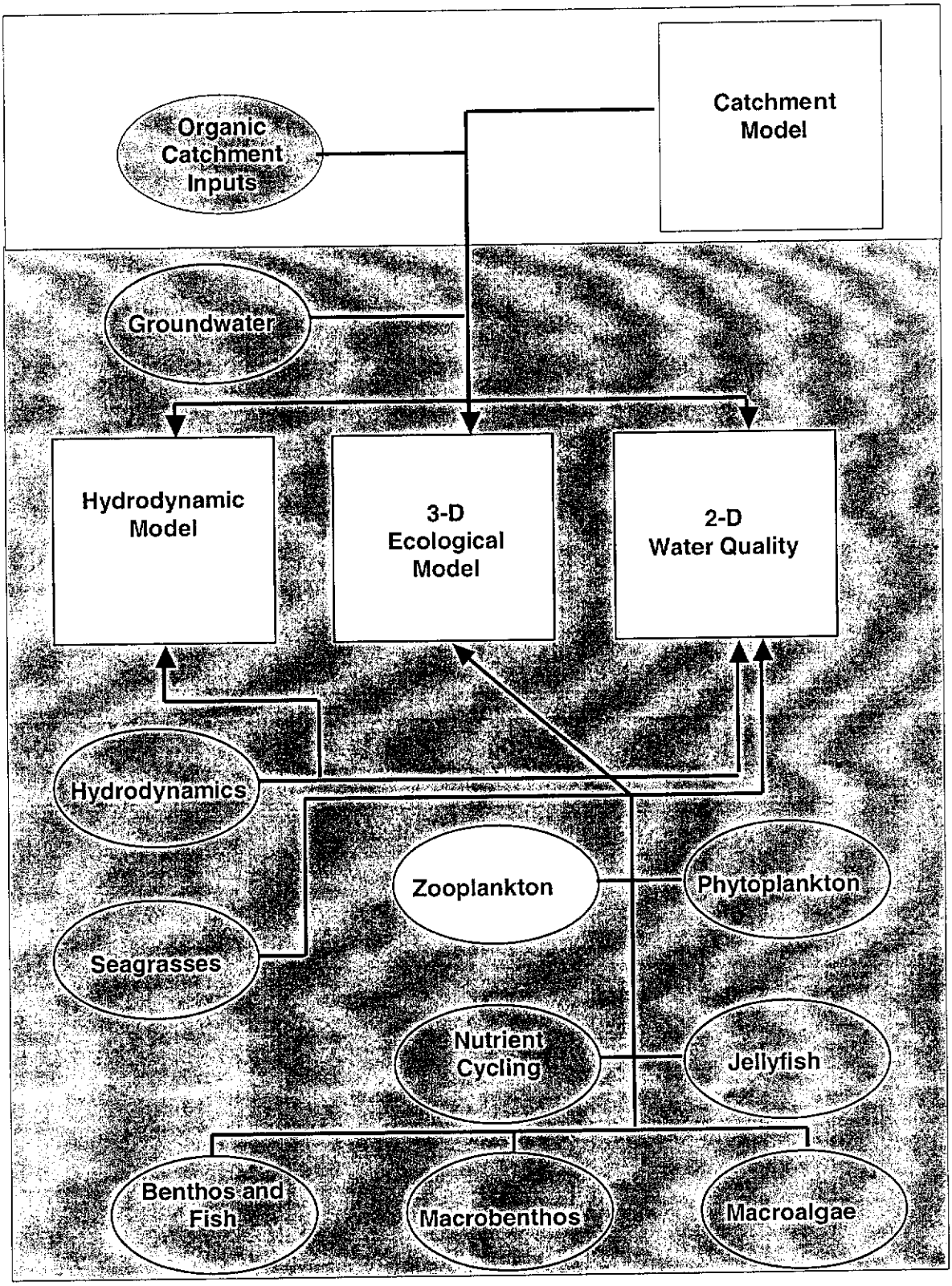

Figure 1.1: Components of CAEDYM.

Source: Hamilton (1996).

Research Aims

This research project focused on one part of the Swan-Canning Estuary – the Swan River estuary, because the Canning River has been substantially modified and has a weir controlling the upstream movement of saline water. The study was multi-faceted, with the following aims:

1) to document the population dynamics of estuarine zooplankton by measuring temporal change in distribution, abundance and species composition in relation to environmental parameters;
2) to determine the ecological role of zooplankton as consumers of primary production through measurement of grazing rates in the laboratory and in the field during algal bloom events;
3) to examine the potential significance of copepod regeneration of nutrients, by measuring metabolic excretion of nutrients and nutrient release from faecal pellets; and
4) to supply data for the development and validation of the 3-dimensional computer model (CAEDYM).

Overall, the study aimed to increase understanding of zooplankton ecology in the Swan River estuary. In doing so, it was hoped that questions pertaining to ecosystem health and estuarine management directions might also be answered.

Description of Study Site

The Swan River estuary (Figure 1.2) is a drowned river valley estuary which receives water from the Avon catchment (~119,000 km^2) and the Swan Coastal catchment (~20,000 km^2) and exchanges water with the Indian Ocean through a narrow inlet channel situated in Fremantle Harbour (Thurlow *et al.*, 1986). Both catchments have been extensively modified as a result of urbanisation and industrial and agricultural expansion, resulting in substantial contributions of nutrients to the Swan River estuary (Donahue *et al.*, 2001).

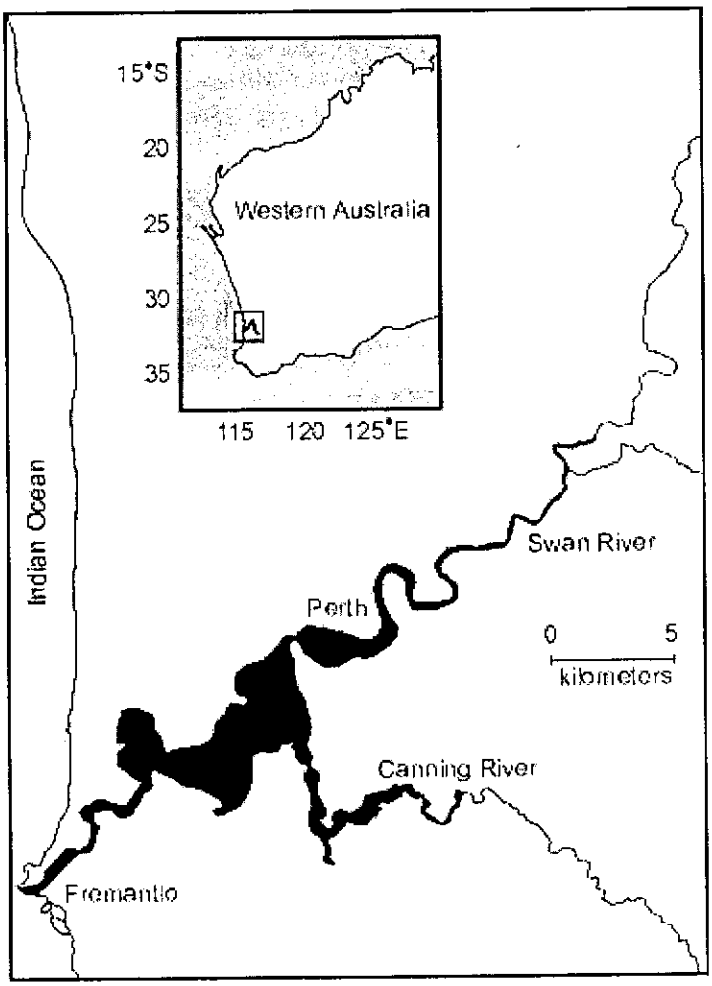

Figure 1.2: Map of Swan River estuary.

The Swan River estuary has a median depth of approximately 3 m in the middle and upper reaches and has a 21 m deep basin in its lower reaches. The relatively shallow middle and upper reaches are punctuated with deeper depressions of approximately 5 m depth (Stephens and Imberger, 1996). The estuary has a 5-10 m channel at its opening, which allows permanent exchange of water with the Indian Ocean.

The Swan River estuary is a micro-tidal estuary, with mean tidal amplitude of ~0.4 m. Water height within the estuary is more influenced by atmospheric pressure than tidal stage, with low atmospheric pressure resulting in high water and high atmospheric pressure resulting in low water (Stephens and Imberger, 1996).

The temperate climate of south-west Western Australia, with most rainfall occurring in winter, causes seasonal fluvial flow of the Swan River estuary. During later winter and early spring, seasonal rainfall results in the upper reaches of the estuary becoming fresh and saline water is progressively pushed down river. During summer and autumn, when fluvial flow has declined, tidal flow has a greater influence, with more dense saline water edging its way upriver on the bottom, creating a 'salt wedge'. It is at this time that haloclines and thermoclines can develop. By the end of autumn, it is possible for saline water to extend ~60 km inland (Stephens and Imberger, 1996).

Rainfall and temperature during the field investigation period are presented in Figures 1.3 and 1.4 respectively, in relation to long-term (1944 – 2001) averages. Winter rainfall was higher than average in 1996, but in 1997, winter rainfall was lower than average (Figure 1.3). Higher rainfall in winter can result in stronger fluvial flow during spring and a delay in movement of the salt wedge upriver. Lower rainfall in winter can reduce the duration and velocity of fluvial flow and allow a more rapid progression of the salt wedge upriver.

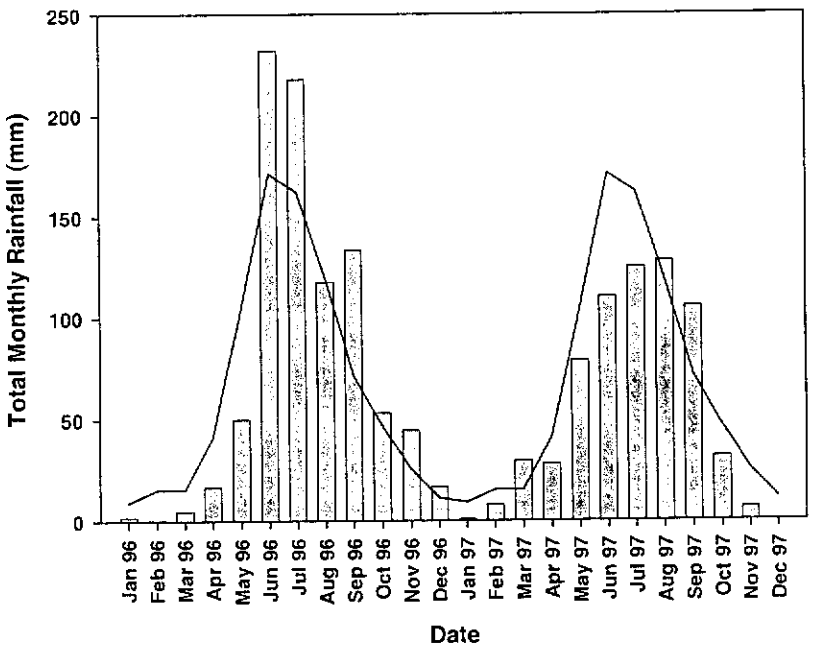

Figure 1.3: Total monthly rainfall during field investigations (column) and long-term monthly average (line), as measured at Perth Airport.

Source: Australian Bureau of Meteorology.

The maximum temperature was higher than average for both years in all seasons (Figure 1.4). Higher than average summer temperatures, combined with lower fluvial flow, promotes algal growth and can lead to persistent nuisance blooms.

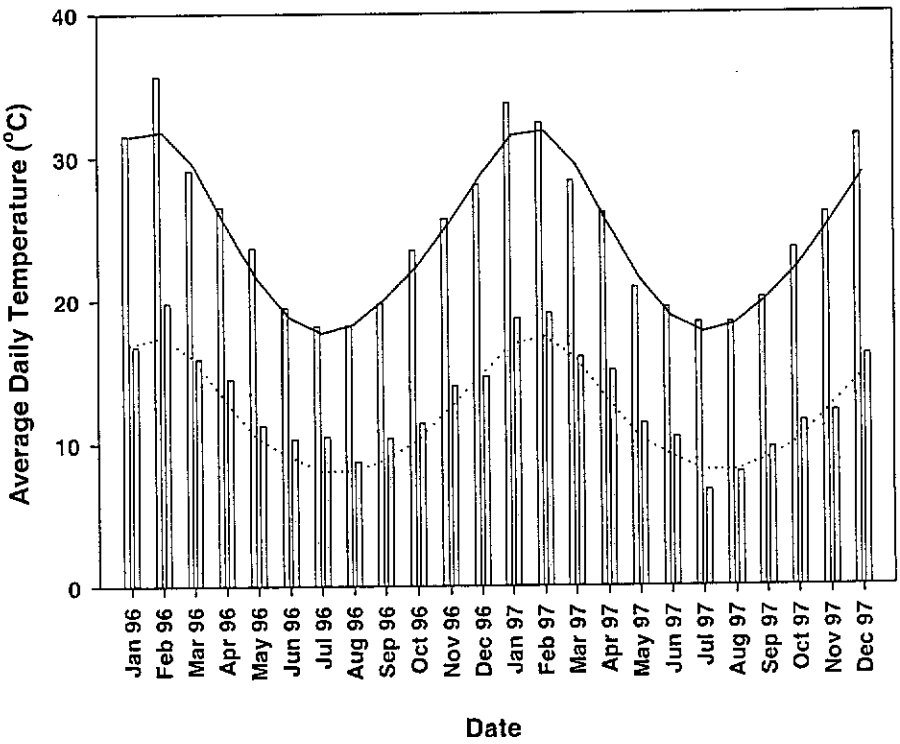

Figure 1.4: Average daily maximum and minimum air temperature during field investigations (columns) and long-term monthly average (lines), as measured at Perth Airport.

Source: Australian Bureau of Meteorology.

Zooplankton Population Dynamics

Chapter 2 of this thesis documents the population dynamics of zooplankton in the Swan River estuary and relates these to environmental parameters. Zooplankton monitoring focused on copepods but all zooplankton collected were enumerated and these unpublished data are also presented.

The basic seasonal cycle of zooplankton in relation to water salinity and hydrology had already been documented (*e.g.* Bhuiyan, 1966; Hodgkin and Rippingale, 1971; Rippingale, 1987). However, a number of questions remained unanswered. For example, what effect do persistent algal blooms have on zooplankton populations? To what extent is salinity the main environmental factor regulating zooplankton population distribution? Is there evidence to support the hypothesis of declining estuarine health as indicated by copepod populations?

Temporal changes in estuarine zooplankton distribution, abundance and species composition and environmental parameters were monitored from summer 1995-1996 to summer 1997-1998 inclusive. This provided biomass estimates of zooplankton grazers and identified the primary mechanisms behind observed shifts in species composition, relative abundance and distribution. It also allowed a comparison with historical data to show whether copepod species composition had changed; a change in grazer type and abundance over both short and long-term scales has implications for the potential of grazers to reduce phytoplankton biomass.

Chapter 2 is based on a manuscript submitted for publication, focussing specifically on copepods, but the chapter also includes unpublished monitoring results for other zooplankton taxa and the results of an unpublished study into vertical distribution and abundance of dominant zooplankton taxa.

Zooplankton Grazing

Zooplankton grazing impact on phytoplankton biomass, and the significance of this impact, has been the focus of many investigations where water quality has been affected by phytoplankton blooms. Very few such studies have been undertaken in Australian estuaries and even fewer in the Swan River estuary.

With the reported increased severity and incidence of algal blooms in the Swan River estuary, it became important to understand the ecological processes that were involved in algal bloom dynamics and to assess the potential for zooplankton to reduce phytoplankton biomass through grazing. Equally as important was the potential for zooplankton grazing to influence phytoplankton species succession.

Chapter 3 of this thesis documents the ecological role of zooplankton as consumers of primary production through *in situ* and laboratory based measurements of ingestion rate. Both zooplankton community and individual taxon ingestion rates were determined, as well as diurnal variation in these rates. This chapter consists of two published papers and the results of unpublished studies into alternative methods of estimating copepod ingestion rate. Each investigation focussed on estuarine copepods, as model zooplankton grazers, but the results were compared with other zooplankton taxa.

Nutrient Interactions

Typically, phytoplankton blooms in the Swan River estuary occur following winter rainfall, when catchment-derived nutrients become available and water temperature and light conditions are favourable for the growth of algae. However, the persistence of algal blooms through to late autumn, when rainfall is generally low, unreliable and unpredictable, can be related to recycling of nutrients within the water column (Caperon *et al.*, 1979; Glibert *et al.*, 1982; Havens *et al.*, 1996; Horner-Rosser and Thompson, 2001).

The role of copepods in nutrient regeneration and, hence, nutrient availability for phytoplankton growth, was examined by measuring the rate of production of faecal pellets by dominant copepods under a variety of feeding regimes, as well as the rate at which these pellets settle. The rate of excretion of soluble nutrients during faecal pellet decomposition and during copepod metabolic activity was also assessed to determine the significance of grazer contributions to nutrients available for phytoplankton growth. These studies resulted in two manuscripts (one published and the other submitted for publication), which are presented in Chapter 4.

Chapter 2 - Zooplankton Population Dynamics

General Introduction

Previous studies of zooplankton in the Swan River estuary have identified a seasonal successional pattern of copepod species composition, abundance and distribution, related to salinity tolerance, riverine flow and inter-species predation (Bhuiyan, 1966; Hodgkin and Rippingale, 1971; Rippingale, 1987; Rippingale, 1994). Hodgkin (1987) described salinity as being the 'ecological master factor' behind observed patterns of zooplankton species distribution. Although salinity is a defining environmental condition, these earlier studies did not document diurnal changes in distribution and did not investigate the effect of other environmental variables on distribution, such as dissolved oxygen, suspended solids and algal species and density.

The aims of the monitoring component of the study were:

1. to verify previously recorded patterns of copepod successional change;
2. to investigate the occurrence of diurnal migration in Swan River zooplankton; and
3. to establish the relative importance of environmental conditions in controlling copepod distribution, relative abundance and species composition.

The following sections review the methods for monitoring zooplankton and describe the methods used for this study, summarise the numerically dominant and commonly occurring zooplankton in this study and summarise patterns of diurnal distribution for numerically dominant zooplankton taxa. The chapter concludes with a copy of a manuscript on copepod monitoring in the Swan River estuary, submitted for publication in the Journal of the Royal Society of Western Australia.

Monitoring Methods

Patchiness of plankton communities is well documented (*e.g.* Levin and Segal, 1976; Mann, 1982; Day *et al.*, 1989; Kotliar and Wiens, 1990; Levin, 1994). In estuarine systems, the distribution of biotic and abiotic conditions occurs over variable spatial scales (patches within patches) and is in a constant state of flux. This occurs because of changes in abiotic conditions, such as tidal movement, internal current generation, wind effects and changes in biotic conditions (predator-prey interactions), over variable temporal scales (diurnal, weekly, monthly, seasonally). Inherent patchiness should be considered in any zooplankton monitoring programme, as patch size can determine the choice of sampling procedure.

For the present study, a range of methods for collecting zooplankton was assessed, including plankton nets, pumps and traps. Pumps were not used because there is evidence for underestimation of zooplankton populations as animals avoid the inlet stream (Singarajah, 1969; Edmondson and Winberg, 1971; Icanberry and Richardson, 1973). Two methods were chosen for zooplankton sample collection based on the aims of the monitoring programme and resource availability. A plankton net was used for long-term monitoring zooplankton populations over a large spatial scale. A plankton trap was used for monitoring zooplankton populations over a short time-frame and small spatial scale.

The use and design of plankton nets for zooplankton sampling has been well researched and the errors associated with this method of sampling are well documented (Tranter and Fraser, 1968). Factors to consider include mesh type and pore size, towing speed and angle, the filtration efficiency of the net diameter and avoidance by zooplankton. Studies have shown that the most appropriate type of mesh to use in plankton nets is nylon or polyester, monofilament, plain weave mesh. In the present study, monofilament, plain weave nylon mesh was used with a pore size of 300 µm. The pore size was chosen based on the dimensions of the most common copepod fauna in the Swan River estuary and the likelihood of the mesh clogging during phytoplankton blooms. It was considered that 300 µm was the greatest pore size that could be used without substantial loss of adult zooplankters. Previous studies have shown that the ratio of mesh area to net mouth area determines the net filtration efficiency, which plateaus when the mesh surface area is three times greater than the mouth area (Tranter and Fraser, 1968). The dimensions of the net used in the present study were such that the mesh surface area was four and a half times greater than the mouth area, effectively providing a greater volume of water filtered efficiently (Tranter and Fraser, 1968). The mouth of the net had a diameter of 0.5 m, being sufficiently large to minimise zooplankton avoidance (Fleminger and Clutter, 1965; M^{c}Gowan and Fraundorf, 1966). To minimise turbulence directly in front of the net and net avoidance behaviour by zooplankton, the net was towed from the top of the mouth rather than from the front. A flow meter was positioned in the centre of the mouth (Tranter and Fraser, 1968). The towing speed was maintained at 0.5 knots to reduce any effect on the filtration efficiency of the net (Tranter and Fraser, 1968). The net was lowered to the bottom of each site (with depth determined using a depth sounder) while the boat was stationary and then slowly hauled in while the boat travelled, creating an oblique haul.

An advantage of the plankton net was that it allowed the filtration of large volumes of water (minimum of 50,000 L of water at each site on each sampling occasion), over both vertical (average 5 m) and horizontal (average 350 m) scales, thereby minimising the effect of patches on the data. Wiebe (1971) found that the larger the patch size encountered the higher the sample accuracy. By filtering over a horizontal, as well as a vertical scale, it was assumed that large patches would be encountered.

The net sampling did not allow any discrimination of vertical zooplankton distribution, so this was examined using a 6.28 L capacity plankton trap, which enabled sampling from discrete depths and repeated sampling over short time scales. A series of sites were located from which sampling could occur from a jetty or boat (Figure 2.1) and these were used for 24 hour monitoring sessions, with samples collected every three hours. Sampling dates were chosen with reference to the location, extent and type of algal blooms present. The data collected allowed observation of diurnal changes in zooplankton distribution in the Swan River estuary.

A major advantage of the trap sampling was that the sample could be filtered on very fine mesh (44 μm) and include nauplii, copepodites and microzooplankton not captured efficiently or consistently with the plankton net. A disadvantage of the trap sampling was that sampling took place from a fixed location in a tidal system. However, by also recording tidal stage, the data could be used to illustrate patches of zooplankton moving within a tidal water body past the fixed sampling location. Any changes in the distribution of zooplankton within the water column as the patch moves past the sampling point could be observed.

The frequency at which both types of sampling were undertaken allowed determination of both long-term and short-term population dynamics. Fortnightly monitoring was chosen for the net sampling because it was the shortest time-frame over which samples could be taken without generating a prohibitive number of samples for processing. Monthly sampling, although it reduces sample processing time was considered to be too infrequent because the dominant copepod fauna of the Swan River estuary can complete their life cycle in approximately 14 days and because previous studies have shown that the time frame for population changes is generally less than one month. For example, predation of one copepod species on another caused a complete shift in the species composition over time scales as small as one week (Rippingale and Hodgkin, 1974b). Three hourly monitoring was chosen as a frequency for the trap monitoring as it allowed a minimum of eight observations of zooplankton distribution within a 24 hour period and two or more tidal changes.

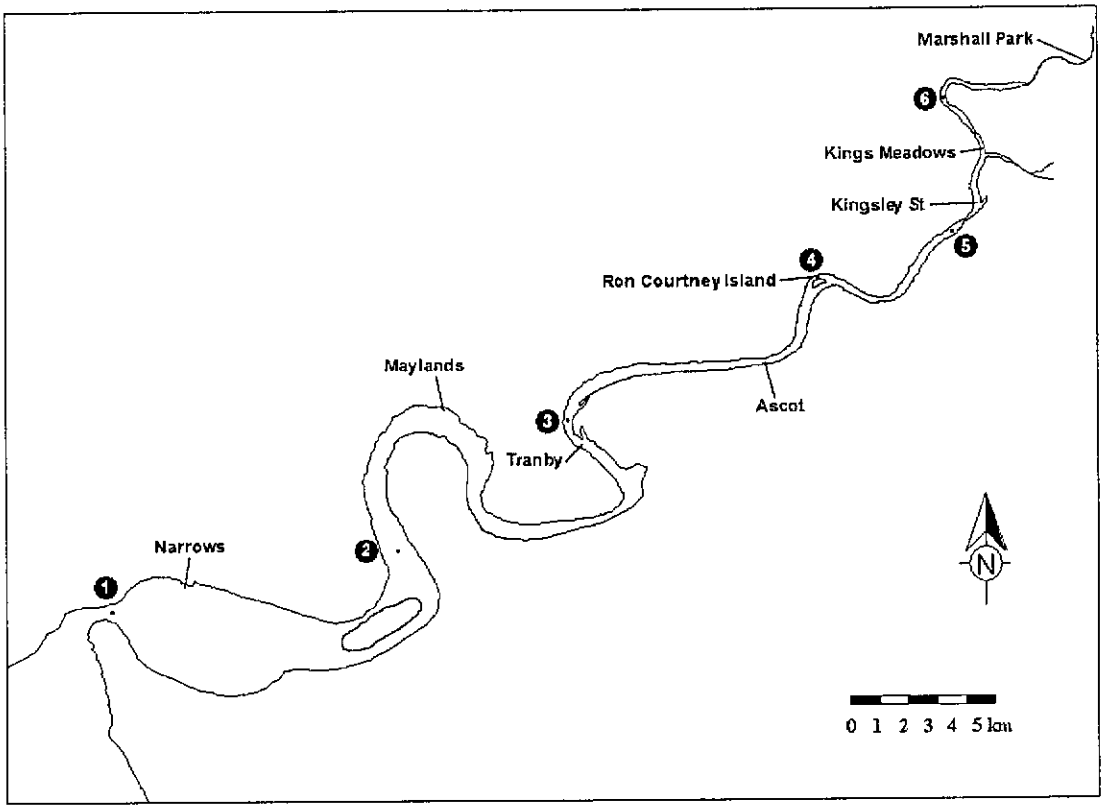

Figure 2.1: Trap sampling locations (with net sampling site numbers shown).

