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The Role of Zooplankton Feeding in Nitrogen and Carbon Cycling in Port Phillip Bay

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EXECUTIVE SUMMARY

1. The zooplankton abundance and species composition of Port Phillip Bay has been characterised in three studies. Zooplankton consists largely of copepods, cladocerans and larvaceans. Microzooplankton (50-150 μm) was dominated by tintinnid ciliates. Differences in methodology between the studies makes comparisons difficult. Variation in estimated standing stocks between years was considerable.

2. Feeding rates for the major Port Phillip Bay taxa were obtained from both local studies and from the international literature. Functional responses are available for the major grazing taxa with the exception of raptorially feeding cladocerans and l arvaceans. Weight-specific parameters generally varied greatly with stage of development. All laboratory estimates are affected by a variety of variables and application to the field situation will be subject to large errors.

3. Assimilation efficiency estimates were not available for most of the major Bay taxa, however, estimates for other zooplankton species are fairly constant. Typical values for assimilation efficiencies range between 0.70 and 0.85. Assimilation efficiencies for microzooplanktonic protozoa were 0.90 to 1.00.

4. Production to biomass (P:B) ratios reported for some Port Phillip Bay taxa in other systems ranged from 0.1-0.5 d^{-1}. Typical values for temperate water communities were around 0.2 d^{-1}.

5. Excreted ammonium is taken up by phytoplankton in preference to nitrate. In some areas remineralised nitrogen from zooplankton is essential for the maintenance of primary production. Size-specific nitrogen excretion rates in other systems varied with season, food quality and size of animals. Few estimates are available for size-specific nitrogen excretion rates for Port Phillip Bay taxa.

6. Literature values for gross growth efficiency for Port Phillip Bay taxa were fairly constant at 0.40 to 0.50. Gross growth efficiency was higher for the cladoceran, *Penilia avirostrus*. No estimates are available for larvaceans or raptorially feeding cladocerans.

7. The role of bacteria in pelagic ecosystems is not well understood, however, there is increasing evidence that they are important consumers of primary production in the form of organic nutrients released by phytoplankton, thereby returning this to the food chain. Bacteria may form the basis of a food chain involving nanoflagellates, ciliates and crustacean zooplankton, as an alternative to direct grazing on phytoplankton. Ciliates are important components in the diets of some copepods nd cladocerans. The importance of picoplankton (< 2 μm) including bacteria in Port Phillip Bay is unknown.

8. Grazing parameters for micro- and nanoplankton were also reviewed. Maximum C-specific ingestion rates ranged from 0.1 to 0.2 d^{-1} for ciliates. Assimilation efficiency ranged between 0.90 and 1.00, and growth efficiency ranged between 0.40 and 0.50. The abundance and composition of heterotrophic microplankton (20-50 μm) and nanoplankton (2-20 μm) in Port Phillip Bay is unknown.

9. For mesozooplankton, an estimated grazing rate of 0.066 d^{-1} was obtained, based on the available information, giving mean clearance time for the entire Bay of 15 d and a range of between 11 and 42 days. However, even with the wide range, this value is considered dubious due to limitations in the data. A conservative estimate for microzooplankton of 0.065 d^{-1} indicated that grazing by this group may be of greater importance than the mesozooplankton.

10. Nutrient regeneration rates, based on an assimilation efficiency of 0.75 and a gross growth efficiency of 0.45, would be approximately 40% of assimilated nutrient.

11. A modern plankton survey including size-specific information in combination with literature derived parameters may provide first order estimates of grazing for modelling, however, errors on estimates would be expected to be large. A better, more cost efficient approach may be to carry out dilution experiments to determine microplankton grazing together with *in situ* assemblage level estimates of mesozooplankton grazing, carried out concurrently with primary production estimates. A possible extension would be to carry out ^{15}N uptake and regeneration experiments, although these are logistically and analytically more complex.

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1.0. INTRODUCTION

One of the aims of the Port Phillip Bay Environmental Study is to determine the environmental status of the Bay in relation to nutrients and toxicants. Various modelling tasks involving evaluation of physical processes, nutrients, toxicants and the ecology of the Bay will be undertaken. Earlier literature reviews have highlighted areas where present understanding of some ecological processes is lacking, and one of these areas concerns the role of zooplankton in the Port Phillip Bay ecosystem. The aim of this review is to provide an assessment of grazing rates, assimilation efficiencies, growth efficiencies and nutrient regeneration rates of zooplankton in Port Phillip Bay, in order to enable the modelling activities to proceed effectively.

Task objectives:

1. To document the state of present knowledge of rates of feeding, assimilation efficiencies and excretion rates and products of zooplankton in Port Phillip Bay.

2. To estimate zooplankton grazing rates, production, and nutrient cycling rates based on existing data on zooplankton biomass and composition in Port Phillip Bay and on national and international literature on zooplankton grazing rates and ecology. To document seasonal and spatial variations in the above where possible.

3. To suggest cost effective experimental designs to obtain an improved quantitative assessment of the role of zooplankton in Port Phillip Bay.

2.0. ZOOPLANKTON OF PORT PHILLIP BAY

Three studies have characterised the species composition and abundance of zooplankton in Port Phillip Bay.

A major study of the zooplankton of Port Phillip Bay was carried out in 1969-70 as part of the Port Phillip Bay Phase One project (MMBW and FWD, 1973), with a view to determining the species composition and estimating standing crop and seasonal variation in the major taxa. The sampling strategy involved sampling the entire water column at twelve stations using a Clarke-Bumpus sampler at six week intervals over a one year period. Three different mesh sizes (159, 190 and 262 μm) were used over this period. Arnott (1974) found that crustacean zooplankton consisted of four main groups - Copepoda (82%), Cladocera (13%), Malacostraca (5%), and Cirripedia (0.4%). Within the copepods *Acartia clausi* (identified as *A. tranteri* in later studies) was dominant over the summer period, while *Paracalanus parvus* (later identified as *P. indicus*) dominated over the winter. These two species represented 35 and 33% of the annual crustacean standing crop respectively. Within the Cladocera, *Evande nordmanni* and *Podon intermedius* were the main species, comprising 8.6 and 4.3% of the total crustacean standing crop respectively. The mean crustacean standing crop for 1969-70 was estimated at 3700 individuals m^{-3}.

Kimmerer and McKinnon (1985) sampled Port Phillip Bay between July 1982 and August 1983. The entire water column was sampled approximately monthly at eight stations using a 200 μm mesh net. The aim of the study was to document spatial and seasonal patterns of zooplankton abundance and to compare the zooplankton of Port Phillip Bay with that of the nearby Western Port. Variation in the abundance of common taxa among central Bay stations was not significant. The holoplankton (>200 μm) was comprised of 48% copepods, 23% cladocerans and 21% larvaceans (*Oikopleura dioica*). The copepod fraction included 32% *Paracalanus indicus* and 6% *Acartia tranteri*. Planktonic carnivores (*Tortanus barbatus*, chaetognaths, ctenophores and medusae) comprised 5% of the plankton. Cladocerans showed strong seasonal variations in abundance patterns. *Evande nordmanni*, abundant in winter, was replaced in summer by *E. tergestina* and *Podon polyphemoides*. *P. intermedius* was common all year, while *Penilia avirostris* appeared only in autumn. Among the copepods, *Paracalanus indicus* was common throughout the year, while *A. tranteri* declined in winter. *Oithona similis* was absent in summer. The seasonal abundances of many taxa were explained on the basis of their temperature tolerance (Kimmerer and McKinnon, 1985). The mean total holoplankton abundance (>200 μm) was 1480 individuals m^{-3}.