Zooplankton of the Swan River Estuary

A total of 57 zooplankton taxa were collected. These were from the invertebrate phyla Arthropoda, Mollusca, Rotifera, Cnidaria, Chaetognatha, Annelida, Ciliophora, Echinodermata and Protozoa and the vertebrate phylum Chordata. Of all taxa collected, 32% were meroplanktonic (temporary members of the plankton) and 68% were holoplanktonic (permanent members of the plankton). A complete list of the taxa collected is provided in Appendix 1.

The most common invertebrate phylum, Arthropoda, was represented by four classes, Ostracoda, Maxillipoda, Malacostraca and Branchiopoda and one sub-class, Cirripedia. Class Maxillipoda (subclass Copepoda) was the most commonly collected arthropod taxon. Twenty-five species of copepod were collected, but five species contributed most to overall abundance. The rotifers *Synchaeta* sp. (Figure 2.2) and *Brachionus plicatilis* (Figure 2.3) and the larvae of the bivalve, *Xenostrobus securis* (Figure 2.4), although not collected often, were numerically dominant during summer 95/96.

Commonly occurring taxa were identified to species level, when possible. The copepods, *Sulcanus conflictus* (Family Sulcanidae) (Figure 2.5) and *Gladioferens imparipes* (Family Centropagidae) (Figure 2.6), have been widely studied in the Swan River estuary and their

taxonomy is well described, as is the taxonomy for *Oithona nana* (Figure 2.7). Less is known about the taxonomy of *Acartiura* sp. (Figure 2.8), which has previously been referred to as *Acartia clausi* (Bhuiyan, 1966; Craig, 1979; Rippingale, 1987) and *Acartia simplex* (Gaughan and Potter, 1995). Bradford (1976) revised the *Acartia* subgenus *Acartiura* to create a new genus, *Acartiura*, based on a close relationship to *Acartia clausi*. The species of *Acartiura* in the Swan River estuary has not yet been confirmed to be any of the new species of *Acartiura* described and so is referred to as *Acartiura* sp.. The cyclopoid copepod referred to as *Halicyclops* sp. (Figure 2.9) was not identified to species level because sufficient reference material was lacking. The taxonomy of species collected infrequently was resolved to Family, when possible.

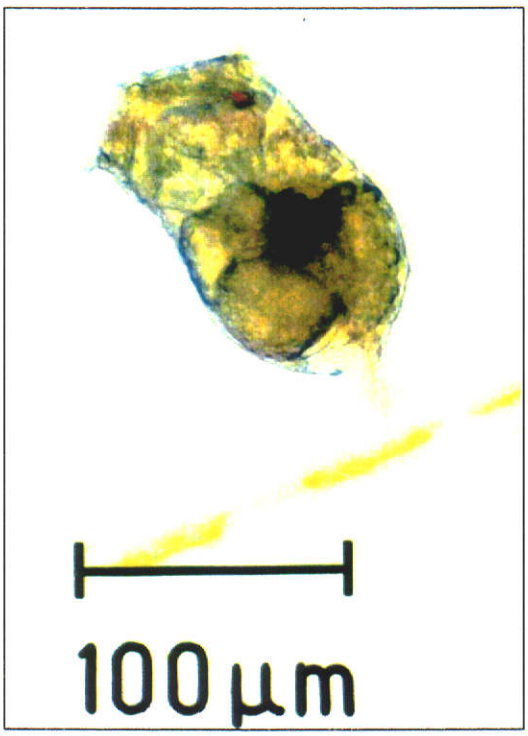

Figure 2.2: *Synchaeta* sp. Ehrenberg, 1832.

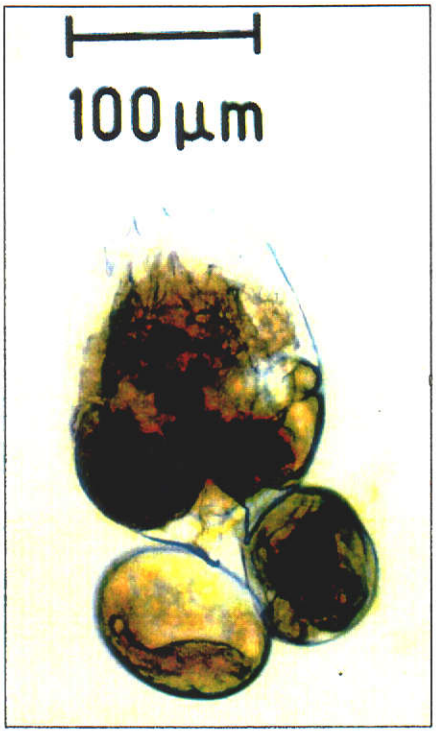

Figure 2.3: ***Brachionus plicatilis*** **Mueller, 1786.**

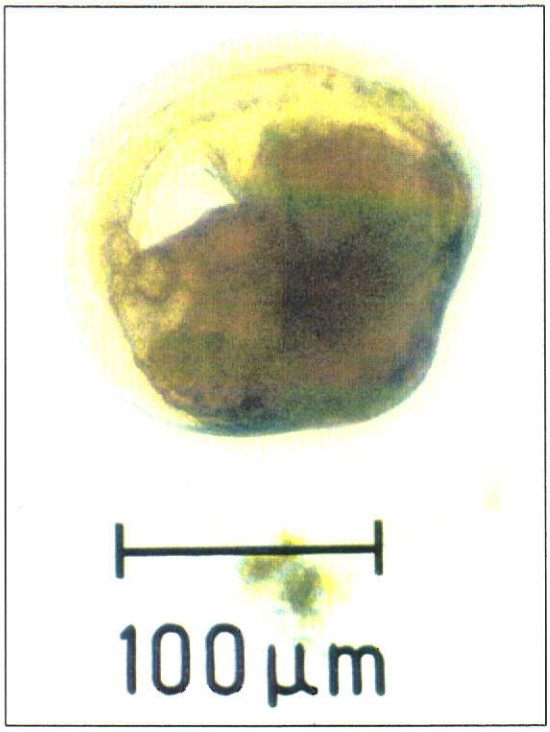

Figure 2.4: ***Xenostrobus securis*** **Mueller, 1786.**

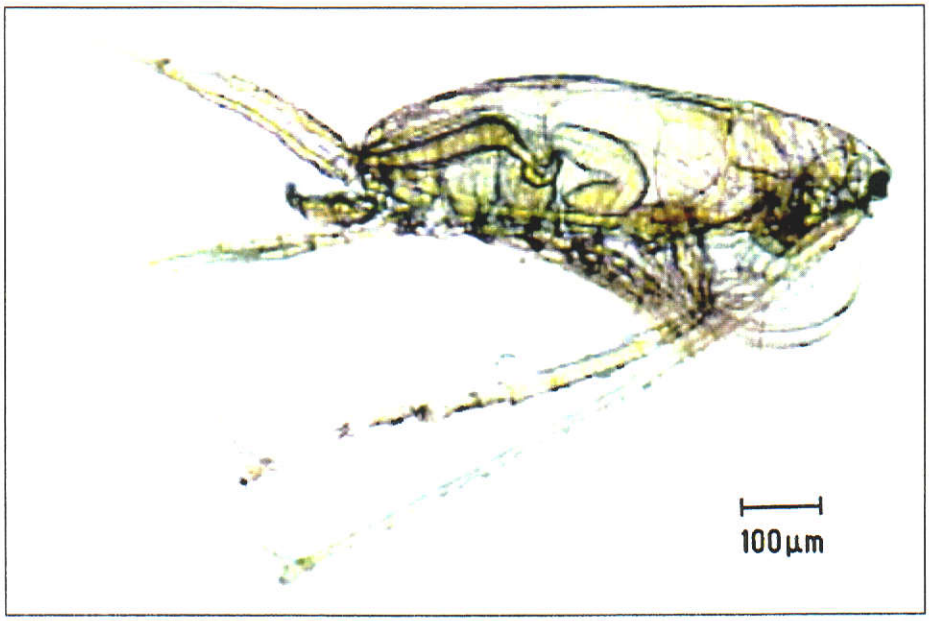

Figure 2.5: ***Sulcanus conflictus*** **Nicholls 1945.**

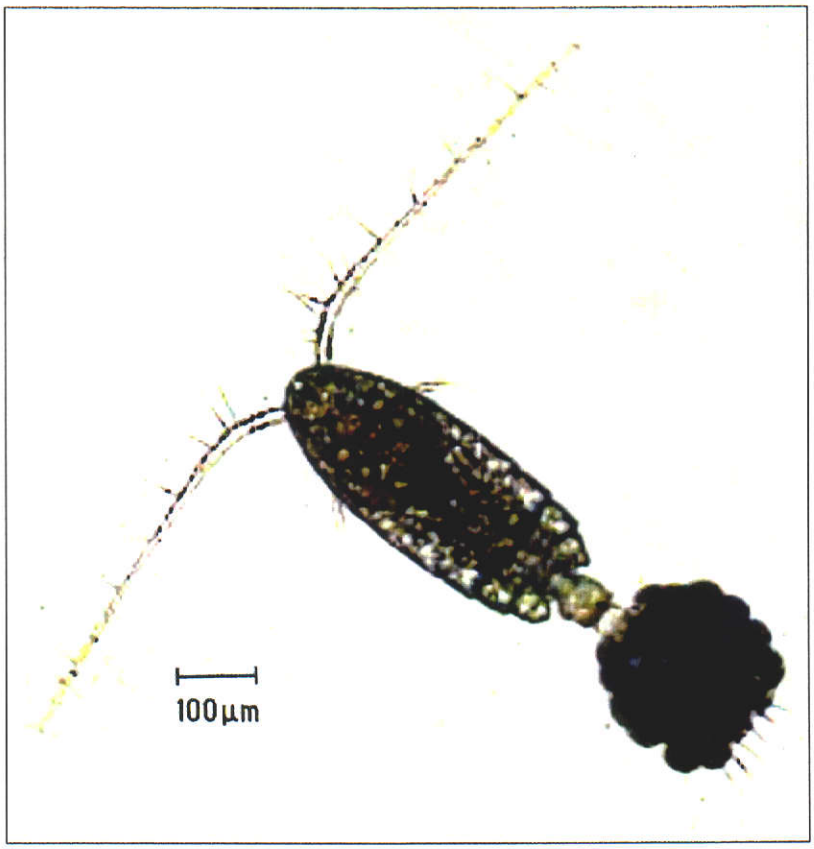

Figure 2.6: ***Gladioferens imparipes*** **Thomson 1946.**

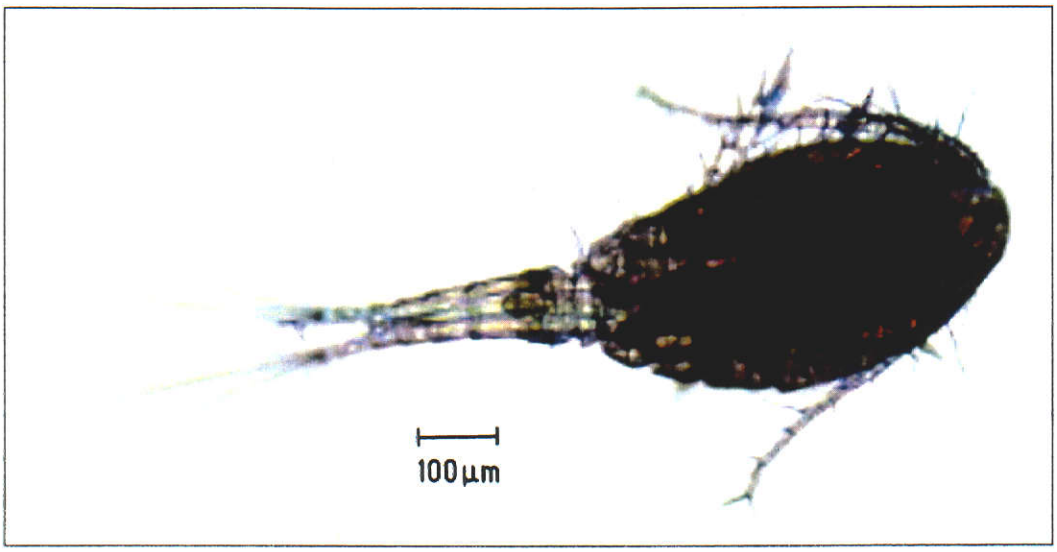

Figure 2.7: ***Oithona nana*** **Giesbrecht, 1892.**

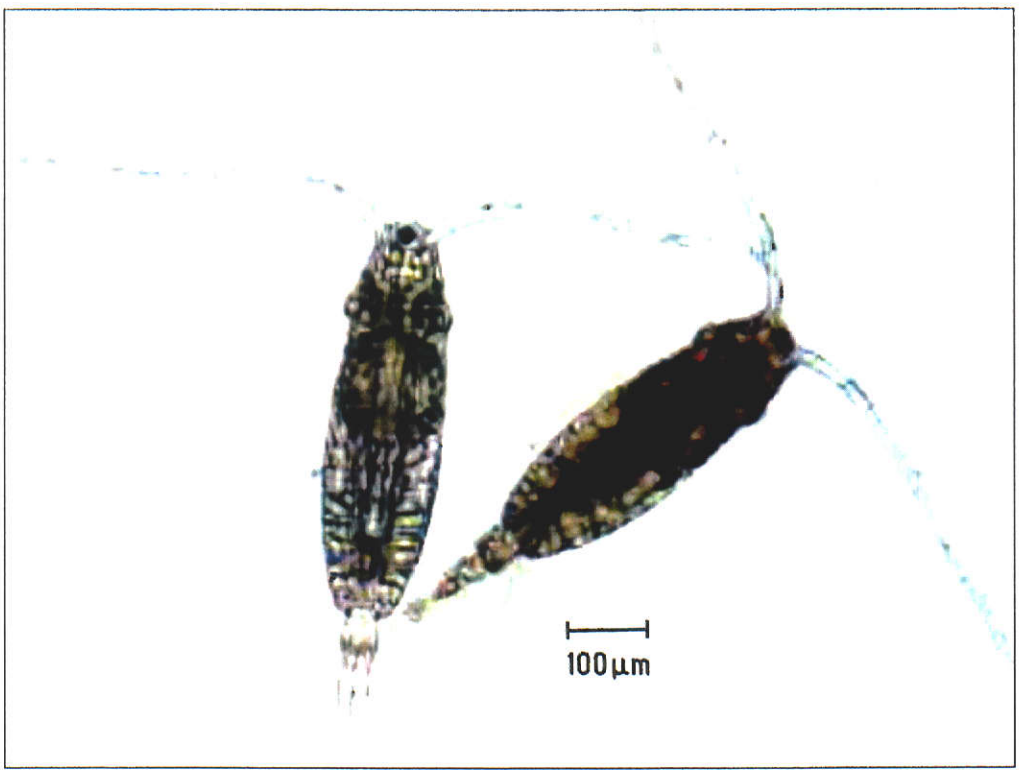

Figure 2.8: ***Acartiura*** **sp. Bradford 1976.**

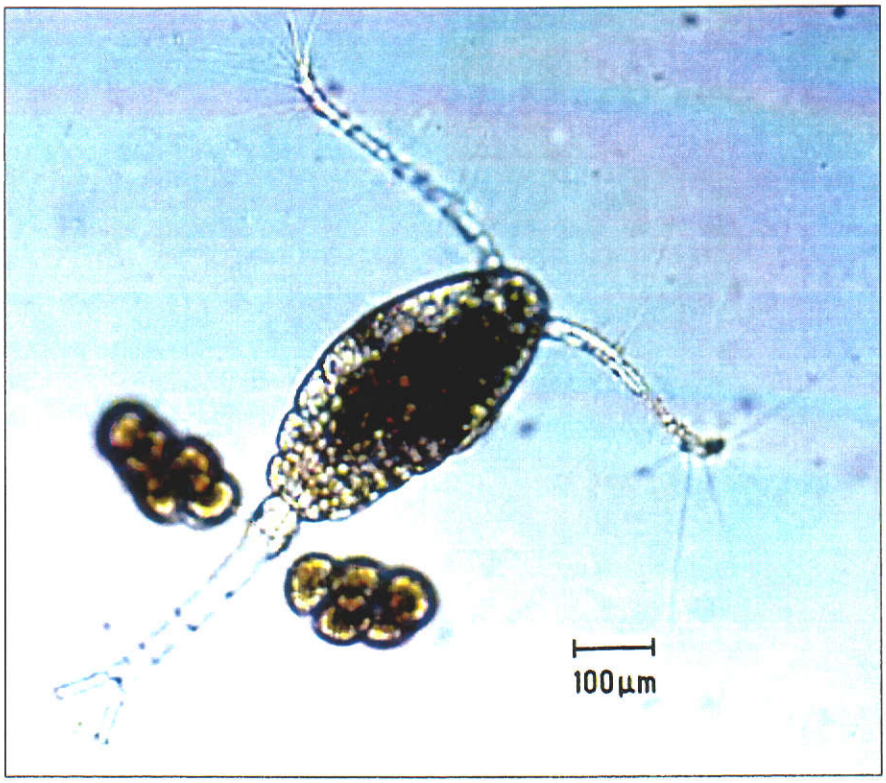

Figure 2.9: *Halicyclops* sp. Lilljeborg, 1853.

Diurnal Distribution

Vertical migration is a commonly observed behaviour in copepods (Day *et al.*, 1989). The control mechanism for, and adaptive significance of, vertical migration has been widely investigated (see reviews in Haney, 1988 and Lampert, 1989). In general, it is considered that daily changes in light intensity and angular distribution provide a primary exogenous stimulus for timing the diel migrations of most zooplankton (M^{c}Laren, 1963; Longhurst, 1976; Haney, 1988), with possible involvement of an endogenous circadian rhythm (*e.g.* Harris, 1963; Enright and Hamner, 1967).

Light as a primary control mechanism for vertical migration does little to explain reverse migration or repeated migrations within a single diel period. Physical water conditions, such as temperature, salinity and current may influence vertical migration (Longhurst, 1976; Haney, 1988). A further hypothesis was that put forward by Gauld (1953), who postulated that food availability could act as a signal for upward or downward migrations in marine copepods. However, it is unlikely that factors controlling or influencing vertical migration would act independently of the changing physical, chemical or biological factors encountered by a migrating organism (Longhurst, 1976; Haney 1988). It is highly probable that a multitude of local factors interact to determine the amplitude and direction of vertical migration, given the diversity of habitats in which zooplankton occur.

Zooplankton commonly show behavioural plasticity in response to particular environmental conditions (Haney, 1988). As such, zooplankton in an estuary could be expected to exhibit migratory behaviour very different from that of zooplankton in open oceans, inland lakes or neritic environments. Factors such as tidal cycles and salinity changes may also influence vertical migration of estuarine zooplankton.

Figures 2.10 to 2.16 show examples of variation in the diurnal distribution of zooplankton and tidally induced changes in water salinity in the Swan River estuary. Although sampling occurred from a fixed point, the graphs show zooplankton patches moving past sampling locations. The tidal currents measured during sampling were used to discern whether a single patch was observed moving up and down the horizontal plane or whether several patches were present. Current direction is indicated in each salinity graph and approximated tide times and heights are provided in Table 2.1.

Not all zooplankton taxa were recorded at each location and sampling time. For example, the rotifers, *B. plicatilis* and *Synchaeta* sp. and larvae of the bivalve, *X. securis*, were recorded in high densities in summer 95-96 but not at all in summer 96-97 (Figures 2.10, 2.11, 2.12 and 2.13). The copepods *Acartiura* sp. and *Halicyclops* sp. were only recorded in summer 96-97 at the trap monitoring sites (Figure 2.14).

Evidence for diurnal vertical migration was found on only three occasions during the observation periods. This occurred with *S. conflictus* at Ron Courtney Island (Figure 2.11), with larvae of the bivalve, *X. securis,* at Ascot (Figure 2.12) and with *Halicyclops* sp. at the Narrows (Figure 2.14). Other patterns of vertical distribution appeared to be more related to tides and salinity.

Previous studies in deeper water (18 m) in the Swan River estuary have indicated that *S. conflictus* does undergo diurnal vertical migration (Bhuiyan, 1966). The sampling sites for the present study were all in shallow water (approximately 3 m) and this may have had an effect on vertical migration. Variation in copepod migratory behaviour has been observed elsewhere. For example, *Acartia erythraea* showed distinct patterns of vertical migration in the eutrophic waters of Tolo Harbour, Hong Kong (Tang *et al.*, 1994), but the same species showed limited vertical migration in the Inland Sea of Japan (Checkley *et al.*, 1992).

Table 2.1: Approximate high and low tide times and water height for the Swan River estuary during diurnal distribution investigations.

Site	Date	Approximate Time (hrs)	Approximate Height ASL (m)
Ron Courtney Island	18/11/95	0820	0.63
		1025	0.64
		1702	0.58
	19/11/95	0026	0.83
		0801	0.56
Ron Courtney Island	23/11/95	1058	0.31
	24/11/95	0223	1.04
		1154	0.29
Ascot	10/01/96	1137	0.43
		1900	0.65
		2000	0.65
	11/01/96	0500	0.83
		1146	0.45
Ascot	31/01/96	0956	0.42
	1/02/96	0015	0.94
Narrows	12/11/96	0851	0.36
		1521	0.58
		1708	0.57
	13/11/96	0039	0.97
		0953	0.35
Maylands	21/11/96	0738	0.55
		1232	0.61
		1648	0.59
		2348	0.85
	22/11/96	0820	0.48
		1345	0.60
Ascot	17/12/96	0138	0.75
	18/12/96	1242	0.53
		2336	0.80
	19/12/96	1044	0.52

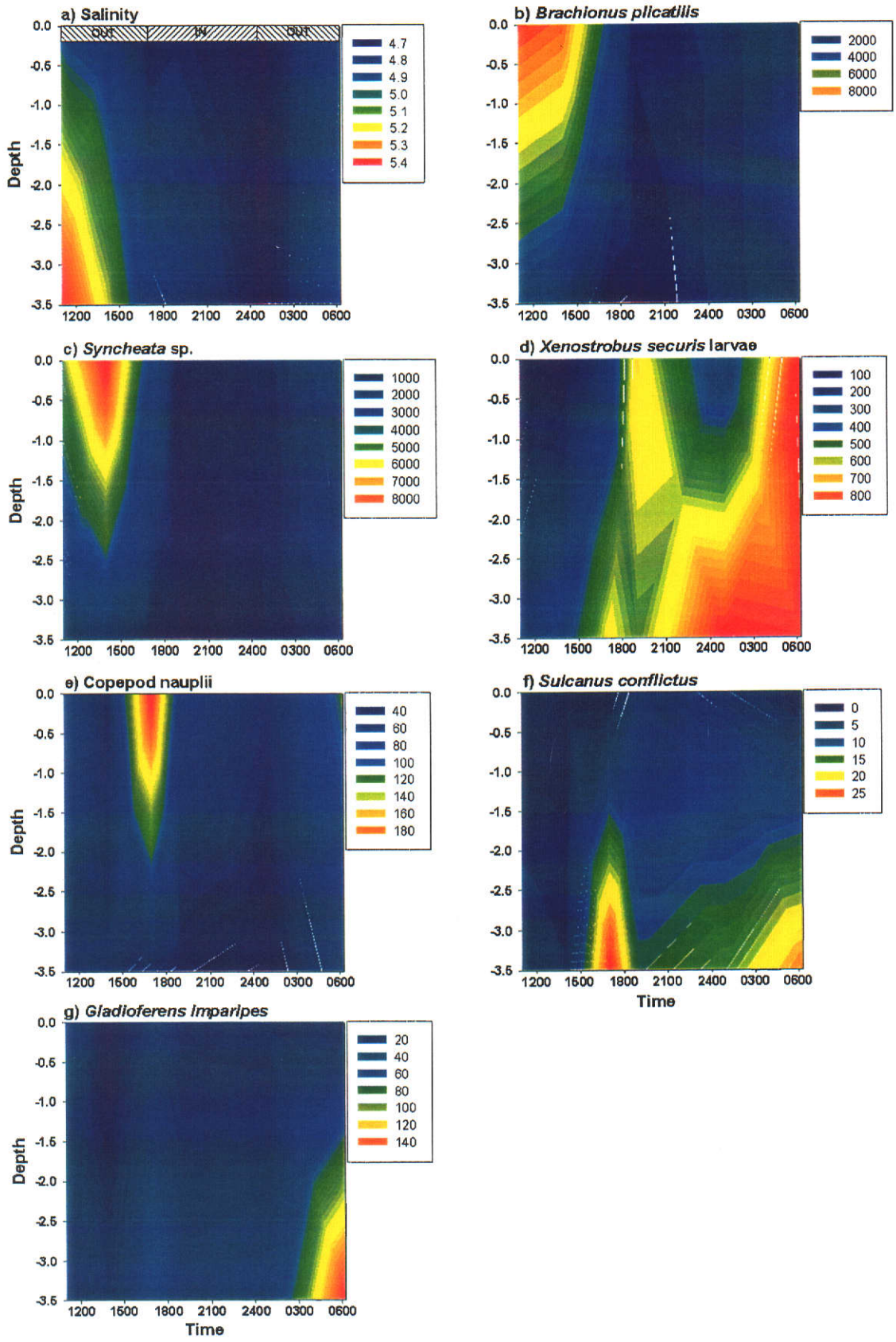

Figure 2.10: Diurnal distribution of zooplankton at Ron Courtney Island, 18-19th November, 1995.

Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)* to *g)*.

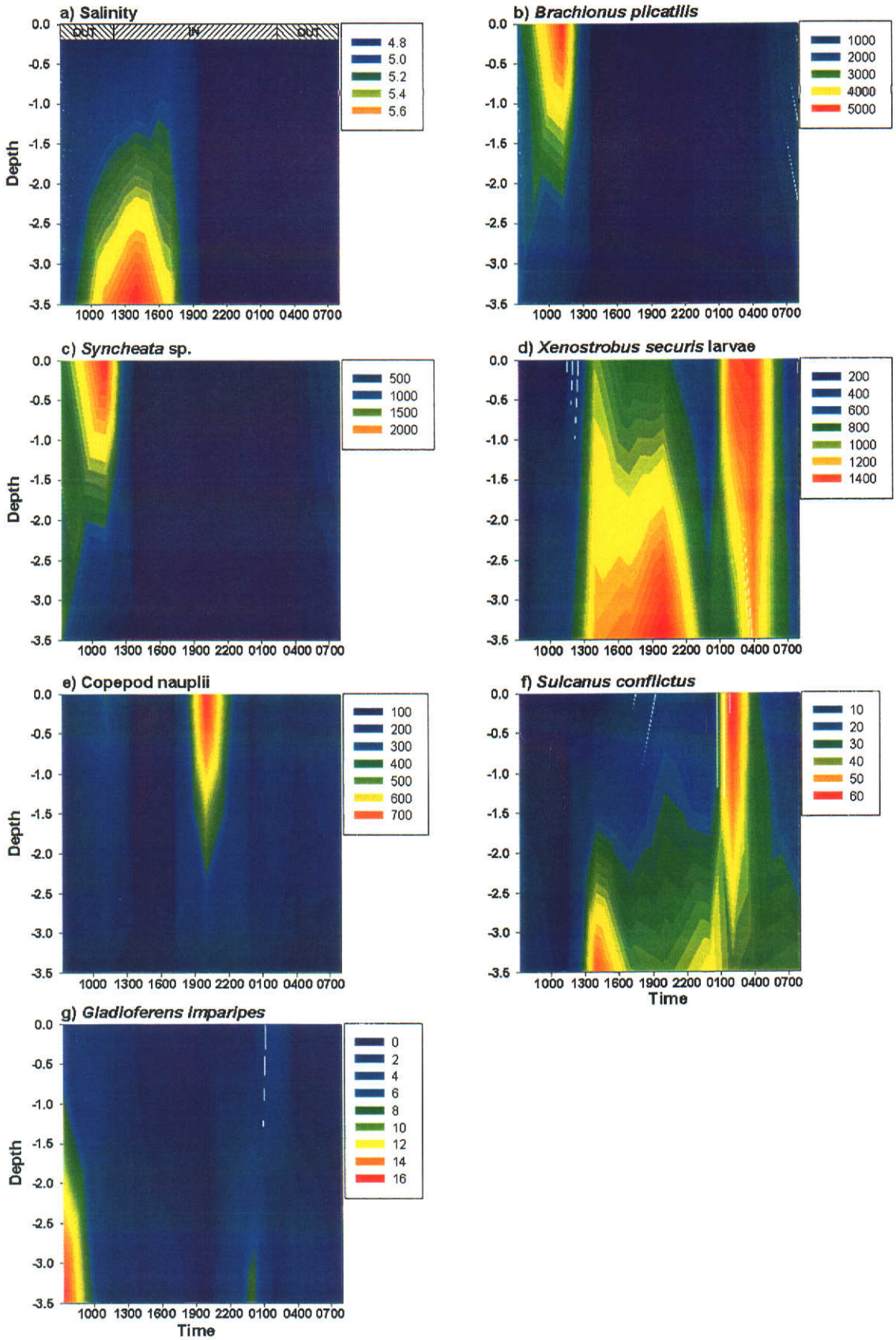

Figure 2.11: Diurnal distribution of zooplankton at Ron Courtney Island, 23-24th November, 1995.

Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)* to *g)*.

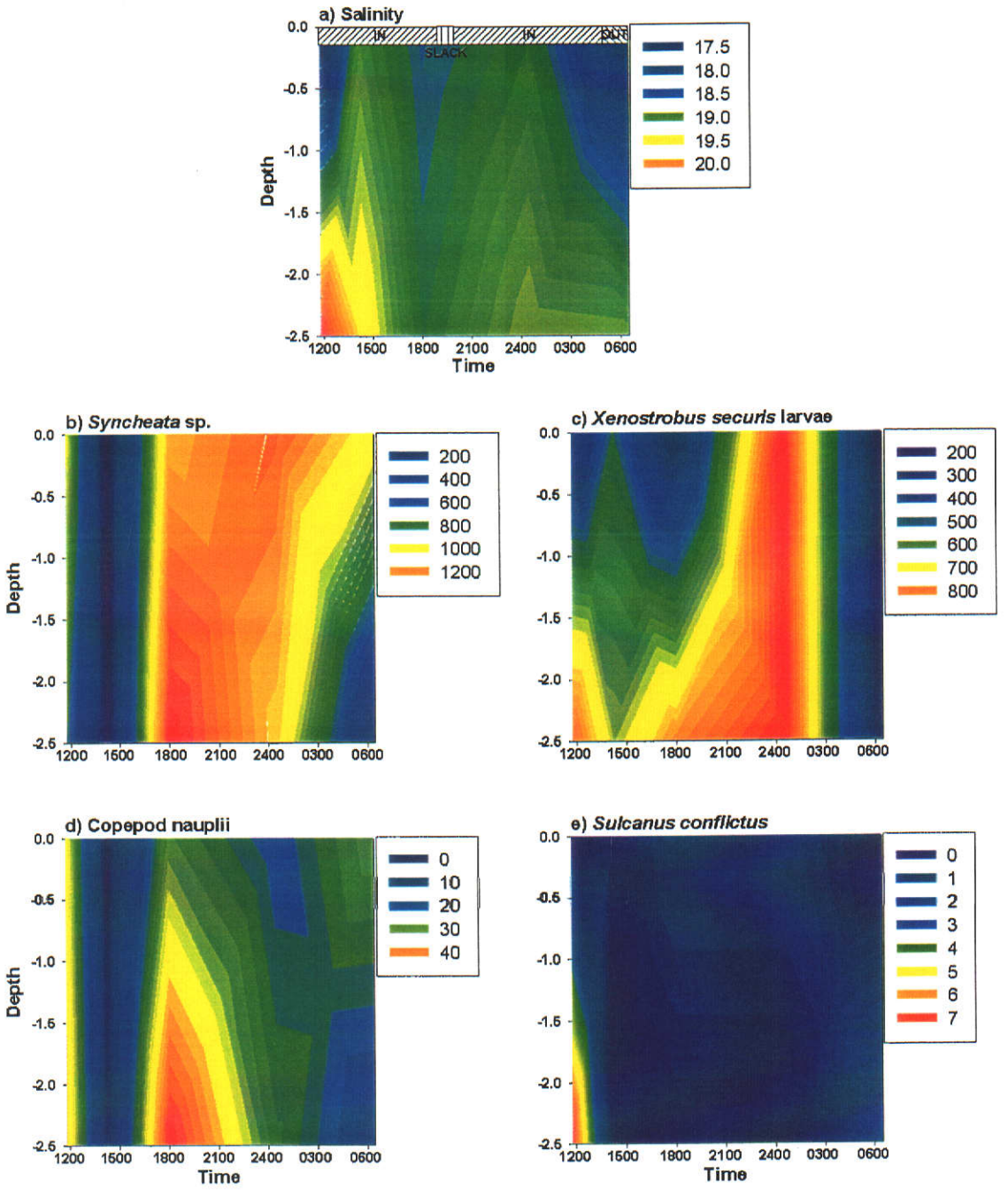

Figure 2.12: Diurnal distribution of zooplankton at Ascot, 10-11th January, 1996.

Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)* to *e)*.

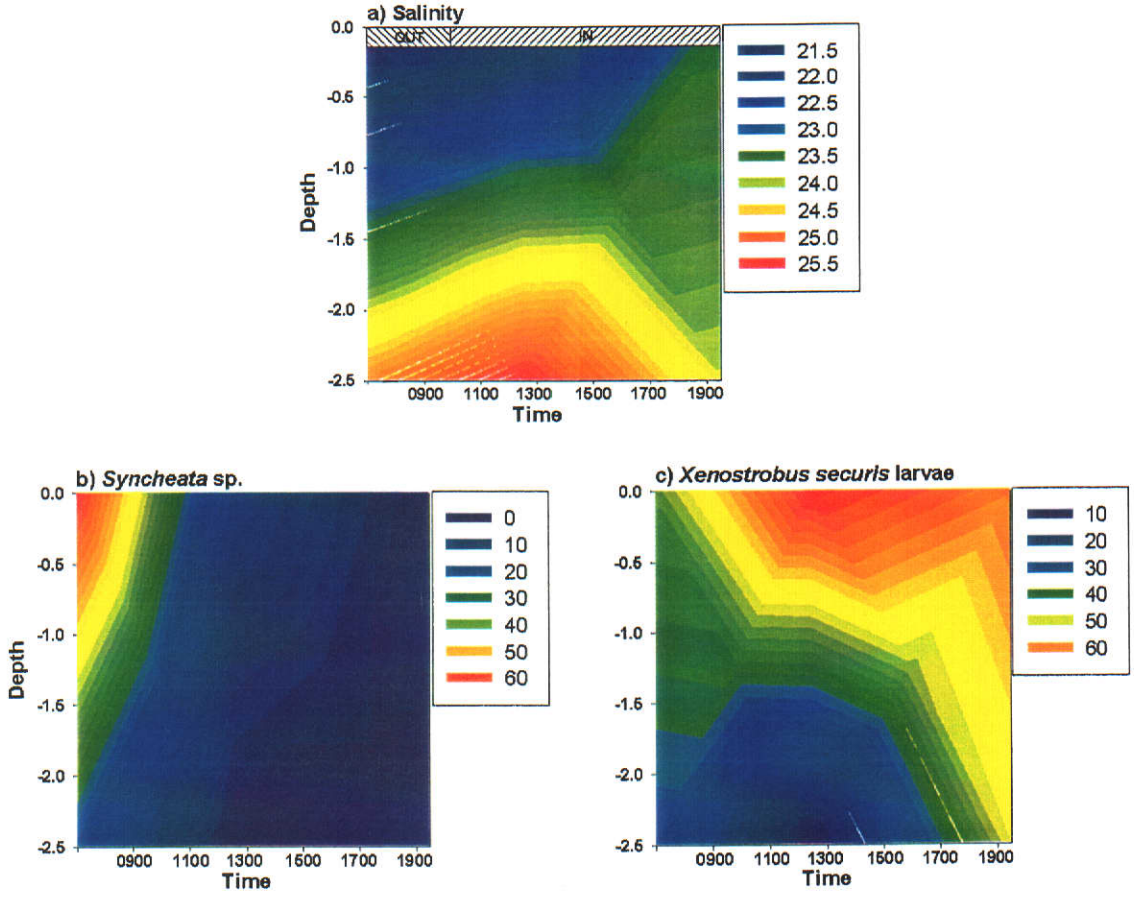

Figure 2.13: Diurnal distribution of zooplankton at Ascot, 31st January, 1996.

Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)* and *c)*.

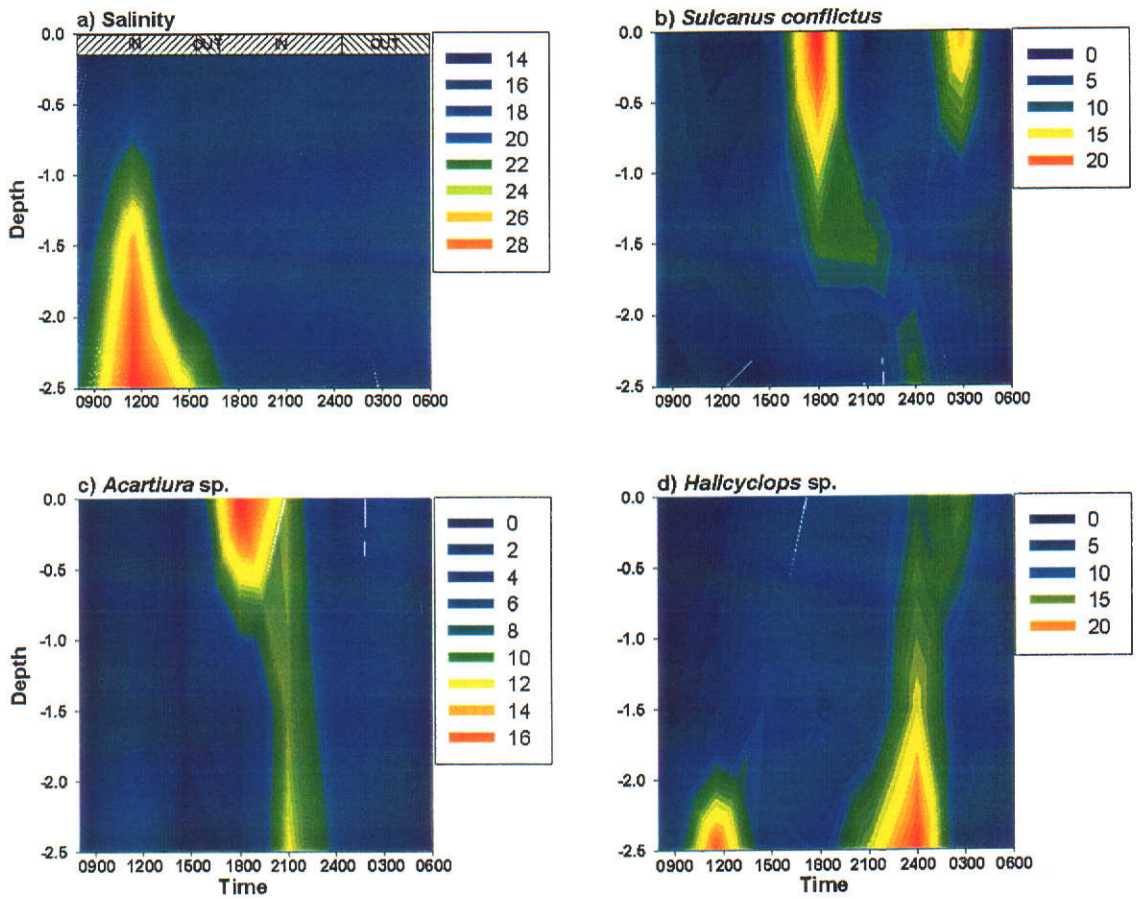

Figure 2.14: Diurnal distribution of zooplankton at Narrows, 12-13th November, 1996.
Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)* to *d)*.

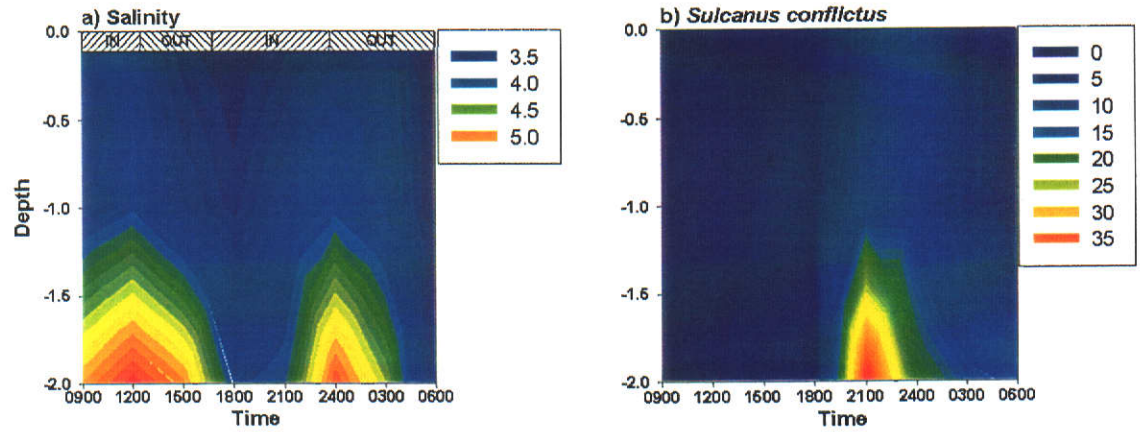

Figure 2.15: Diurnal distribution of zooplankton at Maylands, 21-22nd November, 1996.
Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)*.

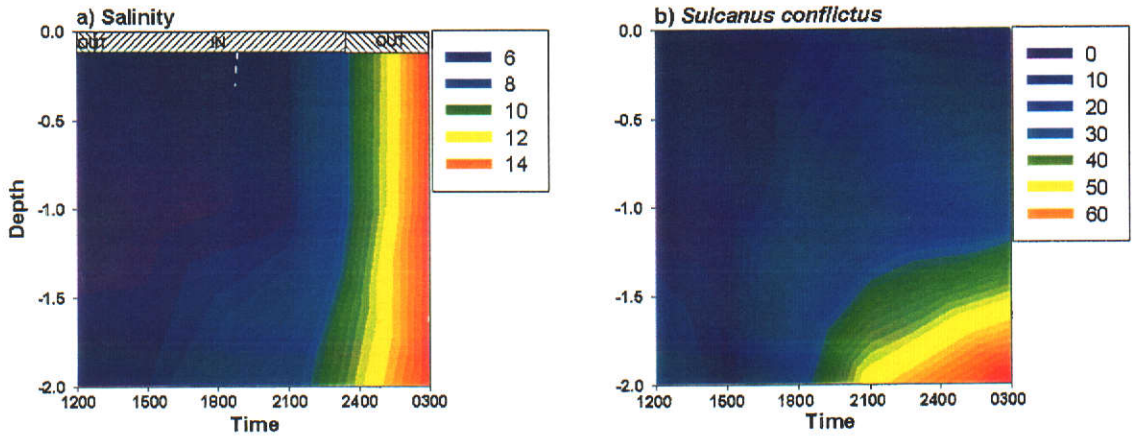

Figure 2.16: Diurnal distribution of zooplankton at Ascot, 18th December, 1996.
Tide direction indicated in *a)*. Legend refers to Salinity in *a)* and zooplankton.L^{-1} in *b)*.

It has previously been demonstrated that estuarine zooplankton exhibit behavioural patterns which maximise their retention in estuarine waters, by concentrating in comparatively slow-flowing bottom waters during ebb tides (Weinstein *et al.*, 1980; Hill, 1991; Schlacher and Wooldridge 1995). In the Swan River estuary, higher velocity tidal currents occur during the flood tide, not the ebb tide (Pattiaratchi and Burling, 1998) and horizontal displacement of copepods would be greater on the flood tide. *S. conflictus* may use this phenomenon to maintain its position in moderate salinity water. It was located in the bottom waters on incoming tides and in the surface waters on outgoing tides. This distribution also coincided with the water salinity most suited to this species' survival (Rippingale and Hodgkin, 1977).

G. imparipes was located on two occasions and also occurred in the bottom waters (Figures 2.10 and 2.11). *G. imparipes* has been shown to move upriver ahead of *S. conflictus* and persist beyond the range of that potential predator of its nauplii (Rippingale and Hodgkin, 1977). This was demonstrated in the present study on one occasion (Figure 2.11). The other time *G. imparipes* was located, it occurred in the same water mass as *S. conflictus* but had an abundance five times greater (Figure 2.10).

Larvae of *X. securis* were located throughout the water column irrespective of time of day or tidal stage when water salinity was low (Figures 2.10 and 2.11) and were confined to lower salinity water when water salinity was high and a halocline was present (Figure 2.13). The rotifers *B. plicatilis* and *Synchaeta* sp. occurred together, when they were both present. They occurred in the surface waters on three occasions on outgoing tides (Figures 2.10, 2.11 and 2.13) and *Synchaeta* sp. was dispersed throughout the water column on one occasion (Figure 2.12), when the tides were unusual in that the water level did not decrease during the outgoing tide, but remained stationary (Table 2.1). Copepod nauplii also were

dispersed throughout the water column at this time, whereas they were only found in surface waters at other times (Figures 2.10, 2.11 and 2.12).

Schlacher and Wooldridge (1995) noted that variation in zooplankton dispersion and density are increased in tidal estuaries and this appears to be the case in the Swan River estuary, despite the low amplitude (mean 0.4 m) and low velocity tides (Pattiaratchi and Burling, 1998). The results of the present study illustrate the variability in zooplankton migratory behaviour under varied environmental conditions (Haney, 1988).

Note: For copyright reasons the following paper in Chapter 2 (pg. 28-55) has not been reproduced in full.

Temporal variation in the distribution and relative abundance of estuarine copepods in the Swan River estuary, Western Australia.

Manuscript submitted to the Journal of the Royal Society of Western Australia

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)

Chapter 3 - Zooplankton Grazing

General Introduction

Phytoplankton growth in the Swan-Canning Estuary is thought to be initiated by nutrients that enter the estuary during winter run-off and develops during spring, when fluvial flow ceases, water temperature rises and photoperiod increases. Phytoplankton biomass subsequently declines as nutrient levels become depleted (John, 1987; Thompson and Hosja, 1996). However, there is increasing evidence to suggest that zooplankton grazers have the potential to play an important role in the reduction of phytoplankton biomass (Griffiths and Caperon, 1979; Stearns *et al.*, 1987; Svensson and Stenson, 1991; Cyr and Pace, 1992).

The potential for herbivorous grazers to remove phytoplankton biomass, is thought to be dependent on the density and size of the herbivores (Martin, 1970; Gamble, 1978; Lampert and Taylor, 1985; Vanni, 1987; Turner and Granéli, 1992), diel variation in feeding rates (Gauld, 1953; McAllister, 1971; Mackas and Bohrer, 1976; Lampert and Taylor, 1985; Peterson *et al.*, 1990a) and phytoplankton abundance (Mullin and Brooks, 1970; Frost, 1972; Reeve and Walter, 1977; Ambler, 1986; Durbin and Durbin, 1992).

There is continuing debate as to the importance of 'top-down' control of algal blooms through grazing (Harris, 1986; Peters, 1991; DeMelo *et al.*, 1992; Boon *et al.*, 1994). However, there is a paucity of studies on the detrimental effect of certain phytoplankton species on grazer survival and fecundity. Similarly, the effect of phytoplankton on water column characteristics (physical and chemical) during periods of peak productivity may be detrimental to the survival of zooplankton. If unsuitable phytoplankton species occur more frequently or if phytoplankton productivity increases, the distribution and abundance of zooplankton grazers may be affected (Sommer, 1989).

The grazing component of this research examined the factors influencing zooplankton grazing, in particular, by copepods, and the ability of zooplankton to reduce phytoplankton biomass. The aims of the grazing component were:

1. to investigate zooplankton community grazing under differing phytoplankton bloom conditions;
2. to investigate diurnal feeding behaviour of copepods;
3. to determine maximum ingestion rates for copepods feeding on different phytoplankton species under laboratory conditions; and
4. to determine which component of the zooplankton contributes most to top-down control of phytoplankton.

The data generated was used in the three dimensional computer model (CAEDYM) to provide insights into the role of zooplankton grazers in relation to each other, phytoplankton and hydrological processes. An integrated assessment of these processes provides a sound framework for formulation of future management strategies for the estuary.

The following sections review the methods used for measuring zooplankton ingestion rates in the present study and the results obtained. The Chapter concludes with two published articles on *in situ* top-down control of phytoplankton and using CAEDYM to determine which component of the zooplankton contributes most to reduction in phytoplankton biomass.

Methods for Measurement of Zooplankton Grazing

Two methods were chosen for measuring zooplankton grazing rate. In one method, grazing rate was calculated by measuring the loss of chlorophyll from incubation chambers over time (Gifford and Dagg, 1988) using the equations of Frost (1972). This technique was used in the field and the laboratory. In the second method, grazing rate was measured using the gut fluorescence technique, which measures chlorophyll in the gut of individuals. Both techniques have their advantages and disadvantages.

One advantage of conducting field-based experiments is that natural assemblages of zooplankton and phytoplankton are used. Grazing rates of zooplankton have been measured using a variety of techniques, both *in situ* and in the laboratory (reviewed in Marshall, 1973; Griffiths and Caperon, 1979; Huntley, 1988). Despite all efforts to obtain predictable and repeatable measures of grazing rates and despite over 50 years of experimentation, researchers still obtain results varying in orders of magnitude. Huntley (1988) asserts that our fundamental thinking towards measurement of grazing rates has a flaw, in that rates are measured without any thought to feeding history or after an arbitrary period of preconditioning. This assertion is supported by experimental evidence that zooplankton preconditioned on a certain food type will select that food type when given a choice of foods (Cowles *et al.*, 1988; Schoeneck *et al.*, 1990; Head and Harris, 1994). Therefore, it would seem that the feeding history of the grazer is of primary importance when measuring the rate at which they remove a given food type.

A disadvantage of the field experiments conducted was that they did not allow measurement of ingestion rates for individual taxa, but provided estimates for size classes of zooplankton. This flaw was addressed by conducting further experiments under controlled laboratory conditions and measurement of ingestion rate for individual taxa. Each technique is discussed further in the following sections.

All measurements of ingestion rate used the fluorescent pigment, chlorophyll *a*, as an indicator of feeding. It is acknowledged that there are problems with the use of chlorophyll *a* (*e.g.* Shuman and Lorenzen, 1975; Riemann, 1978; Gieskes and Kraay, 1983; Baars and Helling, 1985; Carpenter and Bergquist, 1985; Trees *et al.*, 1985; Conover *et al.*, 1986; Jeffrey and Hallegraeff, 1987; Penry and Frost, 1990; Gieskes *et al.*, 1991; Head and Harris, 1992; 1996), mainly through the degradation of chlorophyll to non-fluorescing compounds. Despite this, the use of chlorophyll *a* as an indicator of zooplankton grazing is widely reported in the literature and recommended as an appropriate method in standard texts (*e.g.* Downing and Rigler, 1984; American Public Health Association, 1995; Wetzel and Likens, 1995). In the present study, which was one of several investigations into ecology of the Swan River estuary, it was important to ensure that data collected was comparable to data collected in other studies on the Swan River estuary. All other studies used chlorophyll *a* as an indicator of phytoplankton biomass.

Estimation of Gut Clearance Rate in *Sulcanus conflictus*

Introduction

The measurement of copepod gut fluorescence has emerged as a suitable technique for measuring *in situ* ingestion rates and provides results comparable to other methods (Mann *et al.*, 1984; Baars and Helling, 1985; Kiørboe *et al.*, 1985; Peterson *et al.*, 1990b; Quiblier-Lloberas *et al.*, 1996). The advantages of this technique are many: (i) it avoids handling and confinement of copepods, thereby avoiding artefacts associated with experimental conditions; (ii) it is useful for investigating diurnal feeding rhythms in copepods; (iii) it can be used to estimate ingestion rates over short time periods; and (iv) it allows estimation of ingestion rates of natural densities and mixtures of copepods feeding on natural mixtures of algal species. However, the technique does not provide information on food selectivity and there have been methodological problems associated with the degradation of pigments to non-fluorescing compounds (Baars and Helling, 1985; Durbin *et al.*, 1990; Head and Harris, 1996; Quiblier-Lloberas *et al.*, 1996) and estimation of gut clearance rate (Baars and Helling, 1985; Tsuda and Nemoto, 1987; Dam and Peterson, 1988; Peterson *et al.*, 1990b).