Fancett (1988) sampled the water column monthly during 1986, using two mesh sizes (50 μm and 150 μm) to sample different size fractions of the plankton. Samples were taken from a single station, so spatial variation was not taken into account in this study. During 1986 mesozooplankton (>150 μm) consisted mainly of copepods (58%), larvaceans (18%), bivalve larvae (9%) and cladocerans (5%). *Paracalanus indicus* and *Acartia tranteri* constituted 23% and 6% of the total zooplankton respectively, and *Oithona australis* and *O. similis* comprised 8% and 5% of this fraction. The mean total zooplankton (>150 μm) abundance for the period December 1985 to December 1986 was 4376 individuals m^{-3}. Microzooplankton (50-100 μm) had a mean abundance of 207 x 10^3 individuals m^{-3} and consisted of tintinnid ciliates (39%), copepod nauplii (26%), bivalve larvae (16%), rotifers (9%) and larvaceans (6%). There was little seasonal variation in the total abundance of zooplankton. Among individual taxa, *A. tranteri* and *P. indicus* had maximum abundance over summer and declined in winter. The cladocerans *Evande* were absent over winter. Microzooplankton abundance was variable but showed no seasonal patterns.

The use of different sizes of mesh in the above studies limits analysis of interannual variation in the total and relative abundances of taxa, however some general statements can be made. Arnott (1974) reported *Acartia tranteri* and *Paracalanus indicus* to be equally abundant, while in 1982-83 *P. indicus* outnumbered *A. tranteri* 12:1 (Kimmerer and McKinnon, 1985), and by 4:1 in 1986 (Fancett, 1988). The predatory copepod *Tortanus barbatus* had much lower abundances in 1986 than reported in previous studies, and was apparently replaced by *Coryceaus* sp (Fancett, 1988). The apparently smaller proportion of cladocerans found in 1986 may be an artifact of the smaller mesh used. Actual abundances were not given by Fancett (1988). The larvacean *Oikopleura dioica* was an important component of the zooplankton in 1982-83 and 1986, comprising 21% and 18% of the zooplankton respectively (Kimmerer and McKinnon, 1985; Fancett, 1988), however the abundance of larvaceans was negligible in 1969-70 (Arnott, 1974).

Estimates of total zooplankton abundances varied considerably between the three studies. Aside from the effect of different mesh sizes used, climatic conditions and differences in primary production may have contributed to this variability. Arnott's (1974) study was carried out during a period of exceptionally high rainfall, while that of Kimmerer and McKinnon (1985) was during a drought period. Estimates of primary productivity were 0.8 mg Chl *a* m^{-3} in 1983 and 1.7 mg Chl *a* m^{-3} in 1986 (Kimmerer and McKinnon, 1985).

3.0. FEEDING AND INGESTION RATES

Zooplankton feeding rates are fundamental data for ecological studies. The feeding of zooplankton may be described by four parameters: F, the volume swept clear of food over a given period; I_{max}, the maximum ingestion rate; C_t, the threshold concentration of food below which feeding does not occur; and C_c, the critical concentration at which I_{max} is attained and beyond which F declines (Durbin and Durbin, 1992). It is thought that the clearance rate declines as food supply increases above the critical concentration, however there is some disagreement over this as copepods may be able to adapt over time to increased food concentrations without a decrease in F_{max}. Values of F and I most commonly occur in the literature, while there are fewer estimates of threshold and critical concentrations.

Feeding rates are generally determined in laboratory incubations, involving estimation of the depletion of food particles over a short time period. In order to account for the growth of algal populations during the course of experiments a system of equations developed by Frost (1972) is commonly used. Clearance rate is calculated from the change in cell concentration over time in experimental (with animals) and control containers (without animals). Algal growth over the duration of the incubations are corrected for by using the rate of increase calculated from the control containers. Ingestion rate is then calculated from clearance rate by multiplying by the time averaged concentration of food particles. A criticism of this method is that it assumes that the feeding rate remains constant over the period of incubation, which often may not be the case (McClatchie and Lewis, 1986). An alternative method in which time series measurements of change in algal concentration are used has been proposed (McClatchie and Lewis, 1986), however no comparative data was given for evaluation of the method.

The change in food concentration in experimental containers over time may be estimated in a number of ways. Food particles may be enumerated microscopically or electronically using a Coulter Counter. Paffenhöffer (1982) found that visual counts were more reliable because electronic counts increasingly overestimated the abundance of cells as food was depleted. Chlorophyll concentration can provide an estimate of food concentration in the experimental containers and this value can be converted to cell numbers (e.g. Jagger *et al.*, 1988). Alternatively, radiolabelled phytoplankton can be fed to zooplankton, and the amount ingested is estimated from the activity of the gut contents after a short incubation. Clearance rate is calculated using the activity of water samples (e.g. Kimmerer and McKinnon, 1989).

In an analysis of more than 1600 published data on filtration and ingestion rates for zooplankton species, Peters and Downing (1984) found that experimental conditions significantly affected values obtained. The density of animals used (crowding) and the duration of incubations were both significantly correlated with feeding rates.

Various natural factors may also affect the feeding rates of zooplankton. Filtration and ingestion rates were positively correlated with temperature (Dam and Peterson, 1988; Durbin and Durbin, 1992; Kiørboe *et al.*, 1982), animal size (Berggreen *et al.*, 1988; Peters and Downing, 1984) and negatively correlated with observed food concentration (Kiørboe *et al.*, 1982; Peters and Downing, 1984). Thus variation in published rates (see Table 1) may be due to one or more of the above factors, as well as the method used. The application of feeding rates to ecological studies must be approached with caution, as estimates obtained from short term incubations do not take into account the well documented diel (e.g. Dagg *et al.*, 1989; Dam, 1986; Durbin, *et al.*, 1990) and seasonal (e.g. Bamstedt, 1985; Hassett and Landry, 1990) variation in feeding activity.

In the following sections on feeding rates within the Cladocera and Copepoda, only data on the important genera of Port Phillip Bay are considered. A large amount of data on other taxa, particularly *Calanus*, has been published but is not considered relevant to this review.

3.1 Copepoda

3.1.1 *Paracalanus*

The genus *Paracalanus* is numerically dominant in Port Phillip Bay, in particular the species *Paracalanus indicus*. Kimmerer and McKinnon (1989) examined the feeding of *P. indicus* in Port Phillip Bay. In laboratory incubations using both natural and artificial food, *P. indicus* consumed particles from 2.5-20.3 μm ESD (estimated spherical diameter). 40-120 minute incubations with radiolabelled cultures of the flagellate *Tetraselmis chui* (10 x 20 μm) yielded clearance rates of 2.5-15.1 ml individual^{-1} d^{-1} ([a] 0.8 to 5.0 ml μg body C^{-1} d^{-1} at 3 μg C female body weight).

Checkley (1980) investigated feeding in adult female *Paracalanus parvus* (body weight 3 μg C and 0.74 μg N). No threshold concentration was apparent. The critical concentration occurred at about 47 μg C l^{-1} (8 μg N. l^{-1}). The maximum clearance rate was 30 ml μg C^{-1} d$^{-1.}$. The average maximum rate of ingestion was about 1.5 μg N μg body N^{-1} d^{-1}, or specific ingestion of 1.5 d^{-1}. Specific ingestion rate in terms of C rose to 3.6 d^{-1} for feeding on N-deficient *Thalassioria*, suggesting *Paracalanus* can ingest large amounts of carbon to obtain their ration of nitrogen. Functional relationships are provided.

Feeding in *Paracalanus* has been studied extensively by Paffenhofer (1982, 1984a,b). When fed a mixture of three phytoplankton species between 6 and 25 μm ESD, the two larger species were consumed first. The clearance rate for small cells was much lower than that for the larger species over 48 hours, although the initial concentrations of the three species were equal (ca 0.5 mm^3 l^{-1}). Following depletion of large cells to a concentration of 0.2 mm^3 l^{-1}, *Paracalanus* were able to reduce the concentration of the smaller cells, although the clearance rate for this species did not increase (Paffenhofer, 1982). Clearance rates in this study were between 3 and 30 ml μg body C^{-1} d^{-1}, and varied with food size, but not concentration of food particles. No lower feeding threshold was apparent in *Paracalanus* (Paffenhofer, 1988)

In a similar study, Paffenhofer (1984b) found that weight specific ingestion rates of *Paracalanus* were reduced when a mixture of algal species was offered, compared to copepods feeding on a single algal species.