Gut passage time refers to the time taken for the remains of ingested particles to be egested by the copepod and is calculated as the inverse of the gut clearance rate constant, k (Mackas and Bohrer, 1976). Copepod ingestion rate is estimated from the product of gut fluorescence and the gut clearance rate constant (*e.g.* Mackas and Bohrer, 1976; Bautista and Harris, 1992; Sautour *et al.*, 1996). Therefore, gut clearance rate is an integral part of using gut fluorescence as an indicator of copepod feeding and as such, must be determined with accuracy (Kiørboe and Tiselius, 1987). Inaccurate measurement of gut clearance rate may result in underestimation of copepod ingestion rates (Kiørboe *et al.*, 1985; Kiørboe and Tiselius, 1987; Tsuda and Nemoto, 1987; Peterson *et al.*, 1990b).

Gut clearance rate is commonly estimated by periodic measurement of gut fluorescence of either freshly collected or pre-fed copepods for an hour or more after placement in filtered water (*e.g.* Mackas and Bohrer, 1976; Dagg and Wyman, 1983; Peterson *et al.*, 1990b; Bautista and Harris, 1992; Sautour, *et al.*, 1996). This method makes the assumption that gut clearance rate remains the same independent of whether the experimental animals are feeding or not (Mann *et al.*, 1984; Penry and Frost, 1990; Atkinson *et al.*, 1996). Kiørboe and Tiselius (1987) suggested that the difference in gut clearance rate between feeding and non-feeding copepods is negligible when only the first 30 minutes of the incubation is considered. This prompted the general recommendation by Baars and Helling (1985) and Durbin *et al.* (1990) that only values of gut fluorescence which fall on a straight line when plotted on a semi-logarithmic scale be included for estimation of *k*. This is generally seen to occur within the first 30 to 60 minutes of gut clearance rate incubations (*e.g.* Kiørboe and Tiselius, 1987; Dam and Peterson, 1988; Uye and Yamamoto, 1995). However, many authors have suggested that this assumption may be invalid and that the effect of feeding on gut clearance rate should be investigated (*e.g.* Mann *et al.*, 1984; Baars and Helling, 1985; Dam and Peterson, 1988; Penry and Frost, 1990; Peterson *et al.*, 1990b).

Gut clearance rate has been shown to be a temperature-dependent process, with most authors reporting positive linear relationships (Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Dam and Peterson 1988; Durbin *et al.*, 1990; Uye and Yamamoto, 1995). These studies have reported Q_{10} values ranging between 1.5 and 5.4, but all were carried out at temperatures at or below 20°C. In shallow temperate estuaries, water temperature can often exceed 25°C. Few studies have measured gut clearance rate under these conditions. Irigoien and Castel (1995) and Irigoien *et al.* (1996) made direct measurements of gut clearance rate at 22 and 26°C, but most authors have relied on published regression equations, such as that produced by Dam and Peterson (1988).

The feeding mode and food preference of *Sulcanus conflictus* are unusual among copepods (Rippingale, 1981). It has been hypothesised that *S. conflictus* evolved as a predominately predatory copepod, with elaborate prey-detection structures on the first antennae and anterior mouth-parts, which are most similar to those seen in obligate predators (Rippingale, 1981). However, the structure of the second maxilla and maxilliped is unlike that seen in either predatory or herbivorous copepods and they have been observed to work together to form an elaborate filtering basket. This feature enables *S. conflictus* to exhibit both predatory and herbivorous feeding modes. In a series of laboratory experiments, Rippingale (1981) determined that *S. conflictus* is able to clear water of particles (ranging in size from 6 to 25 μm) at similar rates as other copepods of similar body size, but that in the presence of animal prey, its algal clearance rate was depressed. In the context of the present study, it is unknown whether trophic features of this species, such as having a feeding anatomy

strongly adapted for predation and secondarily suited for filtration, will result in gut clearance rates, which differ from those of other copepod groups.

This study was designed to investigate a) whether gut clearance rate was similar for *S. conflictus* with continuous access to food (feeding) and *S. conflictus* which had previously been feeding but subsequently were denied access to food (non-feeding) and b) the effect of temperature on the gut clearance rate constant. As an ancillary, this study sought to determine whether the gut fluorescence technique could be reliably used for copepod species, such as *S. conflictus*, which can be difficult to maintain under laboratory conditions.

Methods

S. conflictus samples were collected from the Swan River estuary in water with a salinity range of 22.9 to 31.5 and a temperature range of 16.9 to 17.6°C, on the 28th of May, 1996. The specimens were taken to the laboratory, maintained at constant temperature (18 and 25°C) for three days in water of salinity 20 and fed a mixture of the unicellular alga *Dunaliella tertiolecta*, *Nanochloropsis* sp. and *Isochrysis galbana*. The algal cultures had been maintained in the laboratory on Guillard's f/2 medium (Guillard, 1975).

Actively feeding copepods (visible evidence of gut fullness) were removed from their food source and rinsed three times with 1.2 μm filtered water of the same salinity and temperature. This was achieved quickly (in less than one minute) by transferring the copepods to successive water baths using a Nitex ® screen of pore size 300 μm.

Three samples of rinsed copepods were snap frozen with dry ice for initial gut fluorescence measurement (mean=20 copepods, range=7-40). Remaining copepods were then transferred to either 1.2 μm filtered water of salinity 20 (non-feeding) or 1.2 μm filtered water of salinity 20 with actively growing yeast cells added (feeding). Replicate copepod samples (n=3) were removed from the experimental containers at 20 minute intervals for the first hour and then at hourly intervals (t = 0, 20, 40, 60, 120, 240, 300 minutes). All samples were snap frozen with dry ice, and used to show changes in copepod gut fluorescence at different time periods.

The yeast culture was prepared by combining 7 g of dry baker's yeast with 2 g of glucose and one litre of water of salinity 20 and maintained, with aeration, at 18 and 25°C. The yeast cells were examined at 100 times magnification with a compound microscope to ensure they were actively growing and to obtain cell counts using a Sedgewick Rafter Chamber (estimated to be >100,000 cells.mL^{-1}). The copepod culture and filtered water were maintained at the experimental temperatures of 18 and 25°C prior to each experiment. All

experimental containers were softly aerated, to prevent the yeast cells from settling out (feeding copepods) and to ensure uniformity of method (non-feeding copepods).

Frozen copepod samples were examined in chilled saline water, with a binocular microscope fitted with a cool white light. Inspection of individual copepods from the yeast mixture revealed the presence of yeast cells in the gut, so it was assumed that feeding was occurring. Individual intact copepods were removed and placed into a vial with 5 mL of 90% acetone (v/v). The vials were sealed and sonicated for 20 minutes in iced water and then allowed to sit for 24 hrs at 4°C to allow chlorophyll extraction to occur (Thompson and Hosja, 1996; Griffin and Rippingale, 2001). After 24 hours, the vials were centrifuged and the supernatant analysed for concentration of chlorophyll *a* and phaeophytin using an Aminco Colorimeter, previously calibrated against a chlorophyll *a* standard.

Gut pigment was calculated as the sum of chlorophyll *a* and phaeopigment (Dam and Peterson, 1988) and expressed as ng pigment.copepod^{-1}. The extent of pigment degradation to non-fluorescent compounds was not assessed, so pigment values were multiplied by 1.5 to allow for the range of losses most commonly reported (Kiørboe and Tiselius, 1987; Dam and Peterson, 1988). Decline in gut fluorescence over time approximated an exponential decay model, so gut clearance rate constant (k) was calculated for each time period according to:

$$G_t = G_o.e^{-kt} \quad (1)$$

where G_t represents gut pigment after time t and G_o is the initial gut pigment. Gut pigment was not corrected for background fluorescence (Baars and Helling, 1985; Durbin *et al.*, 1990).

Results

Gut pigment decreased over increasing incubation periods at both experimental temperatures and for feeding and non-feeding copepods (Figure 3.1). Feeding and non-feeding copepods had an initial gut pigment level of 0.12 ng pigment.copepod^{-1} at 18°C. At 25°C, initial gut pigment was 0.16 ng pigment.copepod^{-1}. At 18°C, gut pigment in feeding copepods was reduced to 24% of the initial gut pigment within 60 minutes, whereas it took 120 minutes for gut pigment in non-feeding copepods to reduce to 21.4% of the initial level (Figure 3.1a). At 25°C, the difference between feeding and non-feeding copepods was more pronounced; gut pigment in feeding copepods was reduced to 5.8% of the initial gut pigment within 20 minutes, whereas it took 60 minutes for gut pigment in non-feeding copepods to reduce to 4.7% of the initial level (Figure 3.1b).

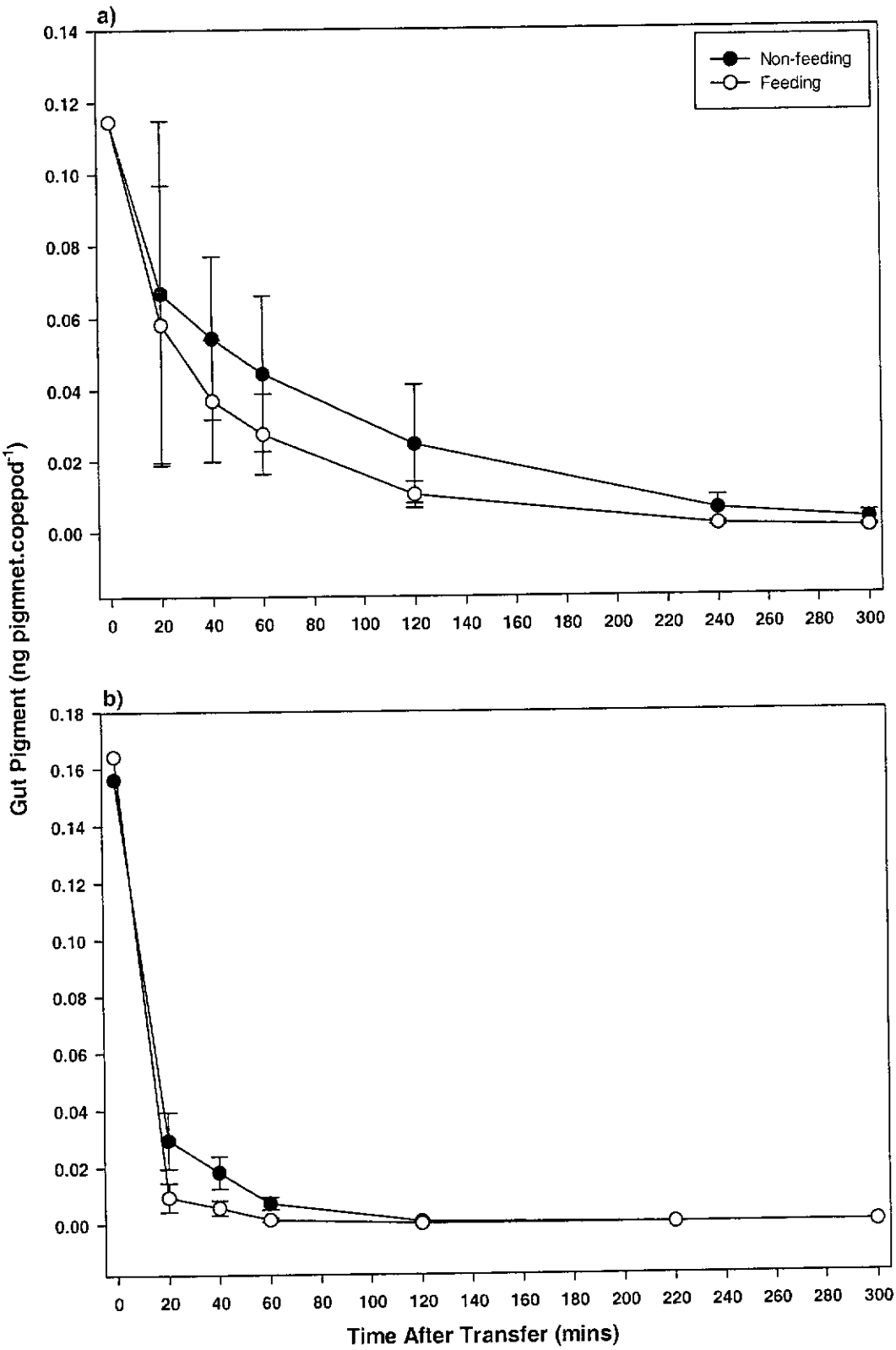

Figure 3.1: *S. conflictus* gut pigment content over time, at a) 18 and b) 25°C.

Bars represent one standard error, n = 3 samples of copepods, except for initial measurement where n=1.

Gut clearance rate constant (k) declined over increasing time periods, representing an increase in gut passage time over the same periods (Table 3.1). Gut clearance rate was greatest for the first 20 minute interval (Table 3.1) and was consistently higher for feeding than for non-feeding copepods. It was also consistently higher at 25°C than at 18°C. A semi-logarithmic plot of gut fluorescence over time showed that the best linear relationship was seen after 40 minutes, for each temperature and feeding and non-feeding copepods (at 18°C, r^2 = 0.94 and 0.90 respectively and at 25°C, r^2 = 0.77 and 0.81 respectively). Therefore, the most accurate value of k was assumed to be that calculated over the first 40 minutes.

Table 3.1. The effect of temperature and feeding on gut clearance rate constant (k) and gut passage time (GPT) for *S. conflictus*, calculated over increasing time periods.

Temperature	Time	Feeding		Non-feeding	
		k	GPT	k	GPT
(°C)	(min)	(min^{-1})	(min)	(min^{-1})	(min)
18	20	0.034	29.6	0.027	37.1
18	40	0.028	35.3	0.019	53.7
18	60	0.024	42.1	0.016	63.3
18	120	0.020	49.6	0.013	77.5
18	240	0.018	55.5	0.012	80.9
18	300	0.017	59.2	0.012	87.1
25	20	0.142	7.0	0.083	12.0
25	40	0.084	11.9	0.054	18.6
25	60	0.079	12.7	0.051	19.6
25	120	0.074	13.6	0.044	22.5
25	240	0.070	14.4	0.042	23.5
25	300	0.066	15.2	0.038	26.5

A linear regression of temperature (T) against k (calculated over 40 minutes, using three measurements at each temperature) gave the following relationships for feeding (2) and non-feeding (3) copepods:

$$k = -0.1142 + 0.0079T \quad (2)$$

$$k = -0.0717 + 0.0050T \quad (3)$$

The regression equations above were plotted with published temperature-k regressions (Kiørboe *et al.*, 1982; Dagg and Wyman, 1983; Dam and Peterson, 1988; Durbin *et al.*, 1990; Irigoien and Castel, 1995; Uye and Yamamoto, 1995; Irigoien *et al.*, 1996) (Figure 3.2). The regression from this study sits within the range reported in the literature.

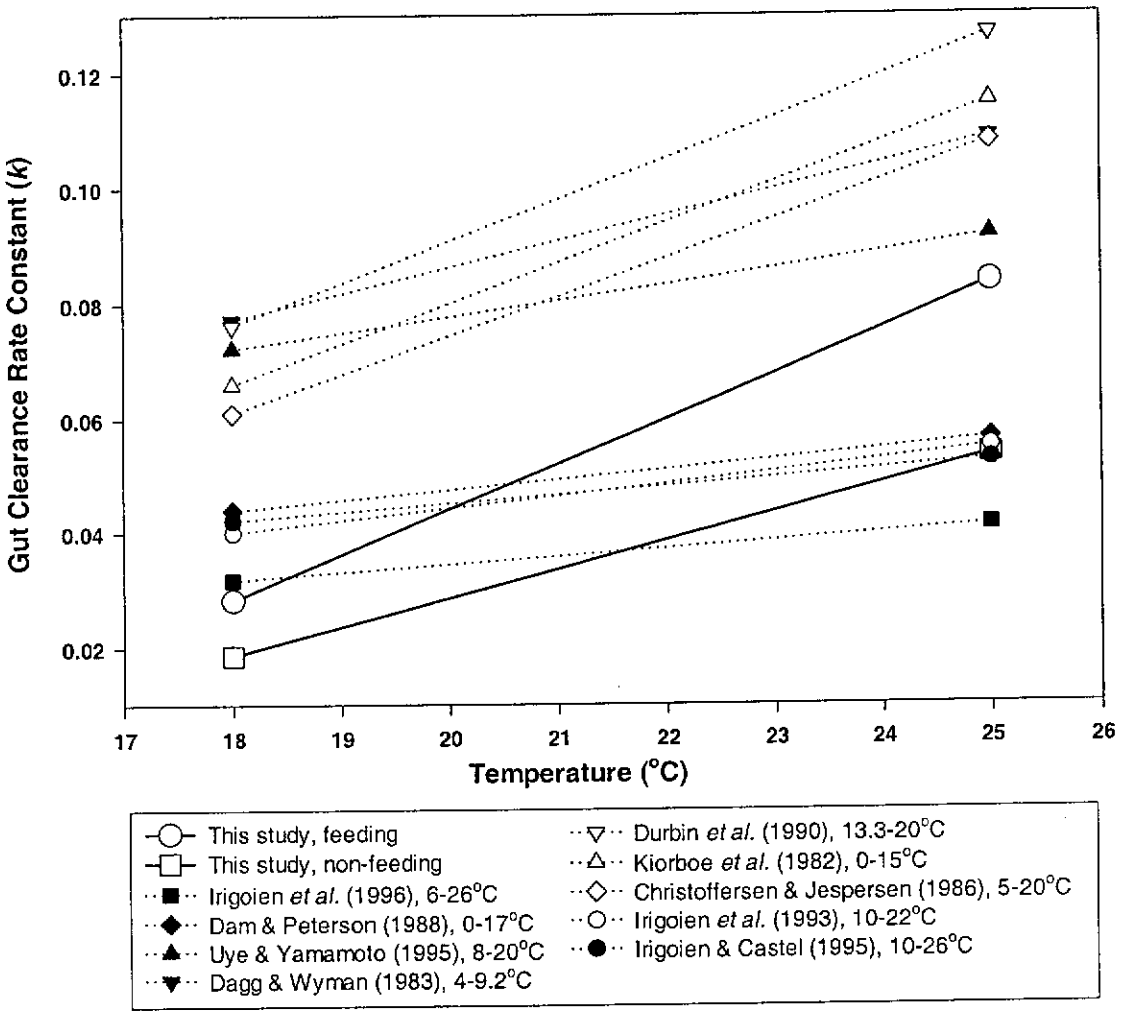

Figure 3.2: Comparison of relationship between temperature (*T*) and gut clearance rate constant (*k*) for copepods in this study with relationships reported in the literature.

Discussion

It has been suggested that the gut clearance rate of feeding and non-feeding copepods should be similar during the initial 30 or so minutes of measurements of copepod gut fluorescence (Baars and Helling, 1985; Durbin *et al.*, 1990). It is during this initial period that copepod gut fluorescence falls on a straight line when plotted on a semi-logarithmic scale (Kiørboe and Tiselius, 1987). In contrast, the results of the present study showed a consistent difference between the value of *k* for feeding and non-feeding copepods, over all periods of measurement and for both temperatures (Table 3.1). At 18°C, average gut clearance rate (calculated over increasing time periods) was 1.5 times higher for feeding copepods than for non-feeding copepods. The difference was more pronounced at 25°C, with gut clearance rate, on average, 1.7 times higher for feeding copepods. These results indicate that copepod gut clearance rate is reduced when food is limited or not available and

support the generally positive relationship seen between ingestion rate and food concentration (*e.g.* Mullin, 1963; McAllister, 1971; Frost 1972; Mullin *et al.*, 1975; Ianora *et al.*, 1995). These results also provide some support for the frequently expressed concern (Baars and Oosterhuis, 1984; Mann *et al.*, 1984; Baars and Helling, 1985; Tsuda and Nemoto, 1987; Dam and Peterson, 1988; Durbin *et al.*, 1990; Peterson *et al.*, 1990a; 1990b; Atkinson *et al.*, 1996) that gut clearance rate (measured in the absence of food) may not provide an accurate estimation of gut passage time (measured in the presence of food).

The gut clearance rate constant decreased over increasing incubation periods for both feeding and non-feeding copepods. This pattern is commonly observed for non-feeding copepods (*e.g.* Baars and Oosterhuis, 1984; Kiørboe and Tiselius, 1987; Dam and Peterson, 1988; Arinardi *et al.*, 1990; Uye and Yamamoto, 1995). Baars and Helling (1985) suggest this decline in k over time reflects a decrease in pellet size as the copepods become more food limited and that this pattern would not be seen in continuously feeding copepods. Presumably, the gut of continuously feeding copepods would be stimulated by food and k would be affected by gut fullness and remain relatively constant. However, feeding copepods in the present study also exhibited a decline in k with increasing period over which it is calculated. In this case, the decline in k does not represent a reduction in pellet size or egestion frequency, but rather the time it takes to completely rid the gut of pigmented food and replace it with non-pigmented food.

It is unlikely that the decline in k over time in feeding copepods was because they became food limited. Although fresh food (yeast cells) was not added to the incubation containers during the experiments and so declining food availability may have limited ingestion rate, the initial yeast culture was dense (>100,000 cells.mL^{-1}) and thus it was assumed that sufficient food particles were available for the entire experimental period. Similarly, ingestion rate is unlikely to have been limited by a change to a different food type, as reported by Christofferson and Jespersen (1986), as the yeast cells were of comparable size (10 μm diameter) to the algae species on which the copepods were maintained in the laboratory (6 to 24 μm diameter) and *S. conflictus* has been shown to feed on particles ranging from 6 to 25 μm in size (Rippingale, 1981). In the present experiments it was assumed that yeast cells would be filtered out of the water because of the density of the culture, the suitable size of yeast cells and the feeding behaviour of *S. conflictus*. This species does not create a steady feeding current through the action of its mouth-parts, but rather it seems to sweep the water with a basket formed by the second maxilla and maxilliped, while its swimming legs propel it through the water. Therefore, normal swimming activity by the copepods would result in the ingestion of yeast cells, whether it be through "accidental" or "active" uptake.

If gut clearance rate in non-feeding copepods is a response to peristaltic movement of the gut (Peterson *et al.*, 1990a; 1990b) rather than gut fullness (Baars and Helling, 1985), it is

plausible that the value of *k* after an extended time period may represent a basal rate of gut activity, which would not be detected in feeding copepods. Approximately 80% of the gut pigment was lost from non-feeding copepods at 18°C within two hours. A further three hours of incubation resulted in only a further 7% loss (Figure 3.1a). At 25°C a similar pattern was seen, but it occurred over a shorter time period. Here, approximately 90% of the initial gut pigment of non-feeding copepods was lost within 40 minutes and a further 80 minutes of incubation resulted in only an extra 5.2% loss (Figure 3.1b). Examination of faecal pellets may lend support to the notion of a basal level of gut activity. If this were the case, copepods incubated at the higher temperature would have produced "empty "pellets after two hours. Faecal pellets were not examined in the present study. Alternatively, the gut pigment remaining after three hours may simply represent background fluorescence, which was not measured in this study.

The gut clearance rates for feeding and non-feeding copepods at 18°C (k = 0.030 and 0.023, respectively) are at the bottom of the range reported in the literature, whereas at 25°C (k = 0.114 and 0.068, respectively) k is very close to other studies conducted at similar temperatures (refer to Figure 3.2).

Figure 3.2 shows two distinct bands of temperature-k regressions. The upper band represents those studies carried out at a lower range of temperatures (0-20°C) and the lower band reflects those studies carried out at a higher range of temperatures (6-26°C) (refer to the legend in Figure 3.2). The central regression is that of Dam and Peterson (1988), which was conducted at temperatures ranging from 0-17°C. The regressions from this study are closest to those studies that included temperatures at or above 20°C. However, the results shown in Figure 3.2 are for a range of copepod species and various methods of estimating the gut clearance rate constant (*e.g.* from pellet production rates, continuously feeding, not feeding, variable time periods for estimation of k). Therefore, some variability between studies can be expected and it is difficult to compare *S. conflictus,* with its unusual feeding mode, to other copepod species.

In summary, the present study has provided direct evidence of an elevated gut clearance rate constant in continuously feeding copepods, compared to previously fed but subsequently non-feeding copepods. Therefore, this technique may not be suitable for use *in situ* under conditions of limited food availability, as it has the potential to underestimate grazing rate. Gut clearance rate was not constant over time for either feeding or non-feeding copepods and it is suggested that, when measured after three hours, the gut clearance rate in non-feeding copepods may represent either a basal rate of gut activity, or simply unmeasured background fluorescence. Further, the positive linear relationship between gut clearance rate constant and temperature supported previous findings in the literature.

Laboratory Measurement of Zooplankton Ingestion Rates

Introduction

There are few published studies on the ingestion rates of zooplankton occurring in the Swan River estuary, Western Australia. Bhuiyan (1966) investigated *Sulcanus conflictus* ingestion of centric diatoms and Rippingale (1981) investigated *Sulcanus conflictus* ingestion of rotifers, copepod nauplii and naturally occurring phytoplankton assemblages. The suitability of different algal species for culture of *Gladioferens imparipes* has been extensively studied (Payne and Rippingale, 2000), but this study did not focus on bloom-forming algal species of the Swan River estuary. Rippingale (1981) found that *S. conflictus* has the potential to clear the entire water column of algal particles (6 to 25 µm in size) in 24 hours at field densities, is an efficient predator of copepod nauplii and ingestion of algal particles is reduced in the presence of copepod nauplii. More recent *in situ* measurements of zooplankton community ingestion rates (Griffin *et al.*, 2001; Griffin and Rippingale, 2001) have indicated that zooplankton communities have variable ingestion rates according to algal species and grazer type and density. How these *in situ* ingestion rates compare to laboratory measurements on the same algal species has not previously been examined for zooplankton in the Swan River estuary.

The measurement of zooplankton ingestion rates in the laboratory has advantages over *in situ* measurements. In the laboratory, factors such as food concentration, feeding history, water temperature and salinity and grazer type and density can be manipulated and the maximum grazing rate and half saturation constant can be estimated. Maximum ingestion and half saturation rates are useful tools for comparing the response of different zooplankton species to different concentrations of food. These may vary considerably between food and grazer types. As such, it is possible to use laboratory measured ingestion rates to determine whether *in situ* zooplankton populations are grazing to their maximum capacity and whether they are food limited.

The effect of food concentration has been well researched and it has been shown that a maximum ingestion rate can be achieved, at which time, there is no further increase in ingestion rate if food concentration is further increased (Frost, 1972). The influence of incubation period on the estimation of ingestion rates is variable and may alter according to the grazer and food type, as well as other factors such as nutrient limitation. Nutrient limitation may be particularly important for field experiments, but in laboratory experiments, using nutrient rich phytoplankton cultures, it is not expected to be an issue.

This study describes laboratory measurements of ingestion rate of zooplankton feeding on phytoplankton species commonly found to occur in the Swan River estuary. In particular, the response of copepod, rotifer and bivalve larvae ingestion rates to varying food

concentrations, temperatures and incubation periods was monitored with a view to determining maximum ingestion and half saturation rates and to examine how these rates compare to previous measurements of *in situ* ingestion rates.

Methods

Plankton collection and maintenance

Zooplankton used in this study were obtained from the Swan River estuary (the rotifer *Brachionus plicatilis* and planktonic larvae of the bivalve *Xenostrobus securis*) and established laboratory cultures (the calanoid copepod *Gladioferens imparipes*) and were maintained on a diet of the prymnesiophyte *Isochrysis galbana*, at room temperature (20 to 25°C). Twenty four hours prior to each experiment, the grazers were removed from their food source and maintained in 0.2 µm filtered water of the appropriate experimental salinity and temperature.

Phytoplankton cultures were obtained from the Commonwealth Scientific and Industrial Research Organization (CSIRO) Microalgae Culture Collection, Hobart, Australia (*Scrippsiella* sp., *Prorocentrum lima*, *Skeletonema costatum*, *Dunaliella tertiolecta*, *Cryptomonas* sp.), or isolated from algal blooms in the Swan River estuary (*Gyrodinium* sp., *Chlamydomonas* sp.). Phytoflagellate and diatom cultures were maintained in the laboratory on Guillard's f/2 culture medium (Guillard, 1975) with silicon being added to the diatom cultures and dinoflagellate cultures were maintained on GSe culture medium (Loeblich and Smith, 1968). All cultures were maintained at room temperature (20-25°C) with constant aeration and a 12 hour light-dark cycle.

Measurement of zooplankton ingestion rates

Zooplankton ingestion rates were measured using the technique and equations of Frost (1972), modified for chlorophyll *a* instead of cell counts. Chlorophyll *a* was measured fluorometrically against chlorophyll *a* standards, after sonification and subsequent extraction in 90% v/v acetone for 24 hours in the dark at 4°C.

Experimental treatments

The range of experimental treatments (food type and concentration, temperature, incubation period and grazer type) used in this study is outlined in Table 3.2. Each experiment used 500 mL food-quality plastic containers for experimental containers, which were rotated at 0.1 $m.s^{-1}$ on a vertical plankton wheel. Grazers were transferred to experimental containers, which were then filled to the brim with the experimental food cultures. Replicate experimental containers and controls were incubated on the plankton wheel for 3, 6, 12 or 24 hours in darkness (Table 4.5). At the end of each incubation period, grazers were removed

from the sample using a 44 μm Nitex® screen and the remaining food mixture was filtered onto glass fibre filter papers (nominal pore size of 1.2 μm) for chlorophyll *a* analysis. A series of preliminary trials were undertaken to determine the loss of chlorophyll *a* incurred by the screening process (<1% total chlorophyll *a*, Griffin, unpublished data).

Data Analysis

The data were tested for differences between mean ranks of ingestion rate using Kruskal Wallace two way and one way ANOVAs for non-normal data (Zar, 1984). Data were pooled when the results of analyses indicated no significant difference between ingestion rate for different treatments, to allow further significance testing for the effect of algal species and temperature.

Table 3.2: Laboratory grazing experiments.

#	Grazer Type	Life Cycle Stage	Algal Species	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Incubation Period (hrs)	Temperature (^{o}C)	Salinity
1	*G. imparipes*	Adult & nauplii	*Scrippsiella* sp.	2.7, 5.8, 10.2	12	15	27
2	*G. imparipes*	Adult & nauplii	*Scrippsiella* sp.	10.6, 22.4	12	20	27
3	*G. imparipes*	Adult & nauplii	*P. lima*	2.4, 5.3, 8.9	12	15	27
4	*G. imparipes*	Adult	*P. lima*	19.6, 26.4	12	20	27
5	*G. imparipes*	Adult	*Gyrodinium* sp.	4.0, 10.7	12, 24	25	10
6	*G. imparipes*	Adult & nauplii	*S. costatum*	1.4, 2.7, 3.6	12	15	27
7	*G. imparipes*	Adult & nauplii	*S. costatum*	6.2, 12.0, 23.2	12	20	27
8	*G. imparipes*	Adult	*S. costatum*	14.7, 22.0, 37.4	12	20	27
	B. plicatilis						
9	*G. imparipes*	Adult	*S. costatum*	36.0, 61.4	12, 24	25	27
10	*G. imparipes*	Adult	*S. costatum*	36.0, 61.4	12	25	27
	X. securis	Planktonic larvae					
11	*G. imparipes*	Adult & nauplii	*D. tertiolecta*	114.2, 250.6, 437.9	12	15	27
12	*G. imparipes*	Adult & nauplii	*D. tertiolecta*	117.3, 210.0, 437.0	12	20	27
13	*G. imparipes*	Adult	*D. tertiolecta*	159.5, 300.4, 598.1	12	20	27
	B. plicatilis						
14	*G. imparipes*	Adult	*D. tertiolecta*	34.0, 116.1, 154.9	12	25	27
15	*G. imparipes*	Adult	*D. tertiolecta*	116.1, 154.9	12, 24	25	27

Table 3.2: Laboratory grazing experiments, *continued.*

#	Grazer Type	Life Cycle Stage	Algal Species	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Incubation Period (hrs)	Temperature (°C)	Salinity
16	*G. imparipes* *B. plicatilis*	Adult	*Cryptomonas* sp.	64.1, 130.8, 243.0	12	20	27
17	*G. imparipes*	Adult	*Cryptomonas* sp.	42.1, 86.8, 178.9	12	25	27
18	*G. imparipes*	Adult	*Cryptomonas* sp.	86.8, 178.9	12, 24	25	27
19	*G. imparipes*	Adult	*Chlamydomonas* sp.	32.0, 54.1, 66.8	12	20	5
20	*G. imparipes*	Adult	*Chlamydomonas* sp.	55.4, 88.1, 106.8	12	25	5
21	*G. imparipes*	Adult	*Chlamydomonas* sp.	88.1, 106.8	12, 24	25	5

Results

Appendix 2 summarises the results of significance testing for the various treatments applied for each experiment. Overall, the length of time over which the grazing experiments were performed (12 hour or 24 hour) did not significantly affect ingestion rate for any grazer, food type or temperature.

Experiments testing for differences between ingestion rate between *G. imparipes* nauplii and adults showed that adult ingestion rate was significantly higher than that of nauplii on two occasions; experiment 1 when the dinoflagellate, *Scrippsiella* sp., was used as a food at a temperature of 15°C and experiment 7 when the diatom, *S. costatum,* was used as a food at a temperature of 20°C. There was no significant difference between ingestion rate of nauplii and adult *G. imparipes* during experiments 2 (*Scrippsiella* sp. at 20°C), 3 (*P. lima* at 15°C), 6 (*S. costatum* at 15°C), 11 and 12 (both *D. tertiolecta* at 15°C and 20°C, respectively).

Experiments testing for differences between ingestion rate between adult *G. imparipes* and the rotifer, *B. plicatilis* and larvae of the bivalve, *X. securis*, showed that there was no significant difference between ingestion rate of *G. imparipes* and *B. plicatilis* when given *S. costatum* or *D. tertiolecta* as food at 20°C (experiments 8 and 13, respectively), but *G. imparipes* had a significantly higher ingestion rate than *B. plicatilis* when given *Cryptomonas* sp. as food at 20°C (experiment 16). *X. securis* larvae had a significantly higher ingestion rate than *G. imparipes* when given *S. costatum* as food at 25°C (experiment 10).

Table 3.3 shows the maximum recorded ingestion rate for each combination of food, temperature and grazer. Maximum average ingestion rate for adult *G. imparipes* was seen when feeding on *Scrippsiella* sp. at 20°C (0.7712 ± 1.427 µg Chl*a*.zooplankton^{-1}.h^{-1}). Maximum average ingestion rate for *G. imparipes* nauplii also occurred when feeding on *Scrippsiella* sp. at 20°C (0.2772 ± 0.731 µg Chl*a*.zooplankton^{-1}.h^{-1}). By comparison, ingestion rate was low for the other dinoflagellates tested.

Overall, ingestion rate increased with increase in temperature. The exception to this is when adult *G. imparipes* were feeding on *D. tertiolecta* and *P. lima*. In these two instances, the reverse was seen – ingestion rate decreased with increasing temperature (Table 3.3).

Table 3.3: Maximum recorded ingestion rates.

Temperature (°C)	Food Type	Grazer	Initial Chl*a* ($\mu g.L^{-1}$)	Maximum Recorded Mean Ingestion Rate (μg Chl*a*.zooplankton^{-1}.h^{-1})
15	*Scrippsiella* sp.	*G. imparipes* adults	10.2	0.0038 ± 0.001
20	*Scrippsiella* sp.	*G. imparipes* adults	10.6	0.7712 ± 1.427
15	*P. lima*	*G. imparipes* nauplii	5.3	0.0008 ± 0.004
20	*P. lima*	*G. imparipes* adults	26.4	0.0003 ± 0.000
25	*Gyrodinium* sp.	*G. imparipes* adults	10.7	0.0011 ± 0.000
15	*S. costatum*	*G. imparipes* adults	3.6	0.0006 ± 0.000
20	*S. costatum*	*G. imparipes* adults	23.2	0.0023 ± 0.001
25	*S. costatum*	*X. securis* larvae	61.4	0.0309 ± 0.001
15	*D. tertiolecta*	*G. imparipes* adults	250.6	0.0054 ± 0.004
20	*D. tertiolecta*	*G. imparipes* adults	210.0	0.0072 ± 0.010
25	*D. tertiolecta*	*G. imparipes* adults	116.1	0.0028 ± 0.001
20	*Cryptomonas* sp.	*B. plicatilis* adults	64.1	0.0040 ± 0.001
25	*Cryptomonas* sp.	*G. imparipes* adults	178.9	0.0070 ± 0.003
20	*Chlamydomonas* sp.	*G. imparipes* adults	66.8	0.0006 ± 0.000
25	*Chlamydomonas* sp.	*G. imparipes* adults	88.1	0.0017 ± 0.000

Discussion

The laboratory-based measurements of ingestion rate were undertaken to provide an estimate of maximum ingestion rate for different grazers, food types and temperatures. The experiments undertaken were limited by the availability of different algal species and grazers and, particularly, the ability to maintain microzooplankton in the laboratory. However, the results did show differences in ingestion rate between different grazers and different chlorophyll *a* concentrations and an effect of temperature. Ingestion rate increased with increase in incubation temperature for most experiments, as was expected.

Ingestion rate, when a difference was present, was higher for adult *G. imparipes* than for nauplii of the same species. Larvae of the bivalve, *X. securis*, showed a higher ingestion rate than adult *G. imparipes* when offered the diatom, *S. costatum*, as food at 25°C. The problems associated with maintaining this micro-zooplankter in the laboratory precluded further testing of this species on other algal types. There were no significant differences between adult *G. imparipes* and the rotifer, *B. plicatilis*, when offered the diatom, *S. costatum*, as food at 20°C and when offered the green alga, *D. tertiolecta*, as food at 20°C. However, adult *G. imparipes* had a higher ingestion rate than *B. plicatilis* when offered

the cryptophyte, *Cryptomonas* sp., as food at 20°C. Despite this overall difference, *B. plicatilis* had a higher ingestion rate at lower food concentrations than adult *G. imparipes.*

The measured ingestion rates were used to calculate the percentage of standing phytoplankton stock potentially able to be removed through zooplankton grazing per day, based on the density of zooplankton used in the experiments. A review of Chapter 2 shows that the natural density of microzooplankton can far exceed the densities used in the experiments. Therefore, the proportion of standing crop removed could be higher for microzooplankton.

The laboratory experiments did not often reveal a significant relationship between initial chlorophyll *a* concentration and ingestion rate. The exceptions for this were *G. imparipes* feeding on *Gyrodinium* sp. at 25°C and *S. costatum* at 15°C (for both, ingestion increased with higher initial concentrations of Chl*a*) and feeding on *Scrippsiella* sp. at 20°C (ingestion decreased with higher initial concentrations of Chl*a*). Although not detected as significant, there were several other instances where ingestion appeared to decrease as initial chlorophyll *a* concentration increased. This pattern was most conspicuous for *G. imparipes* nauplii (when feeding on *Scrippsiella* sp. at 15°C, *P. lima* at 15°C, *S. costatum* at 20°C and *D. tertiolecta* at 20°C). The same pattern was seen for adult *G. imparipes* when feeding on *S. costatum* at 25°C, *D. tertiolecta* at 15°C and 20°C and *Chlamydomonas* sp. at 25°C. Although not conclusive, this pattern may indicate that copepod ingestion is inhibited at high algal densities. *G. imparipes* is capable of feeding on cells within the size range offered (Payne and Rippingale, 2000) but little is known about the palatability of the algal species offered as food.

Note: For copyright reasons the following paper in Chapter 3 (pg. 75-90) has not been reproduced in full.

Griffin, S.L. / Rippingale, R.J. (2001). Zooplankton grazing dynamics: top-down control of phytoplankton and its relationship to an estuarine habitat. *Hydrological Processes* 15(13):2453-2464.

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)

Note: For copyright reasons the following paper in Chapter 3 (pg. 91-120) has not been reproduced in full.

Griffin, S.L., Herzfeld, M. and Hamilton, J.P.(2001). Modelling the impact of zooplankton grazing on phytoplankton biomass, during a dinoflagellate bloom in the Swan River estuary, Western Australia. *Ecological Engineering* 16: 373-394.

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)

Summary of Zooplankton Grazing

The combination of laboratory-based and field-based measurement of zooplankton ingestion rate and the use of these data in a modelling approach have provided previously unknown information on zooplankton grazing dynamics.

Comparing the laboratory-based and field-based measurements of ingestion rate indicates that zooplankton are able to achieve higher rates of ingestion in the laboratory than in the field, even when phytoplankton biomass is similar. This is to be expected as field-based measurements are also influenced by environmental factors such as dissolved oxygen and the presence of detrital particles in the water column. The investigation into gut passage time for the copepod *S. conflictus* indicated that ingestion of phytoplankton particles may be depressed in the presence of other particulates.

The laboratory-based *G. imparipes* ingestion rate measurements were highest when offering the dinoflagellate *Scrippsiella* sp. as food. In contrast, field measurements, made during a dinoflagellate bloom dominated by *Scrippsiella* spp., *Gyrodinium* spp. and *Katodinium* sp., showed low ingestion rates for copepod species but higher rates for microzooplankton. The model of zooplankton grazing verified this pattern of higher ingestion on dinoflagellates by microzooplankton.

The laboratory-based *G. imparipes* ingestion rate measurements were generally low when offering the chlorophyte, *Chlamydomonas* sp. as food. This pattern was repeated in both the field measurements and the model of zooplankton grazing. It was suggested that the observed decline in copepod biomass during field measurements was related to the dominance of *Chlamydomonas* sp. in the water column. The laboratory-based measurements of ingestion rate support this assertion.

The field-based measurements suggest that ingestion rate may be impeded over a certain density of algae (> 320 µg phytoplankton $C.L^{-1}$). This is not supported in the laboratory, where significantly higher densities of phytoplankton were used. However, it is expected that water quality in the laboratory can be maintained, whereas during the field investigations, dissolved oxygen levels declined significantly as a result of algal respiration and water temperatures regularly exceeded 25°C. Both of these factors have the potential to cause rapid deterioration of water quality and hence zooplankton survival.

Although there were few opportunities to undertake laboratory-based measurements of microzooplankton ingestion rate, the measurements made indicated that larvae of the bivalve, *X. securis*, are more efficient at removing phytoplankton biomass than adult *G. imparipes* when offered *S. costatum* as food at 25°C. The difference between adult

G. imparipes and the rotifer, *B. plicatilis*, removal of phytoplankton biomass was negligible in the laboratory in most instances. The field measurements revealed a similar pattern in that the percentage of phytoplankton biomass removed was similar over successive weeks regardless of the composition of the zooplankton community measured.

It can be concluded that the laboratory-based measurements of ingestion provided estimates of maximum potential ingestion by individual zooplankters taxa under controlled conditions. The differences observed between laboratory-based measurements and field-based measurements and the results of modelling grazing are expected as the latter approaches represent naturally dynamics systems. Overall though, the results of each approach gave similar conclusions.

Chapter 4 - Nutrient Interactions

General Introduction

There is much evidence to suggest that zooplankton, though excretion of soluble nutrients during grazing and subsequent production of nutrient rich faecal pellets, have the potential to positively affect phytoplankton productivity (Corner *et al.*, 1965; Mann, 1982; Stearns *et al.*, 1987; Voss, 1991; Checkley *et al.*, 1992). Excretory products can be used immediately by phytoplankton for growth, whereas faecal pellets must be remineralised by bacteria before nutrients become available for phytoplankton use. In the Swan-Canning Estuary, the importance of nutrient release from faecal pellets, or from excretion, is less likely to be significant at times of peak nutrient concentrations, but may become important during summer and early autumn when nutrient levels have been depleted and urban run-off is at a minimum (Stearns *et al.*, 1987). In a well mixed bay Martin (1968) found zooplankton excretory contributions to nutrients ranged from only 2.5% during spring to 100% during autumn. Other studies have given values ranging from 77%, 66% and 43% in one location (Harris, 1959) to negligible contributions in another similarly well-mixed estuary (Stearns *et al.*, 1987).

Copepod faecal pellets are enclosed in peritrophic membranes (Forster, 1953) and serve as a mechanism for downward flux of organic material (Turner and Ferrante, 1979). Studies have indicated that a large percentage of material in the pellets consists of partially or undigested phytoplankton available for recycling by other plankton (Paffenhöffer and Knowles, 1979; Head, 1992; Lee and Fisher, 1992), as well as amino acids (Cowey and Corner, 1966), proteins (Johannes and Satomi, 1966) and carbon (Honjo and Roman, 1978; Paffenhöffer and Knowles, 1979; Turner, 1979). The rate at which pellets sink and the nutritional value of those pellets to microheterotrophs is largely dependent on the type of food eaten (Smayda, 1969; Ferrante and Parker, 1977; Bienfang, 1980; Checkley *et al.*, 1992; Paffenhöffer, 1994). The rate at which pellets are produced appears to be dependent on food availability (Martin, 1968; Checkley *et al.*, 1992; Paffenhöffer, 1994).

Two studies were undertaken examining the role of copepods in the nutrient ecology of the Swan River estuary. The objectives were:

1. to quantify the production rate and settling rate of faecal pellets produced by the estuarine copepod *G. imparipes*; and
2. to investigate the potential significance of nutrients derived from copepod faecal pellets and metabolic respiration.

The remainder of this chapter consists of two manuscripts addressing the aims above.

Note: For copyright reasons the following paper in Chapter 4 (pg. 124-138) has not been reproduced in full.

Griffin, S.L. (2000). Influence of food type on the production and settling rate of faecal pellets produced by an estuarine copepod. *Marine and Freshwater Research* 51(4):371-378.

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)

Note: For copyright reasons the following paper in Chapter 4 (pg. 139-155) has not been reproduced in full.

Nutrient flux associated with copepod excretion and decomposition of their faecal pellets.

Manuscript currently under review after submission for publication in Estuarine, Coastal and Shelf Science

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)

Chapter 5 - General Discussion

This research project aimed to increase understanding of zooplankton ecology in the Swan River estuary, by documenting temporal changes in zooplankton distribution, abundance and species composition in relation to environmental parameters, by determining the ecological role of zooplankton as consumers of primary production and by examining the potential significance of copepod regeneration of nutrients. The data collected was used in a three dimensional computer model (CAEDYM) to predict the role of zooplankton in reducing phytoplankton biomass.

Zooplankton Dynamics

This part of the research confirmed the patterns of distribution described in earlier studies and the strong influence of salinity on horizontal distribution. However, the current study found that water salinity was not the only factor influencing distribution; factors such as temperature, pH, algal production (dissolved oxygen and chlorophyll *a*) and total suspended solids were also shown to be important.

There was little evidence for strong diurnal vertical migration occurring at the sites sampled, which confirmed an *a priori* hypothesis that diurnal vertical migration may not be as marked in shallow (3 m) turbid water, as it has been recorded in deeper water. Salinity and tidal movement are likely to be more influential than migration in the vertical distribution of zooplankton in shallow water where haloclines persist through several months of each year.

Comparison of copepod species composition in the current study and historical data did not show any consistent shifts in species diversity or abundance. Greater variation occurred between different seasons than between years. This is despite accounts of increased nitrogen and phosphorous loading in the estuary over a 30 year span and despite increasing concern over the intensity and frequency of algal blooms. This may be interpreted as being a key characteristic of estuarine zooplankton; an ability to survive under very dynamic biophysical conditions. However, there was some evidence to suggest that there may be localised deleterious effects on zooplankton during short-term declines in water quality associated with algal blooms (>80 $\mu g\ Chla.L^{-1}$).

Zooplankton Grazing

The grazing component of this study, through field and laboratory experiments, identified the ability of zooplankton to exert 'top-down' control over phytoplankton biomass, depending on the type and biomass of zooplankton present. As shown in other studies, in comparison with copepods or other mesozooplankton, the microzooplankton contributed most to loss of phytoplankton biomass, through a combination of high abundance and high grazing rate, relative to mesozooplankton, such as copepods. However, the microzooplankton are a less 'stable' component of the estuarine zooplankton; copepod fauna show predictable patterns of distribution and abundance, whereas the microzooplankton appear as short term opportunists, not consistently present in the water column. This observation suggests that microzooplankton may be more influenced by patterns of phytoplankton productivity than mesozooplankton.

The use of CAEDYM to model the interactions between zooplankton and phytoplankton provided hitherto unknown information about processes occurring in the Swan Rive estuary. It provided evidence that zooplankton were an integral part of algal bloom dynamics, which counters the often-made assumption that phytoplankton blooms are controlled principally by nutrient availability.

The grazing component of the study demonstrated that copepod grazing is inhibited at high phytoplankton densities (>320 μg phytoplankton $C.L^{-1}$). This concurs with the result of the monitoring component, which showed localised deleterious effects on zooplankton during short-term declines in water quality associated with algal blooms. The causal mechanisms behind this, for example algal exudates, has not yet been identified for the Swan River estuary and further research is required on the behaviour and morphology of bloom forming phytoplankton species.

Nutrient Interactions

Historically, the primary focus of management strategies for the Swan River estuary has been the reduction of allochthonous nutrient input. However, the observation that algal blooms can persist for months at a time, when there is no allochthonous input of nutrients, required further investigation into nutrient recycling within the water column. The role of zooplankton in nutrient regeneration had not previously been investigated.

The nutrient component of this research demonstrated that copepods have the potential to provide nutrients for phytoplankton growth, as a by-product of metabolic respiration and through the decomposition of faecal pellets. Although this was always expected to be the

case, it was not clear whether the contribution from copepods was significant in terms of the nutrient budget for the Swan River estuary. The results of the studies undertaken indicate that copepod nutrient contributions are unlikely to be significant except under conditions of much reduced allochthonous nutrient input during late summer and autumn. However, it is during this period that the Swan River estuary typically has the poorest water quality and algal blooms may persist for months. During this time, the role of copepods in recycling of nutrients for phytoplankton growth cannot be dismissed as insignificant

Zooplankton as Indicators of Estuarine Health

In recent years, ecological studies have become more sophisticated. They have moved from a focus on particular species to an emphasis on ecosystem function. In parallel, the concept of ecosystem health is becoming widely recognised and a variety of indicators are used as tools for determining whether ecosystems are functioning in a 'healthy' way. For example, in south-east Queensland, environmental variables, such as turbidity, Chl*a*, nutrient concentrations, dissolved oxygen and seagrass distribution, are used as indicators of the 'healthy' function of estuaries in the area (Dennison and Abal, 1999). Management responses are then formulated on the basis of annual assessments.

From the outset of the current study, there was a question as to whether zooplankton could be a useful indicator of ecosystem health in the Swan River estuary. Although this question did not form part of the research aims, an ancillary aim of this research was to determine whether the data collected could be used to assess whether zooplankton are a useful indicator of ecosystem function. Deeley and Paling (1999), in a review of the ecological health of Australian estuaries, concluded that zooplankton should be assessed for suitability as indicators of estuarine health, because of their important role in trophic transfer from primary producers to secondary consumers higher in the food web. However, the authors acknowledged that estuarine zooplankton are highly dynamic in space and time and therefore may be difficult to use as indicators. The results of the current study did not resolve these difficulties, but, instead, highlighted them.

In order to use zooplankton as an indicator of estuarine ecosystem health, it was necessary to document the 'normal' ecological functions of zooplankton. The current study has provided a greater understanding of the ecological processes in which zooplankton are involved in the Swan River estuary, but it is unlikely that zooplankton would be useful indicator organisms on their own. A more useful approach may be the use of computer models, such as CAEDYM, which incorporates the full range of processes and biological, chemical and physical attributes of the estuary.