Copepods ingested larger particles as they grew, while the relative importance of small particles in the diet declined (Paffenhofer, 1984b). Particle size ingested varied disproportionately with animal size (Paffenhofer, 1984a), that is, the increase in ingestion rate with body size was greater for larger sized particles. There was also evidence for the behavioural control of feeding. Proportions of ingestion rates between algal species varied with increasing copepod size differently at different food concentrations. Ingestion of *Thallasiosira weissflogii* remained constant at two food concentrations (0.1 and 0.3 $mm^3\ l^{-1}$), while ingestion of the smaller *Isochrysis galbana* increased with body size more rapidly at the lower concentration. This could not be explained by mechanical processes alone but was attributed to increased sensitivity of sensors on the food collecting mouthparts (Paffenhofer, 1984a).

Paffenhöfer (1984b) provided relationships between weight specific ingestion in relation to body weight of developmental stages of *Paracalanus* in uni-algal and multi-algal experiments. Specific ingestion ranged from 0.5 to 2 d^{-1} of body N depending on prey species, concentration, developmental stage and phytoplankton species mixture. Of most value to modelling is the ingestion functions for *Paracalanus* formulated by Ambler (1986). This model draws together work described above to relate weight specific ingestion to food concentration for all developmental stages using Ivlev functions. Food concentrations are weighted by selectivity coefficients for phytoplankton size classes. Maximum ingestion rates increased with developmental stage to a peak of about 1.2 μg N μg body $N^{-1}\ d^{-1}$.

3.1.2 *Acartia*

This genus is represented in Port Phillip Bay by the fairly abundant *Acartia tranteri*, although this species is much more abundant in the nearby Western Port (Kimmerer and McKinnon, 1985). There is limited data on feeding of *A. tranteri*, however there are a number of studies on the northern hemisphere species *Acartia tonsa* which is a similar size. A number of studies are also available for *A. hudsonica*, which is slightly larger than *A. tranteri*. Comparisons are complicated by the fact that the population in Port Phillip Bay originally attributed to *A. tranteri* has now been separated into two species, largely on the basis of size (McKinnon *et al*., 1992).

The feeding of *Acartia tranteri* has been studied by Kimmerer and McKinnon (1989). The size range of particles consumed was determined by incubation in natural Port Phillip Bay water with and without the addition of phytoplankton. Incubations were 24 hours in duration and particle counts were performed using a Coulter Counter on control and experimental bottles. The range of particle sizes encountered was 2.5-20.3 μm ESD. *A. tranteri* consumed particles larger than 4 μm, in contrast to *Paracalanus indicus* which consumed all sizes of particles offered. Feeding by *A. tranteri* on the small flagellate *Isochrysis* was negligible. Experiments using radiolabelled *Tetraselmis chui* showed that over the 40-120 minute incubation period, *A. tranteri* had much lower clearance rates than *P. indicus* (0.4-1 ml μg body $C^{-1}\ d^{-1}$ cf. 0.8-5.0 ml μg body $C^{-1}\ d^{-1}$ for *P. indicus*.).

Kiørboe *et al*. (1985) constructed carbon and nitrogen budgets for *Acartia tonsa* feeding on a single phytoplankton species at 18° C. A weight/length relationship was determined [Weight (μg dry weight) = 13.4 $Length^3$), giving an adult weight about 7 μg. The functional relationship between ingestion and food concentration was determined, resulting in an ingestion maximum of 0.28 μg C μg body $C^{-1}\ d^{-1}$ or specific ingestion of 1.8 d^{-1} body carbon.

The maximum clearance rate was about 0.68 ml μg body C^{-1} d^{-1} and the functional relationship with food concentration is given.

Clearance rates for all developmental stages of *Acartia tonsa* feeding on different sized spherical algae were measured by Berggreen *et al.* (1988). Copepods were incubated for 24 hours with each of 10 phytoplankton species presented individually. The initial concentration for all algal species was 0.6-0.7 ppm. Cells were enumerated using a Coulter Counter, except for the largest species (71 and 247 μm ESD) which were counted microscopically. Clearance rates were calculated according to Frost (1972). The lowest size limit of particles ingested was 2-4 μm diameter, and these particles were consumed by copepods at all developmental stages. Not surprisingly the maximum size of particles ingested increased with developmental stage up to the maximum size offered (247 μm). Optimum food size for all developmental stages of *Acartia tonsa* was 2-5% of prosome length.

Clearance rates of *Acartia tonsa* increased 2 to 3 orders of magnitude during development (Berggreen *et al.*, 1988). Figures are presented from which weight specific clearance rates can be determined for different stages of development and food types. The relationship between specific ingestion rate and prey concentration is presented, reaching a maximum of approximately 1.2 d^{-1} body C (Berggreen *et al.*, 1988). The range of food sizes eaten and the clearance rates for the different algal species offered were based on uni-algal experiments, however there is considerable evidence that these parameters may be modified when feeding on mixed diets or natural particle assemblages, due to discrimination on the basis of quality (Paffenhofer and Van Sant, 1985) or size (Paffenhofer, 1984a,b).

Støttrup and Jensen (1990) cultured *Acartia tonsa* on a number of algal species. The critical concentration was about 90 μg C l^{-1}. Maximum clearance rate varied between about 0.4-3.2 ml μg body C^{-1} d^{-1} depending on algal species. Tabulated values of maximum ingestion rate peaked at about 0.5 μg C μg body C^{-1} d^{-1} for two species. This corresponded to a specific ingestion rate of 3.0 d^{-1} body C.

White and Roman (1992) used *in situ* radiolabelling to estimate grazing parameters for *Acartia* in Chesapeake Bay. Weight specific clearance rate for *A. hudsonica* decreased from 0.38 ml μg body C^{-1} d^{-1} for nauplii to 0.053 ml μg body C^{-1} d^{-1} for adults. The values for *A. tonsa* decreased from 2.56 ml μg body C^{-1} d^{-1} for nauplii to 0.36 ml μg body C^{-1} d^{-1} for adults. Carbon specific ingestion rates in *A. hudsonica* decreased from 1.79 μg C μg body C^{-1} d^{-1} for nauplii to 0.11 μg C μg body C^{-1} d^{-1} for adults, and for *A. tonsa* decreased from 2.80 μg C μg body C^{-1} d^{-1} for nauplii to 0.58 μg C μg body C^{-1} d^{-1} for adults.

The effect of temperature and food availability on feeding in *Acartia hudsonica* in Narragansett Bay was studied by Durbin and Durbin (1992). Copepods were incubated at 4.5, 8, 12 and 16° C with the diatom *Thalassiosira constricta* (17 μm ESD) at various concentrations. Maximum clearance rates were similar at all temperatures (20.8-23.9 ml $individual^{-1}$ d^{-1}), but weight specific clearance increased from 3.3 to 6 ml μg C^{-1} d^{-1} depending on temperature (Q_{10}=1.8). Critical concentrations varied between 840 and 1900 cells ml^{-1} (170-230 μg C l^{-1}), and were not related to temperature, and threshold concentrations were 9-20 μg C l^{-1}. Maximum ingestion rate increased from 16460 to 29960 cells $individual^{-1}$ d^{-1} or 0.439 to 0.929 body C d^{-1} (Q_{10}=2.3) over the temperature range examined.

The critical food concentrations reported by Durbin and Durbin (1992) were sometimes exceeded in the field, suggesting that feeding was saturated at least some of the time.

Reeve and Walter (1977) reported a critical concentration of 350 μg C l^{-1} for *A. tonsa* feeding on 3 phytoplankton species, while threshold concentrations were 7-18 μg C l^{-1}. The maximum clearance rate of *A. tonsa* was about 2 ml μg body C^{-1} d^{-1}; declining sharply at concentrations of 10-20 μg C l^{-1}, in contrast to *Paracalanus* which continued feeding at lower food concentrations (Paffenhofer and Stearns, 1988).

Laboratory determined critical and threshold concentrations probably have low applicability to field situations. Threshold concentrations in the field were shown to be much higher, possibly due to the lower proportion of unavailable particulate carbon compared with phytoplankton cultures. For several crustacean species feeding on natural particulate assemblages, no critical concentration was observed (Paffenhofer, 1988; Huntley, 1981).