The Modelling Approach to Management

The creation of the Western Australian Estuarine Research Foundation (WAERF) was a step towards taking a pre-emptive approach to management. Gaps in knowledge of the ecology of the estuary were recognised, but it was also recognised that management tools should to include a predictive process, such as the use of computer modelling. The WAERF directed research into specific areas where information was lacking, to culminate in the validation and operation of CAEDYM.

There is potential for use of validated computer models in estuarine management. Models cannot, and should not, replace well-designed monitoring programmes, but can direct monitoring, to ensure it is occurring at appropriate time scales and targeting appropriate species or elements.

In the Swan River estuary, CAEDYM could be used to predict the effect of management actions, before they are undertaken. For example, in November 1997, a large herbicide spill in the Swan River estuary resulted in the death of an estimated 3,600 fish (*The West Australian*, 25th November 1997). As a result, it was decided to restock fish in the estuary through the introduction of 30,000 juvenile fish at two sites in the Swan River estuary (*The West Australian*, June 4th, 1997). This was undertaken without reference to the possible impact this may have on zooplankton, particularly copepods, which are an important food source for juvenile fish. However, the result of this type of management response could have been predicted using a model such as CAEDYM, prior to the event. Similarly, the results of other remediation techniques being implemented in the Swan and Canning Rivers, such as water oxygenation trials, involving oxygenation of bottom waters to reduce nutrient release from sediments and subsequent algal bloom formation, and sediment remediation, involving the use of a modified clay treatment to remove phosphorous from the water column (Swan River Trust, 2000), could have been predicted using computer modelling. Modelling allows simultaneous examination of all components of an ecosystem, under whatever conditions are prescribed, thereby taking an ecosystem approach to management.

References

Allan, JD 1995. *Stream Ecology: Structure and Function of Running Waters.* Chapman and Hall, London, 388 pp.

Ambler, JW 1986. Effect of food quantity and quality on egg production of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. *Estuarine and Coastal Shelf Science* 23:183-196.

American Public Health Association 1995. *Standard Methods for the Examination of Water and Wastewater.* 19th Edn. American Public Health Association and American Water Works Association, Washington.

Arinardi, OH, Baars, MA and Oosterhuis, SS 1990. Grazing in tropical copepods measured by gut fluorescence, in relation to seasonal upwelling in the Banda Sea (Indonesia). – Proceedings of the Snellius-II Symposium. *Netherlands Journal of Sea Research* 25:545-560.

Arnott, GH and Hussainy, SU 1972. Brackish-water plankton and their environment in the Werribee River, Victoria. *Australian Journal of Marine and Freshwater Research* 23:85-99.

Atkinson, A, Ward, P and Murphy, E 1996. Diel periodicity of subantarctic copepods: relationships between vertical migration, gut fullness and gut evacuation rate. *Journal of Plankton Research* 18(8):1387-1405.

Baars, MA and Helling, GR 1985. Methodical problems in the measurement of phytoplankton ingestion rate by gut fluorescence. *Hydrobiologia Bulletins* 19:81-88.

Baars, MA and Oosterhuis, SS 1984. Diurnal feeding rhythms in North Sea copepods measured by gut fluorescence, digestive enzyme activity and grazing on labelled food. *Netherlands Journal of Sea Research* 18:97-119.

Barans, CA, Stender, BW, Holliday, DV and Greenlaw, CF 1997. Variation in the vertical distribution of zooplankton and fine particles in an estuarine inlet of South Carolina. *Estuaries* 20(3):467-482.

Barlow, JP and Bishop, JW 1965. Phosphate regeneration by zooplankton in Cayuga Lake. *Limnology and Oceanography* 10:R15-R24.

Barnes, RSK and Hughes, RN 1988. *An Introduction to Marine Ecology.* Blackwell Scientific Publications, Oxford, 351 pp.

Bautista, B and Harris, RP 1992. Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Marine Ecology Progress Series* 82:41-50.

Bayly, IAE 1965. Ecological studies on the planktonic copepoda of the Brisbane River with special reference to *Gladioferens pectinatus* (Brady) (Calanoida). *Australian Journal of Marine and Freshwater Research* 16:315-350.

Bhuiyan, AL 1966. *The Biology of Certain Planktonic Organisms of the Swan River Estuary, with Particular Reference to Sulcanus conflictus Nicholls (Crustacea: Copepoda).* PhD Thesis, The University of Western Australia, 251 pp.

Bienfang, PK 1980. Herbivore diet affects faecal pellet settling. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1352–1357.

Boon, PI, Bunn, SE, Green, JD and Shiel, RJ 1994. Consumption of cyanobacteria by freshwater zooplankton: implications for the success of "top-down" control of cyanobacterial blooms in Australia. *Australian Journal of Marine and Freshwater Research* 45:875-887.

Bougis, P 1976. *Marine Plankton Ecology.* North-Holland Publishing Company, Amsterdam-Oxford, 355 pp.

Bradford, JM 1976. Partial Revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae). *New Zealand Journal of Marine and Freshwater Research* 10(1):159-202.

Brand, GW and Bayly, IAE 1971. A comparative study of osmotic regulation in four species of calanoid copepods. *Comparative Biology Chemistry and Physiology* 38b:361-371.

Bright, T, Ferrari, F and Martin, D 1972. Sinking rates of euphausiid fecal pellets. *Limnology and Oceanography* 17:293–301.

Brooks, JL 1969. Eutrophication and change in the composition of zooplankton. In: *Eutrophication: Causes, Consequences, Correctives.* National Academy of Science, Washington, D.C., pp. 236-255.

Burns, CW and Xu, Z 1990. Calanoid copepods feeding on algae and filamentous cyanobacteria: rates of ingestion, defecation and effects on trichome length. *Journal of Plankton Research* 12(1):201–213.

Butler, M and Dam, HG 1994. Production rates and characteristics of fecal pellets of the copepod *Acartia tonsa* under simulated phytoplankton bloom conditions: implications for vertical fluxes. *Marine Ecology Progress Series* 114:81–91.

Butler, EI, Corner, DS and Marshall, SM 1969. On the nutrition and metabolism of zooplankton. 6. Feeding efficiency of *Calanus* in terms of nitrogen and phosphorus. *Journal of the Marine Biology Association of the United Kingdom* 49:977-1001.

Butler, EI, Corner, DS and Marshall, SM 1970. On the nutrition and metabolism of zooplankton. 7. Seasonal survey of nitrogen and phosphorus excretion by *Calanus* in the Clyde Sea area. *Journal of the Marine Biology Association of the United Kingdom* 50:525-560.

Caperon, J, Schell, R, Hirota, J and Laws, E 1979. Ammonium excretion rates in Kaneohe Bay, Hawaii, measured by ^{15}N isotope dilution technique. *Marine Biology* 54:33-40.

Capriulo, GM and Carpenter, EJ 1980. Grazing by 35 to 202 μm micro-zooplankton in Long Island Sound. *Marine Biology* 56:319-326.

Carlsson, P. Granéli, E, Finenko, G and Maestrini, SY 1995. Copepod grazing on a phytoplankton community containing the toxic dinoflagellate *Dinophysis acuminata*. *Journal of Plankton Research* 17(10):1925-1938.

Carpenter, SR and Bergquist, A 1985. Experimental testing of grazing indicators based on chlorophyll degradation products. *Archive fuér Hydrobiologie* 102:303-317.

Carpenter, SR, Kitchell, JF and Hodgson, JR 1985. Cascading trophic interactions and lake productivity: fish predation and herbivory can regulate lake ecosystems. *BioScience* 35(10):634-639.

Castel, J 1993. Long-term distribution of zooplankton in the Gironde estuary and its relation with river flow and suspended matter. *Cahiers Biologie Marine* 34:145-163.

Checkley, DM, Dagg, MJ and Uye, SI 1992. Feeding, excretion and egg production of the marine, planktonic copepods, *Acartia* spp. and *Centropages furcatus*. *Journal of Plankton Research* 14:71-96.

Christofferson, K and Jespersen, A-M 1986. Gut evacuation rates and ingestion rates of *Eudiaptomus graciloides* measured by means of the gut fluorescence method. *Journal of Plankton Research* 8:973-983.

Cloern, JE 1996. Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* 34(2):127-168.

Conover, RJ 1966. Factors affecting the assimilation of organic matter by zooplankton and the question of superfluous feeding. *Limnology and Oceanography* 11:346-354.

Conover, RJ and Corner, EDS 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. *Journal of the Marine Biology Association of the United Kingdom* 48:29-48.

Conover, RJ, Durvasula, R, Roy, S and Wang, R 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. *Limnology and Oceanography* 31(4):878-887.

Corner, EDS, Cowey, CB and Marshall, SM 1965. On the nutrition and metabolism of zooplankton. 3. Nitrogen excretion by *Calanus*. *Journal of the Marine Biology Association of the United Kingdom* 45:429-442.

Cowey, CB and Corner, EDS 1966. The amino-acid composition of certain unicellular algae and of the faecal pellets produced by *Calanus finmarchicus* when feeding on them. In: Barnes, H (ed) *Some Contemporary Studies in Marine Science.* George Allen and Unwin Ltd, London, pp. 225-231.

Cowles, TJ, Olsen, RJ and Chisolm, SW 1988. Food selection by copepods: discrimination on the basis of food quality. *Marine Biology* 100:41-49.

Craig, G 1979. *Zooplankton in Perth Water.* Research Report, Department of Environmental Biology, Curtin University of Technology, Perth.

Cyr, H and Pace, ML 1992. Grazing by zooplankton and its relationship to community structure. *Canadian Journal of Fisheries and Aquatic Science* 49:1455-1465.

Dagg, M and Walser, W Jnr 1986. The effect of food concentration on fecal pellet size in marine copepods. *Limnology and Oceanography* 31(5):1066–1071.

Dagg, MJ and Wyman, KD 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. *Marine Ecology Progress Series* 13:37-46.

Dam, HG and Peterson, WT 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. *Journal of Experimental Marine Biology and Ecology* 123:1-14.

Day, JW Jnr, Hall, C, Kemp, W and Yáñez-Arancibia, A 1989. *Estuarine Ecology.* John Wiley and Sons, New York, pp. 311-337.

Deeley, DM and Paling, EI 1999. *Assessing the Ecological Health of Estuaries in Australia.* LWRRDC Occasional Paper 17/99 (Urban Subprogram Report No. 10).

Delille, D and Razouls, S 1994 Community structures of heterotrophic bacteria of copepod faecal pellets. *Journal of Plankton Research* 16(6):603-615.

DeMelo, R, France, R and McQueen, DJ 1992. Biomanipulation: hit or myth? *Limnology and Oceanography* 37:192-207.

Dennison, WG and Abal, EG 1999. *Moreton Bay Study: A Scientific Basis for the Healthy Waterways Campaign.* South-east Queensland Water Quality Strategy, Brisbane, 245 pp.

den Oude, PJ and Gulati, RD 1988. Phosphorus and nitrogen excretion rates of zooplankton from the eutrophic Loosdrecht lakes, with notes on other P sources for phytoplankton requirements. *Hydrobiologia* 169:379-390.

De Stasio, BT Jnr 1993. Diel vertical and horizontal migration by zooplankton: population budgets and the diurnal deficit. *Bulletins of Marine Science* 53(1):44-64.

Donaghay, PL 1980. Grazing interactions in the marine environment. In: Kerfoot, WC (ed) *Evolution and Ecology of Zooplankton Communities.* University Press of New England, London, pp. 234-240.

Donahue, R, Davidson, WA, Peters, NE, Nelson, S and Jakowyna, B 2001. Trends in total phosphorous and total nitrogen concentrations of tributaries to the Swan-Canning estuary, 1987 to 1988. *Hydrological Processes* 15(13):2411-2434.

Douglas, GJ, Hamilton, DP, Gerritse, RG and Adeney, JA 1995. *An Investigation of Water Quality at Two Sites in the Swan River Estuary.* CSIRO Division of Water Resources Report 96/2.

Douglas, GB, Hamilton, DP, Gerritse, R, Adeney, JA and Coad, DN 1997. Sediment geochemistry, nutrient fluxes and water quality in the Swan Estuary, W.A. In: Davis, RJ (ed) *Managing Algal Blooms: Outcomes from the CSIRO's Multi-Divisional Blue-Green Algal Program.* CSIRO Land and Water, Canberra, ACT, pp. 15-30.

Downing, JA and Rigler, FH 1984. *A Manual on Methods for the Assessment of Secondary Production in Fresh Waters.* 2nd Edn. IBP Handbook 17. Blackwell Scientific Publishers, Oxford.

Dumont, HJ 1977. Biotic factors in the population dynamics of rotifers. *Archive fur Hydrobiologie Beiheft Ergebnisse der Limnologie* 8:98-122.

Dunnett, CW 1980. Pairwise multiple comparisons in the unequal variance case. *Journal of the American Statistical Association* 75:796-800.

Durbin, EG and Durbin, AG 1992. Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*. *Limnology and Oceanography* 37:361-378.

Durbin, AG, Durbin, EG and Wlodarczky, K 1990. Diel feeding behaviour in the copepod *Acartia tonsa* in relation to food availability. *Marine Ecology Progress Series* 68:23-45.

Dussart, BH 1965. Les different categories de plankton. *Hydrobiologia* 26:72-74.

Edmondson, WT and Winberg, GG 1971. *A Manual on Methods for Assessment of Secondary Productivity in Freshwaters.* IBP Handbook #17, Blackwell Scientific Publications, Oxford, 358 pp.

Emerson, CW and Roff, JC 1987. Implications of fecal pellet size and zooplankton behaviour to estimates of pelagic-benthic carbon flux. *Marine Ecology Progress Series* 35:51–257.

Enright, JT and Hamner, W 1967. Vertical diurnal migration and endogenous rhythmicity. *Science* 157:937-941.

Feinberg, LR and Dam, HG 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 175:87-96.

Fenchel, T 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. *Limnology and Oceanography* 15:14-20.

Fenchel, T and Finlay, BJ 1983. Respiration rates in heterotrophic, free-living Protozoa. *Microbial Ecology* 9:99-122.

Ferrante, JG and Parker, JI 1977. Transport of diatom frustules by copepod fecal pellets to the sediments of Lake Michigan. *Limnology and Oceanography* 22:92-98.

Fleminger, A and Clutter, RI 1965. Avoidance of towed nets by zooplankton. *Limnology and Oceanography* 10:96-104.

Forster, GR 1953. Peritrophic membranes in the Caridea (Crustacea Decapoda). *Journal of the Marine Biology Association of the United Kingdom* 32:315-318.

Fowler, SW and Small, LF 1972. Sinking rates of euphausiid fecal pellets. *Limnology and Oceanography* 17:293-296.

Frost, BW 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17(6):805-815.

Frost, BW 1975. A threshold feeding behaviour in *Calanus pacificus*. *Limnology and Oceanography* 20:263-266.

Gamble, JC 1978. Copepod grazing during a declining spring phytoplankton bloom in the northern North Sea. *Marine Biology* 49:303-315.

Ganf, CG and Blazka, P 1974. Oxygen uptake, ammonia and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George, Uganda). *Limnology and Oceanography* 19:313-325.

Gaudy, R 1974. Feeding four species of pelagic copepods under experimental conditions. *Marine Biology* 25:125-144.

Gaughan, DJ and Potter, IC 1994. Relative abundance and seasonal changes in the macrozooplankton of the lower Swan Estuary in south-western Australia. *Records of the Western Australian Museum* 16(4):461-474.

Gaughan, DJ and Potter, IC 1995. Composition, distribution and seasonal abundance of zooplankton in a shallow, seasonally closed estuary in temperate Australia. *Estuarine, Coastal and Shelf Science* 41:117-135.

Gauld, DT 1951. The grazing rate of planktonic copepods. *Journal of the Marine Biology Association of the United Kingdom* 29:695-706.

Gauld, DT 1953. Diurnal variations in the grazing of planktonic copepods. *Journal of the Marine Biology Association of the United Kingdom* 31:461-474.

Geider, RJ 1987. Light and temperature dependence of the carbon to Chl*a* ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. *New Phytology* 106:1-34.

Gerritse, RG 1992. Soils, land use, nutrient losses and algal blooms in the Swan-Canning Estuary. In: *Swan River - The Future.* Swan River Trust, Perth, Western Australia, 30-39.

Gieskes, WWC and Kraay, GW 1983. Unknown chlorophyll a derivatives in the North Sea and the Atlantic Ocean revealed by HPLC analysis. *Limnology and Oceanography* 28:757-766.

Gieskes, WWC, Engelkes, MM and Kraay, GW 1991. Degradation of diatom chlorophyll to colourless, non-fluorescing compounds during copepod grazing. *Hydrologia Bulletins* 25(1):65-72.

Gifford, DJ and Dagg, MJ 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. *Bulletins of Marine Science* 43(3):458-468.

Glibert, PM, Lipschultz, F, McCarthy, JJ and Altabet, MA 1982. Isotope dilution models of uptake and remineralisation of ammonium by marine plankton. *Limnology and Oceanography* 27:639-650.

González, H and Biddanda, B 1990. Microbial transformation of metazoan (*Idotea granulosa*) faeces. *Marine Biology* 106:285-295.

Government Chemistry Laboratories 1983. *River and Effluent Monitoring Terms.* Government Chemistry Laboratories, Perth, Western Australia, pp. 112-113.

Griffin, SL 2000. The influence of food type on the production and settling rate of faecal pellets produced by an estuarine copepod. *Marine and Freshwater Research* 51(4):371-378.

Griffin, SL Submitted. Distribution and abundance of estuarine copepods in the Swan River estuary, Western Australia, 1996-1997. *The Journal of the Royal Society of Western Australia.*

Griffin, SL and Rippingale, RJ 2001. Zooplankton grazing dynamics: top-down control of phytoplankton and its relationship to an estuarine habitat. *Hydrological Processes* 15(13):2453-2464.

Griffin, SL, Herzfeld, M and Hamilton, DP 2001. Modelling the impact of zooplankton grazing on phytoplankton biomass during a dinoflagellate bloom in the Swan River estuary, Western Australia. *Ecological Engineering* 16:373-394.

Griffiths, FB and Caperon, J 1979. Description and use of an improved method for determining estuarine zooplankton grazing rates on phytoplankton. *Marine Biology* 54:301-309.

Guillard, RRL 1975. Culture of phytoplankton for feeding marine invertebrates. In: Smith, WL, Chaney, MH (eds) *Culture of Marine Invertebrate Animals.* Plenum Press, New York, p 29-60.

Hallam, SJ 1987. Aboriginal resource usage along the Swan River. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1, Curtin University of Technology, pp. 21-33.

Hamilton, DP 1996. *An Integrated Ecological Model of Catchment Hydrology and Water Quality for the Swan and Canning Rivers.* 1995/96 Annual Report to the Western Australian Estuarine Research Foundation. Centre for Water Research, Report WP 1005 DH.

Hamilton, DP and Schladow, SG 1997. Prediction of water quality in lakes and reservoirs. Part I - Model description. *Ecological Modelling* 96:91-110.

Hamilton, DP and Turner, JV (eds) 2001. Integrating research and management for an urban estuarine system: the Swan-Canning Estuary, Western Australia. *Hydrological Processes* 15:2383-2385.

Hamilton, D, Thompson, PA, Kurup, R and Horner-Rosser, SMJ 1998. Dynamics of dinoflagellate blooms in the Swan River Estuary. In: M^{c}Combe, AJ and Davis, JA (eds) *Proceedings of the VTH INTECOL International Wetlands Conference.* Perth, 1996, pp. 273-286.

Hamilton, DP, Chan, T, Robb, MS, Pattiaratchi, CB and Herzfeld, M 2001. The hydrology of the upper Swan River estuary with focus on an artificial destratification trial. *Hydrological Processes* 15:2465-2480.

Haney, JF 1988. Diel patterns of zooplankton behaviour. *Bulletins of Marine Science* 43:583-603.

Hansen, B and Bech, G 1996. Bacteria associated with a marine planktonic copepod in culture. I. Bacteria genera in seawater, body surface, intestines and fecal pellets and succession during fecal pellet degradation. *Journal of Plankton Research* 18(2):257-273.

Hansen, B, Fotel, F, Jensen, N and Madsen, S 1996. Bacteria associated with a marine planktonic copepod in culture. II. Degradation of fecal pellets produced on a diatom, a nanoflagellate or a dinoflagellate diet. *Journal of Plankton Research* 18(2):275-288.

Hansen, FC and Boekel, WHM 1991. Grazing pressure of the calanoid copepod *Temora longicornis* on a *Phaeocystis* dominated spring bloom in a Dutch tidal inlet. *Marine Ecology Progress Series* 78:123-129.

Hargrave, BT and Geen, GH 1968. Phosphorus excretion by zooplankton. *Limnology and Oceanography* 13:332-343.

Harris, E 1959. The nitrogen cycle in Long Island Sound. *Bulletins of the Bingham Oceanographic Collection, Yale University* 17:31-65.

Harris, GP 1986. *Phytoplankton Ecology - Structure, Function and Fluctuation.* Chapman and Hall, London, 384 pp.

Harris, GP 1997. Algal biomass and biogeochemistry in catchments and aquatic ecosystems: scaling of processes, models and empirical tests. *Hydrobiologia* 349:19-26.

Harris, JE 1963 The role of endogenous rhythms in vertical migration. *Journal of the Marine Biology Association of the United Kingdom* 43:153-166.

Harris, RP and Malej, A 1986. Diel patterns of ammonium excretion and grazing rhythms in *Calanus helgolandicus* in surface stratified waters. *Marine Ecology Progress Series* 31:75-85.

Havens, KE, East, TL and Beaver, JR 1996. Experimental studies of zooplankton-phytoplankton-nutrient interactions in a large subtropical lake (Lake Okeechobee, Florida, U.S.A.). *Freshwater Biology* 36:579-597.

Head, EJH 1992. Comparison of the chemical composition of particulate material and copepod faecal pellets at stations off the coast of Labrador and in the Gulf of St Lawrence. *Marine Biology* 112:593-600.

Head, EJH and Harris, LR 1992. Chlorophyll and carotenoid transformation and destruction by *Calanus* spp. grazing on diatoms. *Marine Ecology Progress Series* 86:229-238.

Head, EJH and Harris, LR 1994. Feeding selectivity by copepods grazing on natural mixtures of phytoplankton determined by HPLC analysis of pigments. *Marine Ecology Progress Series* 110:75-83.

Head, EJH and Harris, LR 1996. Chlorophyll destruction by *Calanus* spp. grazing on phytoplankton: kinetics, effects of ingestion rate and feeding history, and a mechanistic interpretation. *Marine Ecology Progress Series* 135:223-235.

Hein, RG, Krueger, DM and Richman, S 1993. Feeding and energy relations in *Daphnia galeata-mendotae*. *Bulletins of Marine Science* 53(1):115-127.

Hill, AE 1991. Vertical migration in tidal currents. *Marine Ecology Progress Series* 75:39-54.

Hodgkin, EP 1987. The hydrology of the Swan River estuary: salinity the ecological master factor. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1, Curtin University of Technology, 34-44.

Hodgkin, EP and Rippingale, RJ 1971. Interspecies conflict in estuarine copepods. *Limnology and Oceanography* 16:573-576.

Hodgkin, EP and Vicker, E 1987. A history of algal pollution in the estuary of the Swan River. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1, Curtin University of Technology, 65-70.

Honjo, S and Roman, MR 1978. Marine copepod fecal pellets: production, preservation, sedimentation. *Journal of Marine Research* 36:45-57.

Horner-Rosser, SJM and Thompson, P 2001. Phytoplankton of the Swan-Canning estuary: a comparison of nitrogen uptake by different bloom assemblages. *Hydrological Processes* 15(13):2579-2594.

Hosja, W and Deeley, D 1994. *Harmful Phytoplankton Surveillance in Western Australia.* Waterways Commission of Western Australia Report No. 43.

Huntley, ME 1982. Yellow water in La Jolla Bay, California, July 1980. II. Suppression of zooplankton grazing. *Journal of Experimental Marine Biology and Ecology* 63:81-91.

Huntley, ME 1988. Feeding biology of *Calanus*: a new perspective. *Hydrobiologia* 167/168:83-99.

Huntley, ME, Sykes, P, Rohan, S and Marin, V 1986. Chemically-mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrence and significance. *Marine Ecology Progress Series* 28:105-120.

Ianora, A, Poulet, S and Miralto, A 1995. A comparative study of the inhibitory effect of diatoms on the reproductive biology of the copepod *Temora stylifera*. *Marine Biology* 121:533-539.

Ianora, A, Poulet, S, Miralto, A and Grottoli, R 1996. The diatom *Thalassiosira rotula* affects reproductive success in the copepod *Acartia clausi*. *Marine Biology* 125:279–286.

Icanberry, JW and Richardson, RW 1973. Quantitative sampling of live zooplankton with a filter-pump system. *Limnology and Oceanography* 18:333-335.

Ikeda, T, Carleton, JH, Mitchell, AW and Dixon, P 1982a. Ammonia and phosphate excretion by zooplankton from the inshore waters of the Great Barrier Reef. II. Their *in situ* contributions to nutrient regeneration. *Marine and Freshwater Research* 33:683-698.

Ikeda, T, Hing Fay, E, Hutchinson, SA and Boto, GM 1982b. Ammonia and inorganic phosphate excretion by zooplankton from inshore waters of the Great Barrier Reef, Queensland. I. Relationship between excretion rates and body size. *Marine and Freshwater Research* 33:55-70.

Irigoien, X and Castel, J 1995. Feeding rates and productivity of the copepod *Acartia bifilosa* in a highly turbid estuary, the Gironde (SW France). *Hydrobiologia* 311:115-125.

Irigoien X, Castel, J and Gasparini S 1996. Gut clearance rate as predictor of food limitation situations. Application to two estuarine copepods: *Acartia bifilosa* and *Eurytemora affinis*. *Marine Ecology Progress Series* 131:159-163.

Irigoien, X, Castel, J and Sautour, B 1993. *In situ* grazing activity of planktonic copepods in the Gironde estuary. *Cahiers Biologie Marine* 34:225-237.

Jack, P 1987. Nutrient monitoring in the Swan River estuary. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1, Curtin University of Technology, 45-64.

Jacobsen, TR and Azam, F 1984. Role of bacteria in copepod fecal pellet decomposition: colonization, growth rates and mineralization. *Bulletins of Marine Science* 35:495-502.

Jeffrey, SW and Hallegraeff, GM 1987. Chlorophyllase distribution in ten classes of phytoplankton : a problem for chlorophyll analysis. *Marine Ecology Progress Series* 35:293-304.

Johannes, RE and Satomi, M 1966. Composition and nutritive value of fecal pellets of a marine crustacean. *Limnology and Oceanography* 11:191-197.

John, J 1987. Phytoplankton of the Swan River Estuary. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1. Curtin University of Technology, Perth, pp. 71-90.

John, J 1994. Eutrophication of the Swan River estuary, Western Australia and the management. In: Mitsch, WJ (ed) *Global Wetlands: Old World and New.* Elsevier, Amsterdam, pp. 749-757.

Jørgensen, SE, Kamp-Nielsen, L and Jørgensen, LA 1986. Examination of the generality of eutrophication models. *Ecological Modelling* 32:251-266.

Jumars, PA, Newell, RC, Angel, MV, Fowler, SW, Poulet, SA, Rowe, GT and Smetacek, V 1984. Detritivory. In: Fasham, MJR (ed) *Flows of Energy and Materials in Marine Ecosystems – Theory and Practise.* Plenum Press: New York, pp. 685–693.

Kelso, BHL, Smith, RV, Laughlin, RJ and Lennox, SD 1997. Dissimilatory nitrate reduction in anaerobic sediments leading to river nitrite accumulation. *Applied Environmental Microbiology* 63:4679-4685.

Kidneys, AE, Kovalev, AV, Shulman, G, Gordina, A and Bingel, F 2000. A review of zooplankton investigations of the Black Sea over the last decade. *Journal of Marine Systems* 24(3-4):355-371.

Kimmerer, W and M^{c}Kinnon, A 1985. A comparative study of zooplankton in two adjacent embayments, Port Phillip and Westernport Bays, Australia. *Estuarine, Coastal and Shelf Science* 21:145-159.

Kiørboe, T and Tiselius, PT 1987. Gut clearance and pigment destruction in a herbivorous copepod, *Acartia tonsa*, and the determination of *in situ* grazing rates. *Journal of Plankton Research* 9(3):525-534.

Kiørboe, T, Möhlenberg, F and Nicolajsen, H 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. *Ophelia* 21(2):181-194.

Kiørboe, T, Möhlenberg, F and Riisgård, HU 1985. *In situ* feeding rates of planktonic copepods: a comparison of four methods. *Journal of Experimental Marine Biology and Ecology* 88:67-81.

Komar, PD, Morse, AP, Small, LF and Fowler, SW 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. *Limnology and Oceanography* 26(1):172–180.

Kotliar, NB and Wiens, JA 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.

Kott, P 1955. The zooplankton of Lake Macquarie, 1953-1954. *Australian Journal of Marine and Freshwater Research* 6:429-442.

Krebs, CJ 1985. *Ecology: The Experimental Analysis of Distribution and Abundance.* 3rd Edn. Harper and Row Publishers, New York, 800 pp.

Krebs, CJ 1999. *Ecological Methodology.* 2nd Edn. Benjamin/Cummings, California, 620 pp.

Kurup, GR, Hamilton, DP and Patterson, JC 1999. Modelling the effect of seasonal flow variations on the position of a salt wedge in a microtidal estuary. *Estuarine and Coastal Shelf Science* 47(2):191-208.

Lampert, W 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3:21-27.

Lampert, W and Schober, U 1980. The importance of "threshold" food concentrations. In: Kerfoot, WC (ed) *Evolution and Ecology of Zooplankton Communities.* University Press of New England, London, pp. 264-267.

Lampert, W and Taylor, BE 1985. Zooplankton grazing in a eutrophic lake: implications of diel vertical migration. *Ecology* 66:68-82.

Lampitt, RS, Noji, T and von Bodungen, B 1990. What happens to zooplankton faecal pellets? Implications for material flux. *Marine Biology* 104:15–23.

Landry, MR and Hassett, RP 1982. Estimating the grazing impact of marine microzooplankton. *Marine Biology* 67:283-288.

Lee, BG and Fisher, NS 1992. Decomposition and release of elements from zooplankton debris. *Marine Ecology Progress Series* 88:117-28.

Levin, SA 1994. Patchiness in marine and terrestrial systems: from individuals to populations. *Philosophical Transactions of the Royal Society of London* 343:99-103.

Levin, SA and Segal, LA 1976. An hypothesis for the origin of planktonic patchiness. *Nature* 259:659.

Liang, D, Uye, S and Onbé, T 1996. Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. I. *Centropages abdominalis.* *Marine Biology* 124:527-536.

Loeblich, AR and Smith, VE 1968. Chloroplast pigments of the marine dinoflagellate *Gyridinium resplendens.* *Lipids* 3:5-13.

Longhurst, AR 1976. Vertical migration. In: Cushing, DH and Walsh, JJ (eds) *The Ecology of the Seas.* Blackwell Scientific Publications, Oxford, pp. 124-137.

Mackas, D and Bohrer, R 1976. Fluorescence analysis of zooplankton gut contents and investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology* 25:77-85.

Madhupratap M and Onbé T 1986. Structure and species diversity of the zooplankton community of the Inland Sea of Japan. *Estuarine and Coastal Shelf Science* 23:725-737.

Mann, K 1982. *Ecology of Coastal Waters - A Systems Approach.* Blackwell Scientific Publications, Great Britain, pp. 83-135.

Mann, KH, Frost, B, Guglielmo, L, Huntley, M, Jansson, BO, Longhurst, AR, Radach, G and Williams, R 1984. Herbivory. In: Fasham, MJR (ed) Flows of Energy and Materials in Marine Ecosystems - Theory and Practise. Plenum Press, New York, pp. 671-684.

Marshall, SM 1973. Respiration and feeding in copepods. *Advances in Marine Biology* 11:57-120.

Marshall, SM and Orr, AP 1955. On the biology of *Calanus finmarchicus.* V. Food uptake, assimilation and excretion in adult and stage 5 *Calanus. Journal of the Marine Biology Association of the United Kingdom* 34:495–529.

Martin, JH 1968. Phytoplankton-zooplankton relationships in Narragansett Bay. 3. Seasonal changes in zooplankton excretion rates in relation to phytoplankton abundance. *Limnology and Oceanography* 13:63-71.

Martin, JH 1970. Phytoplankton-zooplankton relationships in Narragansett Bay. 4. The seasonal importance of grazing. *Limnology and Oceanography* 15:413-418.

Mayzaud, P 1976. Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and biochemical composition of some species. *Marine Biology* 37:47-58.

M^{c}Allister, CD 1971. *Some Aspects of Nocturnal and Continuous Grazing by Planktonic Herbivores in Relation to Production Studies.* Fisheries Research Board of Canada Technical Report No. 248.

M^{c}Gowan, JA and Fraundorf, VF 1966. The relationship between size of net used and estimates of zooplankton diversity. *Limnology and Oceanography* 11:456-469.

M^{c}Laren, IA 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada* 20(3):685-727.

M^{c}Lusky, D 1989. *The Estuarine Ecosystem.* 2nd Edn. Blackie and Sons Limited, London, p. 183.

Miralto, A, Ianora, A and Poulet, S 1995. Food type induces different responses in the copepod *Centropages typicus*. *Journal of Plankton Research* 17(7):1521-1534.

Morales, CE 1987. Carbon and nitrogen content of copepod faecal pellets: effect of food concentration and feeding behaviour. *Marine Ecology Progress Series* 36:107–114.

Mullin, MM 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnology and Oceanography* 8:239-250.

Mullin, MM and Brooks, ER 1970. The effect of concentration of food on body size, cumulative ingestion, and rate of growth of the marine copepod *Calanus helgolandicus*. *Limnology and Oceanography* 15:748-755.

Mullin, MM, Stewart, EF and Fuglister, FJ 1975. Ingestion by planktonic grazers as a function of concentration of food. *Limnology and Oceanography* 20:259-262.

Nagasawa, S and Nemoto, T 1988. Presence of bacteria in guts of marine crustaceans and on their fecal pellets. *Journal of Plankton Research* 10:559-564.

Neale, IM and Bayly, IAE 1974. Studies on the ecology of the zooplankton of four estuaries in Victoria. *Australian Journal of Marine and Freshwater Research* 25:337-350.

Nicholls, AG 1945. A new copepod from Australia. *Annuals of the Magazine for Natural History* 12:501-514.

Nielsen, TG 1991. Contribution of zooplankton grazing to the decline of a *Ceratium* bloom. *Limnology and Oceanography* 36(6):1091-1106.

Noji, TT, Estep, KW, MacIntyre, F and Norrbin, F 1991. Image analysis of faecal material grazed upon by three species of copepods. Evidence for coprorhexy, coprophagy and coprochaly. *Journal of the Marine Biology Association of the United Kingdom* 71:465–480.

Oguz, T, Unluata, U, Ducklow, HW and Malanotte-Rizzoli, P 1999. Modelling the Black Sea pelagic ecosystem and biogeochemical structure: a synthesis of recent studies. In: Besiktepe, S, Unluata, U and Bologa, A (eds) *Environmental Degradation of the Black Sea: Challenges and Remedies.* NATO ASI Series, 2-56, Kluwer Academic Publishers, pp. 197-224.

Paerl, HW 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnology and Oceanography* 33(4):823-847.

Paffenhöfer, G-A 1984. Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. *Marine Biology* 80:323-333.

Paffenhöfer, G-A 1994. Variability due to feeding activity of individual copepods. *Journal of Plankton Research* 16(6):617–626.

Paffenhöfer, G-A and Knowles, SC 1979. Ecological implications of faecal pellet size, production and consumption by copepods. *Journal of Marine Research* 37:35–49.

Parsons, TR, Maita, Y and Lalli, CM 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis.* Pergamon, New York, 173 pp.

Pattiaratchi C and Burling, M 1998. Tidal dynamics of the Swan River estuary. In: *Proceedings of the Swan Canning Estuary Conference*, York, Western Australia, April 1998. Western Australian Estuarine Research Foundation, Perth, p 10.

Payne, MF and Rippingale, RJ 2000. Evaluation of diets for culture of the calanoid copepod *Gladioferens imparipes. Aquaculture* 187:85-96.

Penry, DL and Frost, BW 1990. Re-evaluation of the gut-fullness (gut fluorescence) method for inferring ingestion rates of suspension feeding copepods. *Limnology and Oceanography* 35:1207-1214.

Peters, RH 1991. *A Critique for Ecology.* Cambridge University Press, Cambridge, 366 pp.

Peterson, WT, Painting, S and Barlow, R 1990b. Feeding rates of *Calanoides carinatus*: a comparison of five methods including evaluation of the gut fluorescence method. *Marine Ecology Progress Series* 63:85-92.

Peterson, WT, Painting, S and Hutchings, L 1990a. Diel variation in gut pigment content: diel vertical migration and estimates of grazing impact for copepods in the southern

Benguela upwelling region in October 1987. *Journal of Plankton Research* 12:259-281.

Pinto-Coelho, RM, de Moura, RT and Moreira, A 1997. Zooplankton and bacteria contribution to phosphorus and nitrogen internal cycling in a tropical and eutrophic reservoir: Pampulha Lake, Brazil. *Internationale Revue der Gesamten Hydrobiologie* 82:185-200.

Pomeroy, LR, Hanson, RB, McGillivary, PA, Sherr, BF, Kirchman, D and Deibel, D 1984. Microbiology and chemistry of faecal products of pelagic tunicates: rates and fates. *Bulletins of Marine Science* 35:426-439.

Poulet, SA 1973. Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. *Limnology and Oceanography* 18:564-573.

Pourriot, R 1977. Food and feeding habits of Rotifera. *Archive fur Hydrobiologie Beiheft Ergebnisse der Limnologie* 8:243-260.

Quiblier-Lloberas, C, Bourdier, G, Amblard, C and Pepin, D 1996. Impact of grazing on phytoplankton in Lake Pavin (France): Contribution of different zooplankton groups. *Journal of Plankton Ecology* 18(3)305-322.

Raymont, JEG 1980. *Plankton and Productivity in the Oceans. Vol. 1 Phytoplankton.* 2nd Edn. Pergamon, Oxford, 489 pp.

Reeve, MR and Walter, MA 1977. Observations on the existence of lower threshold and upper critical food concentrations for the copepod *Acartia tonsa* Dana. *Journal of Experimental Marine Biology and Ecology* 29:211-221.

Riemann, B 1978. Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton. *Limnology and Oceanography* 23:1059-1066.

Riley, MJ and Stefan, HG 1987. *Dynamic Lake Water Quality Simulation Model "MINLAKE".* St Anthony Falls Hydraulic Laboratory, Project Report 263, University of Minnesota.

Rippingale, RJ 1981. The ecology of plankton fauna in saline river pools. *Hydrobiologia* 82:223-231.

Rippingale, RJ 1987. Zooplankton of the Swan Estuary. In: John, J (ed) *The Swan River Estuary Ecology and Management.* Curtin University Environmental Studies Report #1, Curtin University of Technology, 117-126.

Rippingale, RJ 1994. A calanoid copepod *Gladioferens imparipes*, holding onto surfaces. *Hydrobiologia* 292/293:351-360.

Rippingale, RJ and Hodgkin, EP 1974a. Predation effects on the distribution of a copepod. *Australian Journal of Marine and Freshwater Research* 25:81-91.

Rippingale, RJ and Hodgkin, EP 1974b. Population growth of a copepod *Gladioferens imparipes* Thomson. *Australian Journal of Marine and Freshwater Research* 25:351–360.

Rippingale, RJ and Hodgkin, EP 1977. Food availability and salinity tolerance in a brackish water copepod. *Australian Journal of Marine and Freshwater Research* 28:1-7.

Rivier, A, Brownlee, DC, Sheldon, RW and Rassoulzadegan, F 1985. Growth of microzooplankton: A comparative study of bactiverous zooflagellates and ciliates. *Marine Microbial Food Webs* 1:51-60.

Roman, MR, Ashton, KA and Gauzens, AL 1988. Day/night differences in the grazing impact of marine copepods. *Hydrobiologia* 167/168:21-30.

Rose, TJ 1998. *Swan–Canning Cleanup Programme: Draft Action Plan.* Water and Rivers Commission, Perth, 97 pp.

Roy, S and Poulet, SA 1990. Laboratory study of the chemical composition of aging copepod fecal material. *Journal of Experimental Marine Biology and Ecology* 135:3-18.

Sampson, N, Gerritse, R and Aylmore, G. 1998. The dynamics of soluble organic carbon in the Ellen Brook Catchment. In: *The Swan-Canning Estuary Conference*, York, Western Australia, April, 1998. Conference programme and book of abstracts.

Santer, B 1996. Nutritional suitability of the dinoflagellate *Ceratium furcoides* for four copepod species. *Journal of Plankton Research* 18(3):323-333.

Sapozhnikov, VV and Pasternak, AF 1988. Decomposition of fecal pellet during simulated sinking. *Oceanology* 28:244-248.

Sarnelle, O 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. *Ecological Monographs* 63(2):129-149.

Sautour, B and Castel, J 1993. Feeding behaviour of the coastal copepod *Euterpina acutifrons* on small particles. *Cahiers Biologie Marine* 34:239-251.

Sautour, B and Castel, J 1995. Spring zooplankton distribution and production of the copepod *Euterpina acutifrons* in Marennes-Oléron Bay (France). *Hydrobiologia* 310:163-175.

Sautour, B, Artigas, F, Herbland, A and Laborde, P 1996. Zooplankton grazing impact in the plume of dilution of the Gironde estuary (France) prior to the spring bloom. *Journal of Plankton Research* 18(6):835-853.

Scavia, D 1980. An ecological model of Lake Ontario. *Ecological Modelling* 8:49-78.

Schlacher, T and Wooldridge, T 1995. Small-scale distribution and variability of demersal zooplankton in a shallow, temperate estuary: tidal and depth effects on species-specific heterogeneity. *Cahiers Biologie Marine* 36:211-227.

Schladow, SG and Hamilton, DP 1995. Modelling sediment nutrient release in a stratified reservoir. *Australian Journal of Marine and Freshwater Research* 46(1):189-195.

Schneider, DC 1994. *Quantitative Ecology – Spatial and Temporal Scaling.* Academic Press Inc., Sand Diego, pp. 166-170.

Schoeneck, LJ, Williamson, CE and Stoeckel, ME 1990. Diel periodicity and selectivity in the feeding rate of predatory copepod *Mesocyclops edax*. *Journal of Plankton Research* 12(1):29-40.

Sellner, K and Bundy, M 1987. Preliminary results of experiments to determine the effects of suspended sediments on the estuarine copepod *Eurytemora affinis*. *Continental Shelf Research* 7:62-64.

Sellner, K, Olson, MM and Kononen, K 1994. Copepod grazing in a summer cyanobacteria bloom in the Gulf of Finland. *Hydrobiologia* 292/293:249-254.

Serventy, DL 1955. *The Fauna of the Swan River Estuary.* Report of the Swan River Reference Committee, Perth, 70-77.

Shiel, RJ, Walker, KF and Williams, WD 1982. Plankton of the lower River Murray, South Australia. *Australian Journal of Marine and Freshwater Research* 33:301-327.

Shuman, FR and Lorenzen, CJ 1975. Quantitative degradation of chlorophyll by a marine herbivore. *Limnology and Oceanography* 20:580-586.

Sieburth, JM, Smetacek, V and Lenza, J 1978. Pelagic ecosystem structure: heterotrophic compartments and their relationship to plankton size fractions. *Limnology and Oceanography* 23:1256-1263.

Singarajah, KV 1969. Escape reactions of zooplankton: the avoidance of a pursuing siphon tube. *Journal of Experimental Marine Biology and Ecology* 3:171-178.

Small, LF, Fowler, SW and Unlu, MY 1979. Sinking rates of natural copepod faecal pellets. *Marine Biology* 51:233-241.

Smayda, TJ 1969. Some measurements of the sinking rate of faecal pellets. *Limnology and Oceanography* 14:621–625.

Smayda, TJ 1970. The suspension and sinking of phytoplankton in the sea. *Oceanography and Marine Biology: an Annual Review* 8:353–414.

Smayda, TJ 1974. Some experiments on the sinking characteristics of two freshwater diatoms. *Limnology and Oceanography* 19:628–635.

Smetacek, VS 1980. Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. *Estuarine Coastal and Shelf Science* 11:477-490.

Sommer, U 1989. *Plankton Ecology - Succession in Plankton Communities.* Springer-Verlag, New York, pp. 107-157.

SPSS 1997. *Transforms and Regressions Reference Manual for Windows 95, NT and 3.1.* SPSS Inc, Chicago, Section A1-16.

Statsoft 1994. *Statistica.* Statsoft Incorporated, USA, pp. 551-580.

Stearns, DE 1986. Copepod grazing behaviour in simulated natural light and its relation to nocturnal feeding. *Marine Ecology Progress Series* 30:65-67.

Stearns, DE, Litaker, W and Rosenberg, G 1987. Impacts of zooplankton grazing and excretion on short-interval fluctuations in Chlorophyll *a* and nitrogen concentrations in a well mixed estuary. *Estuarine and Coastal Shelf Science* 24:305-325.

Stephens, R and Imberger, J 1996. Dynamics of the Swan River estuary: the seasonal variability. *Marine and Freshwater Research* 47:517-529.

Sterner, RW 1989. The role of grazers in phytoplankton succession. In: Sommer, U (ed) *Plankton Ecology - Succession in Plankton Communities.* Springer-Verlag, New York, pp. 107-170.

Strickland, JD and Parsons, TR 1972. *A Practical Handbook of Seawater Analysis.* 2nd Edn. Bulletins of the Fisheries Research Board of Canada No. 167.

Svensson, J-E and Stenson, JAE 1991. Herbivoran impact on phytoplankton community structure. *Hydrobiologia* 224:77-84.

Swan River Trust 2000. *Swan-Canning Clean-up Programme: Action Plan Implementation Year 1 in review Summary.* Swan River Trust, Perth.

Tang, KW, Chen, QC and Wong, CK 1994. Diel vertical migration and gut pigment rhythm of *Paracalanus parvus*, *P. crassirostris*, *Acartia erythraea* and *Eucalanus subcrassus* (Copepoda, Calanoida) in Tolo Harbour, Hong Kong. *Hydrobiologia* 292/293:389-396.

Taw, N and Ritz, DA 1978. Zooplankton distribution in relation to hydrology of the Derwent River Estuary. *Australian Journal of Marine and Freshwater Research* 29:763-775.

Tester, PA and Turner, JT 1988. Comparative carbon-specific ingestion rates of phytoplankton by *Acartia tonsa*, *Centropages velificatus* and *Eucalanus pileatus* grazing on natural phytoplankton assemblages in the plume of the Mississippi River (northern Gulf of Mexico continental shelf). *Hydrobiologia* 167/168:211-217.

Thompson, AM, Durbin, EG and Durbin, AG 1994. Seasonal changes in maximum ingestion rate of *Acartia tonsa* in Narragansett Bay, Rhode Island, USA. *Marine Ecology Progress Series* 108:91-105.

Thompson, PA 2001. Temporal variability of phytoplankton in a salt wedge estuary, the Swan-Canning Estuary, Western Australia. *Hydrological Processes* 15(13):2617-2630.

Thompson, PA and Hosja, W 1996. Temporal dynamics of nutrient limitation of phytoplankton from the Swan River estuary, Western Australia. *Marine and Freshwater Research* 47:659-667.

Thompson, PA, John, J, Hamilton, DP and Horner-Rosser, SMJ 1996. Phytoplankton biomass in the Swan and Canning Rivers: studies on factors controlling biomass. In: Hamilton, DP (ed) *An Integrated Ecological Model of Catchment Hydrology and Water Quality for the Swan and Canning Rivers.* Estuarine Research Foundation 1995/96 Annual Report, pp. 36-52.

Thomson, JM 1946. New Crustacea from the Swan River Estuary. *Journal of the Royal Society of Western Australia* 30:35-53.

Thurlow, BH, Chambers, J and Klemm, VV 1986. *Swan-Canning Estuarine System: Environment, Use and the Future.* Western Australia Waterways Commission Report No. 9, Perth.

Tidey, L 1997. *The Effect of Low Dissolved Oxygen on Estuarine Copepods.* Honours Thesis, Department of Environmental Biology, Curtin University of Technology, Western Australia, 72 pp.

Tranter, DJ and Fraser, JH 1968. *Zooplankton Sampling.* UNESCO Press, Paris.

Trees, CC, Kennicutt Mahlon II, C and Brooks, JM 1985. Errors associated with the standard fluorometric determination of chlorophylls and phaeopigments. *Marine Chemistry* 17:1-12.

Tsuda, A and Nemoto, T 1987. The effect of food concentration on the gut clearance time of *Pseudocalanus minutus* Krøyer (Calanoida: Copepoda). *Journal of Experimental Marine Biology and Ecology* 107:121-130.

Tsuda, A and Nemoto, T 1990. The effect of food concentration on the faecal pellet size of the marine copepod, *Pseudocalanus newmani* Frost. *Bulletins of the Plankton Society of Japan* 37(1):83–90.

Turner, JT 1977. Sinking rates of faecal pellets from the marine copepod *Pontella meadii. Marine Biology* 40:249–259.

Turner, JT 1978. Scanning electron microscope investigations of feeding habits and mouth-part structures of three species of copepods of the family Pontellidae. *Bulletins of Marine Science* 28:487–500.

Turner, JT 1979. Microbial attachment to copepod faecal pellets and its possible ecological significance. *Transcripts of the American Microscopy Society* 98:131-135.

Turner, JT 1994. Planktonic copepods of Boston Harbour, Massachusetts Bay and Cape Cod Bay, 1992. *Hydrobiologia* 292/293:405-413.

Turner, JT and Ferrante, JG 1979. Zooplankton faecal pellets in aquatic ecosystems. *Bioscience* 29:670–677.

Turner, JT and Granéli, E 1992. Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. *Journal of Experimental Marine Biology and Ecology* 157:19-31.

Turriff, N, Runge, JA and Cembella, AD 1995. Toxin accumulation and feeding behaviour of the planktonic copepod *Calanus finmarchicus* exposed to the red-tide dinoflagellate *Alexandrium excavatum*. *Marine Biology* 123:55-64.

Tyrell, T and Taylor, AH 1996. A modelling study of *Emiliania huxleyi* in the north east Atlantic. *Journal of Marine Systematics* 9(1/2):83-112.

UNESCO 1981. *The Practical Salinity Scale of 1978 and the International Equation of State Seawater 1980.* 10th Report of the Joint Panel on Oceanographic Tables and Standards. UNESCO technical Papers in Marine Science No. 36, 25 pp.

Urban, JI, Deibel, D and Schwinghamer, P 1993. Seasonal variations in the densities of fecal pellets produced by *Oikopleura vanhoeffeni* (C. Larvacea) and *Calanus finmarchicus* (C. Copepoda). *Marine Biology* 117(4), 607–613.

Uye, S 1994. Replacement of large copepods by small ones with eutrophication of embayments: cause and consequence. *Hydrobiologia* 292/293:513-519.

Uye, S and Sano, K 1995. Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Marine Ecology Progress Series* 118:121-128.

Uye, S and Yamamoto, F 1995. In situ feeding of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan, examined by the gut fluorescence method. *Bulletins of the Plankton Society of Japan* 42(2):123-139.

Vanni, MJ 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology* 68:624-635.

van Rijn, J, Diab, S and Shilo, M 1987. Phytoplankton succession in relation to the nitrogen regime in shallow, brackish-water fishponds. *Archive fuér Hydrobiologie* 111:183-196.

Voss, M 1991. Content of copepod faecal pellets in relation to food supply in Kiel Bight and its effect on sedimentation rate. *Marine Ecology Progress Series* 75:217-225.

Walters, C 1986. *Adaptive Management of Renewable Resources.* Macmillan Publishing Company, New York, 374 pp.