Differential ingestion and clearance rates for *Acartia tonsa* feeding on dinoflagellates (*Heterocapsa triquetra*) and a tintinnid ciliate (*Favella*) were recorded by Stoecker and Sanders (1985). *A. tonsa* were fed monocultures and mixtures of the two food items at concentrations from 0-1500 cells ml^{-1} for *Heterocapsa* and 0-3.5 cells ml^{-1} for *Favella*. Incubations were 8 hours in duration and were performed at night. Cell densities were estimated microscopically, and clearance rates calculated according to Frost (1972). Ingestion rates for *Heterocapsa* increased with increasing density up to 648 cells ml^{-1}, then declined at higher densities. With *Favella* as the sole food, ingestion rate increased with food concentration over the entire range of food offered. When fed combinations of the two food items the ingestion of *Favella* was not affected by the concentration of *Heterocapsa*.

When mixture of the two foods was given, the clearance rate by *Acartia tonsa* was higher for *Favella*, even when the concentration and biomass of *Heterocapsa* was much greater. Clearance rates for both food items declined with increasing concentrations of *Heterocapsa*. Clearance rates were 25-87 ml μg body C^{-1} d^{-1} for *Favella* and 0-40 ml μg body C^{-1} d^{-1} for *Heterocapsa*. The results of this study show that copepods may feed preferentially on tintinnids, thus playing a potentially important role in the regeneration of nutrients through the microbial food web (see below). Feeding by crustacean zooplankton on tintinnids and other microzooplankters may not be evident from studies of fecal pellets (e.g. Kim *et al.*, 1989; Jagger *et al.*, 1988). Gifford and Dagg (1988) found positive selection for heterotrophic microzooplankton by *A. tonsa*. In experiments where natural concentrations of phytoplankton and heterotrophic microzooplankton (mainly aloricate and tintinnid ciliates) were offered, the ratio of microzooplankton carbon:phytoplankton carbon consumed was 0.69 in summer and 0.03 in winter. Ratios offered were 0.03 and 0.004 in summer and winter respectively. Nevertheless, phytoplankton comprised 60% (summer) and 97% (winter) of the diet due to its greater abundance.

3.1.3 *Oithona*

Cyclopoid copepods of the genus *Oithona* made up 10% of the total crustacean zooplankton of Port Phillip Bay in 1969-70 (MMBW and FWD, 1973), and are important world-wide as members of the zooplankton (Paffenhofer, 1993).

Despite this, there is no information on feeding of *Oithona* in Port Phillip Bay, and only a small number of studies on the genus world-wide.

The functional response of *Oithona nana* to several food items was studied by Lampitt and Gamble (1982). Food species were given individually, and included 5 phytoplankton species (4.1-27.5 μm longest dimension) and copepod nauplii of two species (110-300 μm). Incubations lasted 24 h and clearance rates were calculated according to Frost (1972). The relationship between food size and ingestion rate was not clear cut, although rates tended to be lower for smaller foods. Maximum clearance rates ranged from 0.48 to 44.9 ml μg body C^{-1} d^{-1} depending on food species. Ingestion rate ranged from 0.004 to 0.37 μg C μg body C^{-1} d^{-1} and specific ingestion ranged from 0.04 to 0.415 body C d^{-1}. Maximum clearance and ingestion rates were obtained using *Acartia clausi* nauplii (110 μm) as the food source. *Oithona nana* is a raptorial feeder and was capable of feeding on a wide range of prey sizes.

Landry and Fagerness (1988) obtained maximal clearance rates of 45 ml individual^{-1} d^{-1} for *Oithona spinirostris* (at an adult size of 2 μg this equates to about 56.3 ml μg body C^{-1} d^{-1}) feeding on nauplii of *Calanus pacificus*. The incubations ran for 24 hours at prey concentrations of 40-150 individuals ml^{-1}.

The feeding of the cyclopoid *Oncaea mediterranea* was studied in 24 hour incubations using two phytoplankton species offered simultaneously (Paffenhofer, 1993). Feeding rates were determined according to Frost (1972). The maximum clearance rate was 3.6 ml individual^{-1} d^{-1}, and the maximum ingestion rate was 5 x $10^6 \mu^3$ algae individual^{-1} d^{-1}. These feeding rates are considerably lower than those reported for similarly sized copepods (e.g. 5-20 ml μg body C^{-1} d^{-1} for *Paracalanus* [Paffenhofer, 1984b]). The fact that clearance rates of *Oithona* are higher for animal prey than for phytoplankton (Lampitt and Gamble, 1982; Landry and Fagerness, 1988) suggest that omnivory or carnivory may be an important component in the diet of these copepods.

In situ estimates of grazing parameters for *Oithona colcarva* have been estimated by White and Roman (1992) using radiolabelled natural plankton. Clearance rate was estimated at 4.7 ml μg body C^{-1} d^{-1} and ingestion rate at 1.42 μg C μg body C^{-1} d^{-1}.

3.2 Cladocera

Despite considerable diversity within the Cladocera, only eight species are known to be truly marine. These belong to three genera, *Evadne*, *Penilia* and *Podon*, all of which are represented in Port Phillip Bay (Kimmerer and McKinnon, 1985). Cladocerans are often an important component of the zooplankton, particularly in productive nearshore waters, however they have also been reported to occur in continental shelf upwellings and open oceanic waters. Paffenhoffer and Orcutt (1986) reported that *Penilia avirostris* is able to grow and reproduce at low food levels (6 μg C l^{-1}), indicating that this species can survive in open ocean waters characterised by low nutrient levels.

Five species of marine cladocerans are residents of Port Phillip Bay, and collectively they comprise 23% of the total zooplankton numbers (Kimmerer and McKinnon, 1985).

The species are *Evande nordmanni, Evadne tergistina, Podon intermedius, Podon polyphemoides* and *Penilia avirostris*. Of these, *P. intermedius* is the most abundant, occurring in 89% of samples taken from Port Phillip Bay. Seasonal variation in the abundance of cladocerans is not pronounced, although there is a peak in abundance in spring and summer (Fancett, 1988).

The natural food of five marine cladocerans, *Evande nordmanni, Evadne tergestina, Penilia avirostris, Podon leuckarti* and *Podon polyphemoides* was investigated by Kim *et al.* (1989). Microscopic examination of gut contents revealed that centric diatoms were the most common food. Food size ranged from 4-115 μm, with a mean of 16.5 μm. *Skeletonema costatum*, the most common food species, measured from 4-15 μm. Gore (1980) investigated the feeding of *P. avirostris* using spherical plastic beads as a controlled particle source. He found that ingestion was limited to particles of 20 μm and smaller. Turner *et al.* (1988) found that the smallest food particles ingested by *P. avirostris* were 2-5 μm flagellates. There was no evidence of direct ingestion of bacterioplankton (< 1 μm).

Penilia avirostris was found to feed mainly on small particles up to 18 μm from natural particle assemblages, with maximum ingestion in the range 3.5-7 μm (Paffenhofer and Orcutt, 1986). Ingestion rates increased and clearance rates decreased with increasing food concentration. No maximum feeding threshold was observed. Maximum weight specific clearance rates decreased from about 11 to 3.3 ml μg body N^{-1} d^{-1} with increasing weight. Maximum weight specific ingestion rates decreased from 2.5 to 0.8 body N d^{-1} with increasing body weight.

Turner *et al.* (1988) examined feeding of *Penilia avirostris* on a variety of foods including bacterioplankton (0.5-2 μm), microflagellates (2-5 μm), naturally occurring and cultured phytoplankton. Incubations took place over 4-5 hours, food concentration was determined microscopically, and clearance rates were calculated using the equations of Frost (1972). *P. avirostris* did not ingest bacterioplankton except at unnaturally high concentrations where cells were clumped, nor did it ingest larger naturally occurring phytoplankton species. Heterotrophic microflagellates and two species of cultured phytoplankton were ingested, however, covering a sized range of 2-12 μm. Average clearance rates were 96 ml $individual^{-1}$ d^{-1} and 33.6 ml $individual^{-1}$ d^{-1} for heterotrophic microflagellates and phytoplankton respectively. It was concluded that *P. avirostris* may be an important component of the microbial loop through the consumption of bacterivorous microflagellates.