Weinstein, MP, Weiss, SL, Hodson, RG, Gerry, LR 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fisheries Bulletins* 782:419-436.

Wetzel, RG and Likens, GE 1995. *Limnological Analysis.* 2nd Edn. Springer, New York, 391 pp.

Wiebe, PH 1971. A computer model study of zooplankton patchiness and its effects on sampling error. *Limnology and Oceanography* 16:29-38.

Wiesse, T and Rudstam, LG 1989. Excretion and respiration rates of *Neomysis integer* (Mysidaceae): effects of temperature, sex and starvation. *Hydrobiologia* 178, 253-258.

Zaitsev, YP 1992. Recent changes in the trophic structure of the Black Sea. *Fisheries and Oceanography* 2:180-189.

Zar, JH 1984. *Biostatistical Analysis.* 2nd Edn. Prentice-Hall, New Jersey, 718 pp.

Zettler, ER and Carter, JCH 1986. Zooplankton community and species responses to a natural turbidity gradient in Lake Temiskaming, Ontario - Quebec. *Canadian Journal of Fisheries and Aquatic Science* 43:665-673.

Zhang, X, Daro, M and Tackx, M 1993. Comparison of Coulter Counter and 14C measurements of *Acartia tonsa* (Copepoda, Calanoida) grazing on *Chlamydomonas* sp. (Volvocales). *Hydrobiologia* 252(3):193-198.

Appendix 1: Zooplankton Taxa Recorded in the Swan River Estuary from 3rd October 1995 to 19th February 1997

Phylogeny follows that of the Integrated Taxonomic Information System[8].

Phylum Annelida

Class	Genus	Species	Comments
Polychaeta	Unknown	spp.	larvae and adults

Phylum Arthropoda, Subphylum Crustacea

Subclass	Genus	Species	Comments
Cirripedia	Unknown	spp.	larvae

Class	Subclass	Order	Suborder	Suborder	Infraorder	Family	Genus	Species	Comments
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Anomopoda	Daphniidae	*Ceriodaphnia*	sp.	
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Anomopoda	Daphniidae	*Daphnia*	sp.	
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Anomopoda	Bosminidae	*Bosmina*	sp.	
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Anomopoda	Chydoridae	*Chydorus*	sp.	
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Anomopoda	Chydoridae	*Pleuroxus*	sp.	
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	-	Ctenopoda	Sididae	*Penilia*	sp.	larvae

[8] Retrieved January, 2003, from the Integrated Taxonomic Information System on-line database, http://www.itis.usda.gov.

Class	Subclass	Order	Suborder	Suborder	Infraorder	Family	Genus	Species	Comments
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	Eucladocera	Onychopoda	Polyphemidae	*Podon*	sp.	larvae?
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	Eucladocera	Onychopoda	Polyphemidae	*Evadne*	sp.	larvae?
Branchiopoda	Phyllopoda	Diplostraca	Cladocera	Eucladocera	Onychopoda	Moinidae	*Moina*	sp.	

Class	Subclass	Superorder	Order	Suborder	Infraorder	Superfamily	Family	Genus	Species	Comments
Malacostraca	Eumalacostraca	Peracarida	Mysida	-	-	-	Mysidae	Unknown	sp.	larvae
Malacostraca	Eumalacostraca	Peracarida	Isopoda	-	-	-	-	Unknown	spp.	
Malacostraca	Eumalacostraca	Eucarida	Decapoda	Pleocymata	Anomura	-	-	Unknown	spp.	larvae
Malacostraca	Eumalacostraca	Eucarida	Decapoda	Pleocymata	Brachyura	-	-	Unknown	spp.	larvae
Malacostraca	Eumalacostraca	Eucarida	Decapoda	Dendrobranchiata	-	Sergestoidea	Luciferidae	*Lucifer*	sp.	
Malacostraca	Eumalacostraca	Eucarida	Decapoda	Dendrobranchiata	-	Penaeoidea	-	Unknown	spp.	larvae
Malacostraca	Eumalacostraca	Eucarida	Euphausiacea	-	-	-	Euphausiidae	Unknown	spp.	larvae

Class	Subclass	Infraclass	Superorder	Order	Family	Genus	Species	Comments
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	*Halicyclops*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Oithonidae	*Oithona*	*nana*	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	Unknown	sp. 1	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	Unknown	sp. 2	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	Unknown	sp. 3	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	Unknown	sp. 4	

Class	Subclass	Infraclass	Superorder	Order	Family	Genus	Species	Comments
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	Unknown	sp. 5	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Cyclopoida	Cyclopidae	*Cyclops*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Poecilostomatoida	Oncaeidae	*Oncaea*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Podoplea	Harpacticoida	Ectinosomidae	*Microsetella*	spp.	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Acartiidae	*Acartiura*	sp.	formerly referred to as *Acartia clausi*
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	*Gladioferens*	*imparipes*	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	*Boeckella*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	*Calamoecia*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	*Calamoecia*	*attenuata*	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	Unknown	sp. 1	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	Unknown	sp. 2	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Centropagidae	Unknown	sp. 3	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Acartiidae	*Acartia*	*longiremis*	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Paracalanidae	*Paracalanus*	sp. 1	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Paracalanidae	*Paracalanus*	sp. 2	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Pontellidae	*Labidocera*	sp.	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Temoridae	*Temora*	*longicornis*	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Sulcanidae	*Sulcanus*	*conflictus*	
Maxillipoda	Copepoda	Neocopepoda	Gymnoplea	Calanoida	Tortanidae	*Tortanus*	sp.	

Class	Genus	Species
Ostracoda	Unknown	spp.

Phylum Chaetognatha

Class	Order	Suborder	Family	Genus	Species	Comments
Sagittoidea	Aphragmophora	Ctinodontina	Sagittidae	Unknown	spp.	larvae

Phylum Chordata

Subphylum	Superclass	Class	Order	Family	Genus	Species	Comments
Tunicata	-	Appendicularia	Copelata	Oikopleuridae	Unknown	spp.	larvae
Vertebrata	Osteichthyes	-	-	-	Unknown	spp.	larvae and eggs

Phylum Ciliophora

Class	Subclass	Order	Suborder	Family	Genus	Species
Ciliatea	Spirotricha	Oligotrichida	Tintinnina	Tintinnidae	Unknown	spp.

Phylum Cnidaria

Class	Order	Suborder	Family	Genus	Species
Scyphozoa	Semaeostomeae	-	Ulmaridae	*Aurelia*	*aurita*
Scyphozoa	Rhizostomeae	Kolpophorae	Mastigiidae	*Phyllorhiza*	*punctata*

Phylum Echinodermata

Genus	Species	Comments
Unknown	spp.	larvae

Phylum Mollusca

Class	Subclass	Order	Family	Genus	Species	Comments
Bivalvia	Pteriomorphia	Mytiloida	Mytilidae	*Xenostrobus*	*securis*	larvae
Gastropoda	-	-	-	Unknown	spp.	larvae

Phylum Protozoa

Subphylum	Superclass	Class	Order	Genus	Species
Sarcodina	Rhizopoda	Granuloreticulosea	Foraminiferida	Unknown	spp.

Phylum Rotifera

Class	Order	Family	Genus	Species
Monogononta	Ploima	Brachionidae	*Brachionus*	*plicatilis*
Monogononta	Ploima	Synchaetidae	*Synchaeta*	sp.

Appendix 2: Results of Laboratory Based Measurement of Zooplankton Ingestion Rates

In each of the tables below, the following symbols are used:

g grazing coefficient

F filtration rate (ml.zooplankton^{-1}.hr^{-1})

I ingestion rate (µg Chla.zooplanton^{-1}.hr^{-1})

SE Standard error of the mean

All experiments used seawater of salinity 27, unless otherwise stated. % Standing Crop Removed Per Day was calculated by multiplying the Ingestion Rate (I) by the mean number of animals per litre used in the incubations. The number of zooplankton per litre reflects densities observed during field monitoring of zooplankton populations (as discussed in Chapter 2). Significance testing was based on a Kruskal-Wallace 1-Way ANOVA for non-parametric data.

Experiment 1, *G. imparipes* grazing on *Scrippsiella* sp. at 15°C, for 12 hours

Grazer	Initial Chl*a* Concentration (µg.L^{-1})	Mean ± SE *g*	Mean ± SE F	Mean ± SE I	% Standing Crop Removed per Day	Results of Significance Testing
Adult	2.7	0.080 ± 0.000	1.082 ± 0.146	0.0021 ± 0.000	141.4	Reject Ho – adult ingestion rate higher than nauplii
	5.8	0.051 ± 0.010	0.473 ± 0.056	0.0022 ± 0.000	96.8	Accept Ho - no effect of Chla concentration on ingestion rate
	10.2	0.032 ± 0.008	0.402 ± 0.091	0.0038 ± 0.001	69.8	
Nauplii	2.7	0.019 ± 0.016	0.095 ± 0.096	0.0002 ± 0.000	41.5	Accept Ho - no significant interaction between grazer age and food concentration
	5.8	0.025 ± 0.003	0.109 ± 0.007	0.0029 ± 0.001	273.6	

10.2	0.008 ± 0.003	0.034 ± 0.012	0.0004 ± 0.000	19.7

Experiment 2, *G. impariples* grazing on *Scrippsiella* sp. at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adult	10.6	0.008 ± 0.007	0.050 ± 0.064	0.7712 ± 1.427	52,306.8	Accept Ho - no difference between adult and nauplii ingestion rate
	22.4	0.014 ± 0.012	0.044 ± 0.082	0.3979 ± 1.424	33,547.5	Reject Ho - ingestion rate decreased with increase in Chl*a* concentration
Nauplii	10.6	0.004 ± 0.010	0.031 ± 0.084	0.2772 ± 0.731	4,791.0	Accept Ho - no significant interaction between grazer age and food concentration
	22.4	-0.018 ± 0.007	-0.095 ± 0.053	-1.1509 ± 0.657	0.0	

Experiment 3, *G. impariples* grazing on *Prorocentrum lima* at 15°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adult	2.4	-0.052 ± 0.024	-0.686 ± 0.327	-0.0012 ± 0.001	0.0	Accept Ho - no difference between adult and nauplii ingestion rate
	5.3	-0.002 ± 0.026	0.047 ± 0.323	-0.0001 ± 0.001	20.3	Accept Ho - no effect of Chl*a* concentration on ingestion rate
	8.9	0.003 ± 0.018	0.036 ± 0.335	-0.0002 ± 0.002	16.8	
Nauplii	2.4	-0.001 ± 0.000	-0.023 ± 0.008	0.0000 ± 0.000	0.0	Accept Ho - no significant interaction between grazer age and food concentration
	5.3	0.021 ± 0.025	0.702 ± 1.558	0.0008 ± 0.004	25.1	
	8.9	0.001 ± 0.018	-0.066 ± 0.715	-0.0012 ± 0.004	15.1	

Experiment 4, *G. impariples* adults grazing on *Prorocentrum lima* at 20°C, for 12 hours

Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
	g	F	I		
19.6	0.000 ± 0.012	-0.004 ± 0.021	-0.0001 ± 0.000	0.0	Accept Ho - no effect of Chl*a* concentration on ingestion rate
26.4	0.009 ± 0.006	0.015 ± 0.010	0.00034 ± 0.000	12.4	

Experiment 5, *G. impariples* adults grazing on *Gyrodinium* sp. at 25°C

Time	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
12 hr	4.0	0.154 ± 0.072	0.209 ± 0.070	0.0003 ± 0.000	87.7	Accept Ho - no effect of incubation period on ingestion rate Reject Ho - ingestion rate increased with increase in Chl*a* concentration Accept Ho - no significant interaction between incubation period and food concentration
	10.7	0.273 ± 0.080	0.343 ± 0.046	0.0011 ± 0.000	102.3	
24 hr	4.0	0.125 ± 0.037	0.139 ± 0.057	0.0002 ± 0.000	57.5	
	10.7	0.148 ± 0.047	0.242 ± 0.105	0.0006 ± 0.000	59.4	

Experiment 6, *G. imparipes* grazing on *Skeletonema costatum* at 15°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adult	1.4	-0.051 ± 0.019	-0.359 ± 0.187	-0.0006 ± 0.000	0.0	Accept Ho - no difference between adult and nauplii ingestion rate Reject Ho - ingestion rate increased with increase in Chla concentration Accept Ho - no significant interaction between grazer age and food concentration
	2.7	0.006 ± 0.014	0.082 ± 0.125	-0.0001 ± 0.000	0.0	
	3.6	0.042 ± 0.007	0.138 ± 0.032	0.0006 ± 0.000	65.7	
Nauplii	1.4	-0.087 ± 0.011	-0.025 ± 0.004	0.0000 ± 0.000	0.0	
	2.7	0.005 ± 0.005	0.001 ± 0.001	0.0000 ± 0.000	8.2	
	3.6	0.009 ± 0.012	0.003 ± 0.003	0.0000 ± 0.000	15.2	

Experiment 7, *G. imparipes* grazing on *Skeletonema costatum* at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adult	6.2	0.087 ± 0.030	0.158 ± 0.053	0.0007 ± 0.000	84.0	Reject Ho – adult ingestion rate higher than nauplii Accept Ho - no effect of Chla concentration on ingestion rate Accept Ho - no significant interaction between grazer age and food concentration
	12.0	0.057 ± 0.000	0.095 ± 0.019	0.0011 ± 0.000	18.5	
	23.2	0.076 ± 0.013	0.126 ± 0.031	0.0023 ± 0.001	90.1	
Nauplii	6.2	0.031 ± 0.007	0.016 ± 0.001	0.0001 ± 0.000	40.0	
	12.0	0.030 ± 0.013	0.021 ± 0.016	0.0003 ± 0.000	76.5	
	23.2	0.005 ± 0.013	0.002 ± 0.007	0.0000 ± 0.000	2.9	

Experiment 8, grazing on *Skeletonema costatum* at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
G. imparipes adults	14.7	-0.038 ± 0.011	-0.095 ± 0.029	-0.0014 ± 0.000	0.0	Accept Ho - no difference between adult *G. imparipes* and adult *B. plicatilis* ingestion rate Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between grazer type and food concentration
	22.0	-0.003 ± 0.001	-0.007 ± 0.002	-0.0002 ± 0.000	0.0	
	37.4	0.009 ± 0.013	0.021 ± 0.028	0.0008 ± 0.001	14.9	
B. plicatilis adults	14.7	-0.042 ± 0.005	-0.594 ± 0.060	-0.0062 ± 0.003	0.0	
	22.0	-0.008 ± 0.001	-0.108 ± 0.035	-0.0028 ± 0.001	0.0	
	37.4	0.000 ± 0.004	0.016 ± 0.062	0.0006 ± 0.003	1.4	

Experiment 9, *G. imparipes* adults grazing on *Skeletonema costatum* at 25°C

Time	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
12 hr	36.0	0.023 ± 0.008	0.068 ± 0.018	0.0022 ± 0.001	27.4	Accept Ho - no effect of incubation period on ingestion rate Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between incubation period and food concentration
	61.4	0.016 ± 0.010	0.035 ± 0.025	0.0008 ± 0.001	7.0	
24 hr	36.0	0.022 ± 0.003	0.056 ± 0.010	0.0016 ± 0.000	25.6	
	61.4	0.032 ± 0.005	0.075 ± 0.012	0.0038 ± 0.001	36.0	

Experiment 10, grazing on *Skeletonema costatum* at 25°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
G. imparipes	36.0	0.023 ± 0.008	0.068 ± 0.018	0.0022 ± 0.001	27.4	Reject Ho - *X. securis* ingestion rate higher than *G. imparipes*
	61.4	0.016 ± 0.010	0.035 ± 0.025	0.0008 ± 0.001	7.0	Accept Ho - no effect of Chl*a* concentration on ingestion rate
X. securis larvae	36.0	0.205 ± 0.025	1.017 ± 0.219	0.0143 ± 0.002	109.5	Accept Ho - no significant interaction between grazer type and food concentration
	61.4	0.163 ± 0.016	1.023 ± 0.074	0.0309 ± 0.001	107.9	

Experiment 11, *G. imparipes* grazing on *Dunaliella tertiolecta* at 15°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adults	114.2	0.0108 ± 0.009	0.0465 ± 0.039	0.0043 ± 0.004	13.9	Accept Ho - no difference between adult and nauplii ingestion rate
	250.6	0.0169 ± 0.013	0.0329 ± 0.028	0.0054 ± 0.004	17.7	Accept Ho - no effect of Chl*a* concentration on ingestion rate
	437.9	-0.0095 ± 0.003	-0.0205 ± 0.007	-0.0084 ± 0.003	-11.6	Accept Ho - no significant interaction between grazer age and food concentration
Nauplii	114.2	0.0198 ± 0.017	0.0031 ± 0.003	0.0003 ± 0.000	21.2	
	250.6	-0.0143 ± 0.001	-0.0024 ± 0.000	-0.0005 ± 0.000	-17.6	
	437.9	0.0385 ± 0.047	0.0040 ± 0.006	0.0006 ± 0.001	11.7	

Experiment 12, *G. impariped* grazing on *Dunaliella tertiolecta* at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
Adults	117.3	-0.0037 ± 0.004	-0.0114 ± 0.012	-0.0014 ± 0.002	-6.3	Accept Ho - no difference between adult and nauplii ingestion rate Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between grazer age and food concentration
	210.0	0.0103 ± 0.013	0.0421 ± 0.053	0.0072 ± 0.010	11.8	
	437.0	-0.0106 ± 0.001	-0.0475 ± 0.004	-0.0226 ± 0.002	-15.7	
Nauplii	117.3	-0.0030 ± 0.006	-0.0011 ± 0.002	-0.0001 ± 0.000	-4.7	
	210.0	0.0015 ± 0.009	0.0004 ± 0.005	-0.0001 ± 0.001	-1.6	
	437.0	-0.0134 ± 0.003	-0.0059 ± 0.002	-0.0029 ± 0.001	-21.5	

Experiment 13, grazing on *Dunaliella tertiolecta* at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
G. imparipes adults	159.5	0.0155 ± 0.004	0.0049 ± 0.001	0.0002 ± 0.000	-7.1	Accept Ho - no difference between adult *G. imparipes* and adult *B. plicatilis* ingestion rate Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between grazer type and food concentration
	300.4	-0.0108 ± 0.001	-0.0166 ± 0.003	-0.0037 ± 0.001	-11.0	
	598.1	-0.0017 ± 0.003	-0.0019 ± 0.003	-0.0008 ± 0.001	1.7	
B. plicatilis adults	159.5	0.0054 ± 0.001	0.0024 ± 0.000	0.0003 ± 0.000	2.8	
	300.4	-0.0058 ± 0.002	-0.0065 ± 0.004	-0.0012 ± 0.001	-4.6	
	598.1	0.0007 ± 0.001	0.0007 ± 0.001	0.0003 ± 0.000	1.3	

Experiment 14, *G. imparipes* adults grazing on *Dunaliella tertiolecta* at 25°C, for 12 hours

Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
	g	F	I		
34.0	0.0073 ± 0.007	0.0101 ± 0.010	0.0003 ± 0.000	10.4	Accept Ho - no effect of Chl*a* concentration on ingestion rate
116.1	0.0159 ± 0.009	0.0309 ± 0.013	0.0028 ± 0.001	18.2	
154.9	0.0111 ± 0.011	0.0182 ± 0.017	0.0025 ± 0.002	11.5	

Experiment 15, *G. imparipes* adults grazing on *Dunaliella tertiolecta* at 25°C

Time	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
12 hr	116.1	0.0159 ± 0.009	0.0309 ± 0.013	0.0028 ± 0.001	10.4	Accept Ho - no effect of incubation period on ingestion rate Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between incubation period and food concentration
	154.9	0.0111 ± 0.011	0.0182 ± 0.017	0.0025 ± 0.002	18.2	
24 hr	116.1	0.0193 ± 0.010	0.0205 ± 0.007	0.0018 ± 0.001	11.5	
	154.9	0.0068 ± 0.002	0.0093 ± 0.003	0.0015 ± 0.000	18.2	

Experiment 16, grazing on *Cryptomonas* sp. at 20°C, for 12 hours

Grazer	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
G. imparipes adults	64.1	0.0189 ± 0.007	0.0303 ± 0.010	0.0016 ± 0.001	21.3	Reject Ho - adult *G. imparipes* ingestion rate higher than adult *B. plicatilis* Accept Ho - no effect of Chl*a* concentration on ingestion rate Accept Ho - no significant interaction between grazer type and food concentration
	130.8	0.0145 ± 0.004	0.0234 ± 0.006	0.0027 ± 0.001	17.4	
	243.0	0.0075 ± 0.003	0.0133 ± 0.007	0.0028 ± 0.002	10.1	
B. plicatilis adults	64.1	0.0038 ± 0.001	0.0052 ± 0.000	0.0040 ± 0.001	21.3	
	130.8	0.0035 ± 0.003	0.0104 ± 0.009	0.0008 ± 0.001	6.2	
	243.0	0.0063 ± 0.009	0.0078 ± 0.013	0.0014 ± 0.003	5.4	

Experiment 17, *G. imparipes* adults grazing on *Cryptomonas* sp. at 25°C, for 12 hours

Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
	g	F	I		
42.1	0.0095 ± 0.010	0.0067 ± 0.019	0.0002 ± 0.001	3.3	Accept Ho - no effect of Chl*a* concentration on ingestion rate
86.8	-0.0084 ± 0.004	-0.0191 ± 0.009	-0.0018 ± 0.001	-13.5	
178.9	0.0201 ± 0.009	0.0439 ± 0.018	0.0070 ± 0.003	24.0	

Experiment 18, *G. imparipes* adults grazing on *Cryptomonas* sp. at 25°C

Time	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
12 hr	86.8	-0.0084 ± 0.004	-0.0191 ± 0.009	-0.0018 ± 0.001	-13.5	Accept Ho - no effect of incubation period on ingestion rate
	178.9	0.0201 ± 0.009	0.0439 ± 0.018	0.0070 ± 0.003	24.0	
24 hr	86.8	-0.0036 ± 0.001	-0.0154 ± 0.007	-0.0015 ± 0.001	-6.1	Accept Ho - no effect of Chl*a* concentration on ingestion rate
	178.9	-0.0041 ± 0.003	-0.0140 ± 0.012	-0.0028 ± 0.002	-9.0	Accept Ho - no significant interaction between incubation period and food concentration

Experiment 19, *G. impariped* adults grazing on *Chlamydomonas* sp. at 20°C, for 12 hours and salinity 5

Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
	g	F	I		
32.0	-0.0054 ± 0.002	-0.0076 ± 0.002	-0.0006 ± 0.000	-16.3	Accept Ho - no effect of Chl*a* concentration on ingestion rate
54.1	-0.0061 ± 0.002	-0.0126 ± 0.007	-0.0007 ± 0.000	-10.9	
66.8	0.0134 ± 0.005	0.0201 ± 0.005	0.0006 ± 0.000	7.4	

Experiment 20, *G. impariped* adults grazing on *Chlamydomonas* sp. at 25°C, for 12 hours and salinity 5

Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
	g	F	I		
55.4	0.0030 ± 0.002	0.0048 ± 0.002	0.0002 ± 0.000	3.2	Accept Ho - no effect of Chl*a* concentration on ingestion rate
88.1	-0.0039 ± 0.013	-0.0098 ± 0.018	-0.0009 ± 0.001	-11.5	
106.8	-0.0154 ± 0.006	-0.0183 ± 0.007	-0.0028 ± 0.001	-30.4	

Experiment 21, *G. impariped* adults grazing on *Chlamydomonas* sp. at 25°C

Time	Initial Chl*a* Concentration ($\mu g.L^{-1}$)	Mean ± SE			% Standing Crop Removed per Day	Results of Significance Testing
		g	F	I		
12 hr	88.1	-0.0039 ± 0.013	-0.0098 ± 0.018	-0.0009 ± 0.001	-11.5	Accept Ho - no effect of incubation period on ingestion rate
	106.8	-0.0154 ± 0.006	-0.0183 ± 0.007	-0.0028 ± 0.001	-30.4	
24 hr	88.1	0.0195 ± 0.007	0.0224 ± 0.007	0.0017 ± 0.000	23.3	Accept Ho - no effect of Chl*a* concentration on ingestion rate
	106.8	0.0102 ± 0.006	0.0141 ± 0.009	0.0009 ± 0.001	6.6	Accept Ho - no significant interaction between incubation period and food concentration

Appendix 3: Phytoplankton and Zooplankton Parameters Used in CAEDYM.

Phytoplankton Symbols	
β_{ep}	value of f(S) when salinity is 2 x S_{opt} (freshwater) or zero (marine)
c_4	maximum upward migration velocity
c_5	maximum downward migration velocity
I_K	initial slope for photosynthesis-irradiance curve
IN_{max}	maximum internal N concentration
IN_{min}	minimum internal N concentration
k_c	specific light attenuation coefficient for chlorophyll *a*
K_N	half saturation constant for nitrogen
K_P	half saturation constant for phosphorous
$k_{r,p}$	rate coefficient for respiration
K_{Si}	half saturation constant for silica
P_{max}	maximum potential growth rate
S_{opt}	optimum salinity
T_{max}	maximum temperature, where growth rate is zero
T_{opt}	optimum temperature, where growth rate is maximal
T_{sta}	minimum temperature, where growth rate is no longer exponential
θ_{pg}	temperature multiplier for respiration
θ_{pr}	settling velocity
W_s	temperature multiplier for growth
Y_{CC}	ratio of carbon to chlorophyll *a*

Zooplankton Symbols	
A	assimilation rate
β_z	value of f(S) when salinity is zero
k_r	respiration rate coefficient
k_i	grazing rate
K_i	half saturation constant for grazing
k_z	fraction of total loss contributed by excretion
P_{ij}	preference of zooplankton group i for grazing phytoplankton group j
P_{ik}	preference of zooplankton group i for grazing zooplankton group k
θ_z	temperature dependence

Appendix 4: Co-Author Statements

Attached are letters from the co-authors of published papers, attesting to their relative contributions.

Note: For privacy reasons Appendix 4 has not been reproduced in full.

(Co-ordinator, ADT Project (Retrospective), Curtin University of Technology, 11/02/2004)