Faecal pellets of *Podon intermedius*, which is the most abundant cladoceran in Port Phillip Bay, contained mainly fragments of the pennate diatom *Rhizosolenia* (150 x 10 μm) (Jagger *et al.*, 1988). Fragments of other species were occasionally found. Feeding experiments were conducted using single species of cultured phytoplankton over the size range 8-150 μm (maximum dimension), over an incubation period of 24 h. Only *Rhizosolenia* were consumed in significant numbers. Clearance rates, calculated using the equations of Frost (1972), varied inversely with food concentration and ranged from 2-12 ml $individual^{-1}$ d^{-1}.

In general, species of the genera *Podon* and *Evadne* appear to be 'raptorially feeding herbivores' preying on relatively large particles, particularly diatoms and dinoflagellates (Jagger *et al.*, 1988; Kim *et al.*, 1989). It is possible that these species are not sufficiently active to capture animal prey.

There is evidence that cladocerans may be more efficient grazers of dinoflagellate blooms than copepods (Nielsen, 1991). In contrast, *Penilia* , which is less common in Port Phillip Bay, feeds on very fine particles down to the nanoplanktonic range (Turner *et al.*, 1988). Little information is available on the grazing parameters of *Evadne* and *Podon*, to some extent due to difficulties in maintaining these species in the laboratory.

3.3 Larvaceans

The larvacean *Oikopleura dioica* comprised approximately 20% of the zooplankton numbers in Port Phillip Bay in 1983-84 (Kimmerer and McKinnon, 1985) and 1986 (Fancett, 1988). These animals are filter feeders, pumping suspended material through incurrent filters on which large particles are retained, while material of ingestible size pass through to the mouth (Alldredge, 1981). Deibel and Lee (1992) examined the feeding of *Oikopleura vanhoeffeni* for particles from 0.6-7 μm. Retention efficiencies ranged from 44% for the smallest particles to 91% for the largest particles tested. They concluded that this species is capable of transporting microbial biomass directly from picoplankton to large metazoans such as fish.

Clearance rates for *Oikopleura dioica* were determined by Alldredge (1981) *in situ* using suspensions of plastic beads 2-15 μm diameter. Maximum clearance rate was 300 ml individual^{-1} d^{-1} (approximately 42 ml μg body C^{-1} d^{-1} at ca. 30 μg body weight). Using population estimates from field samples made simultaneously with feeding experiments, it was estimated that up to 37% of each cubic meter could be filtered in 24 hours. Thus *Oikopleura* may have a significant impact on particulate populations.

Further estimates of the grazing impact of *Oikopleura* species indicate that when they are abundant, these animals may clear significantly more of the water column than crustacean zooplankton (Knoechel and Steel-Flynn, 1989). *O. vanhoeffeni* cleared up to 13% of the standing stock of ingestible food particles each day (Deibel, 1988). Alldredge (1981) estimated that at the height of its abundance (4587 individuals m^{-3}), *O. dioica* grazed primary production faster than it could be replaced. The abundance of *O. dioica* in Port Phillip Bay in 1986 was 100-3000 individuals m^{-3}, and did not vary seasonally (Fancett, 1988), therefore the grazing impact of this species on particles in the Bay is probably significant.

3.4 Conclusion

From the results of Kimmerer and McKinnon (1989) it appears that *Paracalanus indicus* can feed on smaller particles, and at a higher clearance rate than *Acartia tranteri*. The available data on feeding in *Oithona* indicate much lower feeding rates on phytoplankton compared to *Paracalanus* and *Acartia*. Higher feeding rates have been reported for zooplankton feeding on heterotrophic flagellates and ciliates (Stoecker and Sanders, 1985; Gifford and Dagg, 1988; Turner *et al.*, 1988). Clearance rates obtained using single food species must be interpreted with caution. Schnack (1979) found that clearance rates for particular prey species may be up to 5 times higher or lower in a mixture than when offered singly. Critical and threshold concentrations determined in the laboratory may not be applicable to field conditions due to different food conditions. The high variability among reported rates may be due to experimental conditions, as well as natural variations due to daily and seasonal cycles. From the studies reviewed above it is clear that feeding by crustacean zooplankton is not a simple filtration of particles at a constant rate.

This rate can vary with food concentration, food size, food quality, temperature, season and the developmental stage and physiological state of the animal. Therefore any estimate of a general grazing rate applicable to Port Phillip Bay from published values in other systems will necessarily be subject to large errors.

4.0 ASSIMILATION EFFICIENCY

Assimilation efficiency is defined as the fraction of ingested material that is absorbed across the gut wall of an animal. Assimilated material (carbon and nutrients) is available to the organism for growth, reproduction and metabolism, the waste products of which are excreted and thus regenerated. The unassimilated fraction, on the other hand, is contained in the faeces and usually sinks out of the surface layer and is lost to the system. Estimates of assimilation efficiency are therefore important in determining what proportion of the ingested material remains in the surface layer and is potentially available to higher (via predation) and lower (via excretion) trophic levels.

Despite the importance of zooplankton assimilation efficiency to understanding marine ecosystems there have been relatively few studies in this area. There is only limited information on assimilation in the genera represented in Port Phillip Bay. Most studies have concentrated on the calanoid copepods *Calanus*. Conover (1966a) developed a formula for calculation of carbon assimilation efficiency based on the ratio of ash free dry weight to dry weight in samples of food and faeces. It was assumed that the inorganic or ash fraction of the ingested food would be unaffected by the digestive process. Field-based estimates for assimilation efficiencies of mixed zooplankton obtained by this method varied widely from 39-92%. Laboratory estimates for *Calanus hyperboreus* feeding on the dinoflagellate *Exuviella* also varied, from 39-86% (Conover, 1966a). Conover (1968) concluded that zooplankton assimilated phytoplankton with 60-95% efficiency. Assimilation efficiency was largely unaffected by temperature, food concentration or amount ingested (Conover, 1966b).
Later studies have invalidated Conover's (1966a) assumption that the inorganic fraction of the food is not assimilated (Forster and Gabbott, 1971; Lasenby and Langford, 1973). Landry *et al.* (1984) proposed a method for the estimation of assimilation efficiency based on Conover's (1966a) technique, but using chlorophyll a as the unassimilated reference fraction of the ingested material. Experimenting on *Calanus pacificus*, they derived values of 68.5-85.4% for carbon, and 73.9-92.5% for nitrogen. Assimilation efficiency was closely related to the feeding history of the individuals. Individuals were acclimated for two weeks before the experiment in the laboratory at four different densities of food (the diatom *Thalassiosira weissflogii*) from 1000 to 8000 cells ml^{-1}. At the experimental concentration of 8000 cells ml^{-1} individuals acclimated at the lowest food levels had the highest assimilation efficiencies. The results were ascribed to higher enzyme activities of zooplankton acclimated to lower food levels (Hassett & Landry, 1983; Landry *et al.*, 1984).

Seasonal changes in enzyme activity and assimilation efficiency in *Calanus pacificus* were reported by Hassett and Landry (1990). Assimilation efficiencies were estimated from the the difference between ingested (measured in food) and egested (measured in faecal pellets) nutrients. The highest assimilation efficiencies coincided with high field-based estimates of enzyme activities in spring. Throughout the study assimilation efficiencies ranged from 30-85%, but were generally around 75%.

While short term (hours-days) variation in food availability may affect feeding rates (e.g. Durbin *et al.*, 1990), it had little effect on the assimilation efficiency of *Calanus pacificus* (Hassett and Landry, 1988).

Downs and Lorenzen (1985), using the carbon to phaeopigment (C:Phe) ratio method, reported assimilation efficiencies of 73-81% (mean of 77%) for actively grazing *Calanus pacificus*, while diapausal animals had an average assimilation efficiency of 46%. Faecal pellets from field samples of zooplankton between 0.5 and 7mm yielded much higher C:Phe ratios, indicative of omnivory or carnivory.

Tande and Slagstad (1985) developed a method for measuring assimilation efficiency, also based on Conover's (1966a) method, but using biogenic silica as the unassimilated reference fraction and using ^{14}C to measure the proportion of food absorbed. This method is restricted to experiments using diatoms as food, as other potential food sources do not contain silica. The application of this method to *Calanus hyperboreus* feeding on *Thalassiosira anguste-lineata* yielded assimilation rates of between 84.2% and 87.7%. The reduction in assimilation efficiency was inversely correlated with a threefold increase in food concentration. The low variability of this method compared to others indicates that assimilation efficiency in copepods may be higher than previously thought (Tande and Slagstad, 1985).

Reinfelder and Fisher (1991) used radiolabelled diatoms (*Thalassiosira pseudonana*) to measure the assimilation efficiency of copepods for several elements, including carbon and phosphorous. The experiments were conducted with monospecific assemblages of each of three species; *Acartia tonsa, Acartia hudsonica* and *Temora longicornis*. Assimilation efficiency was calculated by dividing the amount of radiotracer retained after gut evacuation by the amount ingested. Values of 70% for phosphorous and 85% for carbon were obtained. Kiørboe *et al.* (1985) estimated that the assimilation efficiency based on C of *Acartia tonsa* varied between 0.51-0.81.

Assimilation efficiency has been shown to vary seasonally (Downs and Lorenzen, 1985; Hassett and Landry, 1990). It is interesting to note that most of the above studies used *Thalassiosira weisflogii* as the only food source. Assimilation efficiency is likely to vary between individual phytoplankton species for herbivorous zooplankton. There have been no estimates of assimilation efficiency for zooplankton grazing on natural particle assemblages. Since the work of Conover (1966a, b, 1968), a number of ecological studies have simply assumed an average value of somewhere between 70% and 80% for carbon assimilation efficiency. For example, such values have been used to estimate carbon flux (Downs and Lorenzen, 1985), calculation of community ingestion from values of respiration (James and Wilkinson, 1988), and for calculation of energy budgets for zooplankters (Bamstedt *et al.*, 1990).

5.0 ZOOPLANKTON PRODUCTION

Zooplankton production has not been studied in Port Phillip Bay. Kimmerer and McKinnon (1987) measured the secondary production of *Acartia tranteri* in Western Port, where this species comprised 77% of the holoplankton (>200 μm, Kimmerer and McKinnon, 1985). Growth rates and related variables were measured on 19 occasions between 1982 and 1984.

Growth rate was determined by an *in situ* incubation technique and was highly variable and usually food limited. The mean value for growth rate was 0.11 d^{-1}, and secondary production was estimated to be 0.36 mg C $m^{-3}d^{-1}$. This value represented <1% of phytoplankton primary production. This relatively low value for secondary production was attributed to the low growth rate and biomass of *A. tranteri* in Western Port, and the fact that food was limiting. Addition of phytoplankton to experimental containers resulted in an increase in growth rate of up to 77%, and the maximum growth rate obtained with added food was 0.2 d^{-1}. It was concluded that zooplankton production was a minor constituent of the Bay's energy budget compared to benthic production.

Secondary production of *Acartia* species in other systems has been found to be much higher than that reported by Kimmerer and McKinnon, for example 6.3-7.7 mg C $m^{-3}d^{-1}$ (Durbin and Durbin, 1981) and 7.5-12 mg C $m^{-3}d^{-1}$ (Landry, 1978), but this may have been due to higher biomass. Perhaps a more relevant measure of production is the production to biomass (P:B) ratio, also known as the specific productivity. The P:B ratio of *A. tranteri* in Western Port was 0.10 d^{-1} (Kimmerer and McKinnon, 1987).

Conover (1979) summarised a large number of published data on P:B ratios for both individual species and planktonic communities. Values for *Acartia*, *Oithona*, paracalanids and cladocerans (all important Port Phillip Bay taxa) ranged between 0.033 and 0.52 d^{-1}, while typical values for temperate water communities were 0.07-0.16 d^{-1}.

Based on a large volume of previously published data, Baird and Ulanowicz (1989) examined the flow of energy through the Chesapeake Bay ecosystem. The results of their model suggested that zooplankton production varied seasonally, with the highest P:B ratio in summer (0.65 d^{-1}) and the lowest in winter (0.01 d^{-1}). Overall production was highest in spring however, due to higher biomass. The average P:B ratio over an entire year was estimated as 0.37 d^{-1}.

6.0 EXCRETION RATES AND NUTRIENT REGENERATION

Those products of zooplankton excretion which may be important for phytoplankton production include ammonia, urea and inorganic phosphate. Both ammonia and urea may be taken up by phytoplankton in preference to nitrate (Harrison *et al.*, 1983). A considerable fraction of excreted phosphorous is in organic forms, and is thus unavailable to phytoplankton (Bamstedt, 1985). Bamstedt (1985) examined the weight specific ammonia, urea, inorganic phosphate and total dissolved phosphorous excretion rates for 17 species of zooplankton from the Swedish west coast during spring, summer and autumn. Seasonal variation was apparent, with lower rates during summer. Zooplankton excretion amounted to between 4 and 50% of the nitrogen requirement and 14 to 102% of the phosphate requirement for primary production.

In some species at least, ammonia excretion rate appears to be independent of ingestion rate (Miller and Landry, 1984). Many studies of excretion have concentrated on adult stages of zooplankters, even though juveniles often constitute a large proportion of zooplankton biomass. When food was abundant, similar weight specific excretion rates (0.65-0.94 μg NH_4^+-N μg body wt^{-1} d^{-1}) were found for all developmental stages of the copepod *Eucalanus pileatus* (Paffenhofer and Gardner, 1984).

However at low food concentrations later stages had significantly lower weight specific excretion rates than earlier stages. In fact the excretion rate of juveniles was constant under varying food concentrations.

No direct measurements of excretion by grazers from Port Phillip Bay have been undertaken, and few measurements have been made on the same genera from other areas. Amongst the copepods, Kiørboe *et al.* (1985) found that excretion rates for *Acartia tonsa* in the laboratory varied between 0.038 and 0.188 μg NH_4^+-N μg body $N^{-1}d^{-1}$ (assuming C:N = 5:1), increasing with increasing food concentration. Checkley *et al.* (1992) measured excretion for freshly collected *Acartia* from the inland Sea of Japan and found a range of 0.053 to 0.245 μg NH_4^+-N μg body N^{-1} d^{-1}, giving an approximate specific excretion rate of 0.12 d^{-1} (0.045-0.21).

Ammonia and phosphate excretion rates for the larvacean *Oikopleura dioica* were measured by Gorsky *et al.* (1987). Excretion rates were significantly affected by temperature over the range 15-24^o C and were also correlated with body mass. Ammonia excretion rates at 20^o C ranged from 1 x 10^{-4} to 18 X 10^{-4} mol NH_4^+-N individual$^{-1}h^{-1}$, while phosphate excretion was 0.33 x 10^{-5} to 7.4 x 10^{-5} mol PO_4-P individual$^{-1}h^{-1}$. The weight specific excretion rates decreased with increasing body size.

6.1 Growth efficiency

Excretion rate can be determined indirectly from growth efficiency. Growth efficiency (GE) is the growth of an organism expressed as a fraction of ingestion (Gross Growth Efficiency - GGE) or assimilation (Net Growth Efficiency - NGE). That portion of assimilated food not used for growth is assumed to be metabolised (respired C or excreted N). Growth efficiency has not been determined for zooplankton from Port Phillip Bay, but has been widely reported for similar taxa elsewhere.

Growth efficiency for adult copepods is considered to be equivalent to efficiency of egg production in females. GGE can be converted to NGE if an assimilation efficiency of 0.75 is assumed.

Efficiency of egg production in terms of nitrogen for *Paracalanus parvus* was 0.37 (Checkley, 1980). For carbon, GGE ranged from 0.15 to 0.41 depending on C:N ratio of food.

Kiørboe *et al.* (1985) estimated from egg production that NGE for *Acartia tonsa* was between 0.60 and 0.76 for C and for N was between 0.5 and 0.65. GGE was between 0.39 and 0.49 for C and for N was between 0.40-0.49. GGE decreased and NGE increased with increasing food concentration. This estimate was very similar to an estimated GGE of juvenile *A. tonsa* of 0.44 (C) estimated by Berggreen *et al* (1988). When *A. tonsa* was fed on a number of algal species the highest value of GGE based on egg production was 0.33 for C and 0.40 for N (different algal species) (Støttrup and Jensen, 1990).

Lampitt and Gamble (1982) estimated carbon respired by *Oithona nana* collected monthly over one year. The specific rate ranged from 0.06 to 0.40; a similar proportion of N excretion can be assumed.

GGE of the cladoceran, *Penilia avirostrus*, reared at two food concentrations was 0.49 to 0.74 (N) at the lower food level and 0.40 to 0.58 (N) at the higher level (Paffenhofer and Orcutt, 1986). Weights of developing young in female brood chambers were included in the calculations. Efficiencies were similar over the first 3 days of life and then decreased with increasing age (or size). Efficiencies varied with food species. No estimates are available for raptorial feeding cladocerans or larvaceans.

7.0 THE MICROBIAL LOOP

Trophic relationships among the smallest fractions of the plankton, the nano- and picoplankton (0.2-20 μm), have not been investigated in Port Phillip Bay. The importance of such relationships in nutrient cycling has only recently been recognised. This was mainly due to the development of techniques using epifluorescence microscopy and appropriate stains (Hobbie *et al.*, 1977; Porter and Feig, 1980; Caron, 1983; Sherr and Sherr, 1983). Bacteria and other micro-organisms are very abundant in coastal waters and their main source of energy comes from the release of dissolved organic matter (DOM) by phytoplankton (Azam *et al.*, 1983). It has been estimated that bacteria use between 10 and 50% of the carbon fixed by photosynthesis (Azam *et al.*, 1983). The microbial loop hypothesis holds that nutrients are recycled in the surface layers via a food chain comprising bacteria, flagellates, microzooplankton and mesozooplankton. Mineral nutrients are returned to the water column at each step in the food chain. However, as bacteria can absorb mineral nutrients and carbon, the major role of remineralization is carried out by flagellates and zooplankton (Figure 1). This is contrary to the traditional view of bacteria as the major remineralisers of nutrients.

Naturally occurring bacterial populations have not been enumerated for Port Phillip Bay, however these organisms are ubiquitous in the world's oceans. Estimates of bacterial numbers in coastal waters range from 10-50 x 10^8 l^{-1} (5-200 μg C l^{-1}) (from Azam *et al.*, 1983). Fuhrman *et al.* (1980) found that bacterial and phytoplankton populations off the coast of California were strongly correlated on a scale of tens of kilometres. Bacteria are consumed by heterotrophic flagellates (Azam *et al.*, 1983) and ciliates (Heinbokel, 1978). There is increasing evidence that these animals are in turn consumed by crustacean zooplankton (Gifford and Dagg, 1988).

Malone *et al.* (1991) found that seasonal variation in the abundance of bacterioplankton in Chesapeake Bay was closely coupled to the release of dissolved organic carbon (DOC) by phytoplankton. Bacteria took up 54% and 83% of phytoplankton exudates in spring and summer respectively. On average 9% of primary production was cycled through bacterioplankton. The input of allochthonous nutrients appeared to be coupled to higher bacterial production via increases in the productivity and DOC release of phytoplankton. This would presumably lead to increased flow of carbon through the microbial food web.

The efficiency of the microbial loop in returning energy and nutrients to the surface layer is likely to be fairly low. Losses of nutrients and energy are likely to result from egestion of unassimilated materials as faeces. Therefore the transport of organic material through several microbial links would not result in increased food chain efficiency. However, given the large proportion of primary production which is hypothesised to travel through this system, it may be of considerable importance as a food source for the mesozooplankton (Turner *et al.*, 1988).

There is no evidence of direct ingestion of bacteria by mesozooplankton, which would lead to improved efficiency of remineralization, in marine systems, although it is well documented in freshwater systems (Hart and Jarvis, 1993).

Tintinnid ciliates and rotifers are relatively abundant in Port Phillip Bay and show little seasonal variation (Fancett, 1988). The microbial food web is probably well developed in the Bay, however there is too little quantitative information available to make an estimate of its importance in relation to nutrient regeneration. Evidence from other systems indicates that bacterioplankton production is transported through a microbial loop (e g. Malone *et al.*, 1991), and the remineralisation of nutrients via zooplankton may support a considerable proportion of primary production. However, understanding of the trophic relations among the smallest fractions of the plankton is poor, and many studies are inconclusive (e g. Rosenberg *et al.*, 1990).

8.0 MICROPLANKTON GRAZING

Microzooplankton (20-200 μm), although usually less important than mesoplankton in terms of biomass, may be of greater importance in terms of grazing due to their high growth rates. Fancett (1988) recorded a dominance of tintinnids and copepod nauplii in the microzooplankton > 50 μm. Tintinnids in Port Phillip Bay are dominated by the genera *Tintinnopsis* and *Favella* (Jenkins, unpublished data). Aloricate oligotrich ciliates may be of even greater importance than these groups but, due to their small size and fragility, are often overlooked by traditional zooplankton sampling methods (Gifford, 1988).

Tintinnids feed primarily on plastidic nanoflagellates but also consume picoplankton, including cyanobacteria (Bernard and Rassoulzadegan, 1993). Oligotrich ciliates feed mainly on small plastidic nanoflagellates (Bernard and Rassoulzadegan, 1990). Verity (1991) cultured *Strobilidium* (an oligotrich) and *Tintinnopsis* on plastidic and aplastidic nanoplankton. Maximum clearance for *Strobilidium* was approximately 0.1 ml individual^{-1} d^{-1}, maximum C-specific ingestion ranged from 2.88-3.6 d^{-1} and gross growth efficiency ranged from 0.47 to 0.54. For *Tintinnopsis*, maximum clearance was 0.19-0.26 ml individual^{-1} d^{-1}, maximum C-specific ingestion was about 2.4 -3.1 d^{-1} and gross growth efficiency ranged from 0.38 to 0.54. Highest growth rates for both groups are recorded for diets of plastidic rather than aplastidic nanoplankton and some preference for the former is apparent.

Verity (1985) cultured two species of *Tintinnopsis* and tabulated specific ingestion, growth, respiration and excretion for each species at three temperatures. The maximum clearance rate of *T. acuminata* was about 0.04-0.064 ml individual^{-1} d^{-1} (tintinnid 850 pg N) and for *T. vasculum* was about 0.15-0.19 ml individual^{-1} d^{-1} (tintinnid 8600 pg C). Assimilation efficiencies ranged from 0.91 to 1.00 and GGE ranged from 0.35 to 0.57.

Functional dynamics of five tintinnid species was studied by Heinbokel (1978). Maximum clearance rates for two species was approximately 0.07 ml individual^{-1} d^{-1}, maximum specific ingestion ranged from 0.1 to 0.2 d^{-1} body C and GGE was approximately 0.50.

Maximum clearance rates for three species of oligotrichous ciliates in culture ranged from 0.01 to 0.62 ml individual^{-1} d^{-1} and the GGE was approximately 0.40 (Jonsson, 1986). Fenchel and Johnson (1988) estimated a clearance rate of approximately 0.048 ml individual^{-1} d^{-1} and a GGE of approximately 0.50 for the oligotrich *Strombidium*.

In summary, these studies suggest that maximum clearance rates are variable from about 0.05 to 0.3 ml individual^{-1} d^{-1} for tintinnids and about 0.01 to 0.5 ml individual^{-1} d^{-1} for oligotrichs (clearance in terms of C or N can be calculated in some cases and would reduce variability). Maximum C- specific ingestion ranges from 0.1 to 0.15 d^{-1}, assimilation efficiency is approximately 0.90 to 1.00 and GGE is 0.40 to 0.50.

Another potentially important group of grazers in the microplankton are heterotrophic dinoflagellates (Hansen, 1991). Grazing rates by the herbivorous dinoflagellate *Gymnodinium* on a plastidic nanoflagellate and a cyanobacterium were investigated by Strom (1991). Total clearance rates ranged from 0.005 to 0.04 ml individual^{-1} d^{-1} (individual 300 pg C), maximum carbon specific ingestion was 4.5 d^{-1} and maximum GGE was 0.53. Grazing by *Gyrodinium* (individual = 1404 pg C) on a red tide flagellate (individual = 996 pgl C) resulted in an ingestion rate of 3.8 prey individual^{-1} d^{-1} and a C specific GGE of 0.31 (Nakamura *et al.*, 1992).

Grazing rates of microzooplankton have been estimated *in situ* by Lessard and Swift (1985) using radiolabelled natural heterotrophic and autotrophic food. Clearance rates by ciliates and heterotrophic dinoflagellates were comparable to, but sometimes exceeded, the range determined in laboratory studies described above.

An additional important group of microzooplankton are the juvenile stages of mesozooplankton. Copepod nauplii are typically much more abundant than older stages, as reported in section 3.1, and although absolute grazing rates are lower than in older stages, weight-specific grazing rates are much higher. White and Roman (1992) estimated grazing of microzooplankton *in situ* using radiolabelling of food and obtained clearance rates of 0.5 ml individual^{-1} d^{-1} for *Acartia hudsonica* nauplii and 2.0 ml individual^{-1} d^{-1} for *A. tonsa* nauplii. Another common microzooplankton group studied by White and Roman (1992) were rotifers which had clearance rates of about 0.5 ml individual^{-1} d^{-1}.

9.0 NANOPLANKTON GRAZING

The importance of grazing in this group (2-20 μm) is being increasingly recognised (Caron *et al.*, 1991). This group may include ciliates and heterotrophic dinoflagellates at the lower end of their size range (see above); together with naked heterotrophic flagellates (Fenchel, 1982b) and choanoflagellates (Buck *et al.*, 1991) which are usually less than 5 μm. This group is the most difficult to study in terms of grazing by individual components. Caron *et al.* (1991) investigated grazing by two nanoplanktonic ciliate species and a heterotrophic flagellate on heterotrophic bacteria and cyanobacteria and found highest growth efficiency (yield) of up to 100% on a diet of heterotrophic bacteria. Marchant and Scott (1993) tabulated clearance rates of choanoflagellates from various studies of between 9.6-384 x 10^{-6} ml individual^{-1} d^{-1}. Their study also indicated that these organisms could take up DOM directly. Parslow *et al.* (1986) estimated the maximum clearance rate of a heterotrophic zooflagellate on a picoplanktonic prasinomonad at 10 x 10^{-6} ml individual^{-1} d^{-1}. This compared well with the range of 12-24 x 10^{-6} ml individual^{-1} d^{-1} determined by Sherr *et al.* (1983) for a heterotrophic nanoflagellate feeding on bacteria. Fenchel (1982a) studied six species of heterotrophic nanoflagellates in batch culture. Maximum clearance rates ranged from 33.6 to 1896 x 10^{-6} ml individual^{-1} d^{-1}. Gross growth efficiency for two species (C basis) was 0.34 and 0.43, net growth efficiency was 0.60.

Grazing rates of nanoplanktonic flagellates have been estimated *in situ* by Sherr *et al.* (1981) using fluorescently labelled algae (FLA). Clearance rates ranged from 0.1 to 20 x 10^{-3} ml individual^{-1} d^{-1}. The possible importance of algivory by < 20 μm phagotrophic flagellates was emphasised.

10.0 ESTIMATION OF ZOOPLANKTON GRAZING IN PORT PHILLIP BAY

10.1 Clearance rates

The best estimates for feeding rates are probably those of Jagger *et al.* (1988) for *Podon intermedius* and Kimmerer and McKinnon (1989) for *Acartia tranteri* and *Paracalanus indicus*. These estimates have been chosen because they were performed on Port Phillip Bay residents and are comparable to literature estimates for similar species. Other species of copepods are assumed to have the same clearance rate as *Paracalanus*, and the clearance rate of *Podon* is assummed to be representative of all cladoceran species. Clearance rates of *Oikopleura dioica* are taken from Alldredge (1981). Using the mid-range values obtained in these studies, and applying them to the abundance and species composition data of Kimmerer and McKinnon (1985) for zooplankton > 200 μm, a figure of 0.066 d^{-1} is obtained, which represents the fraction of the water column swept clear of particles per day. This figure gives a clearance time for the entire Bay of approximately 15 days. Interestingly, the larvacean *Oikopleura dioica* accounts for 88% of this figure.

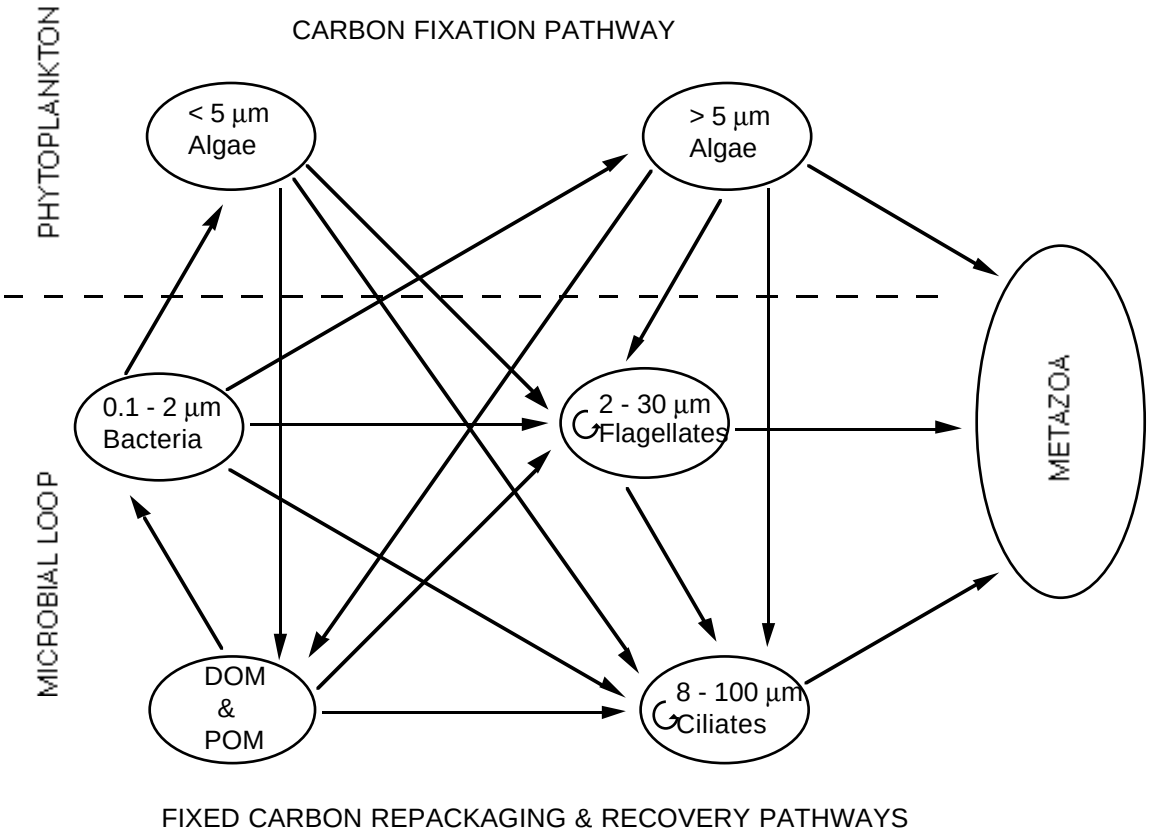

Figure 1. Trophic interactions within the microbial food web, which is separated here into phytoplankton and 'microbial loop' (i.e. bacteria and protozoal components. Nonliving pools of dissolved and particulate organic matter (DOM and POM) are also included. Note the many direct links between heterotrophic and autotrophic microbes, such as ingestion of phytoplankton by flagellates and ciliates and ingestion of bacteria by mixotrophic phytoplankton. The curved arrows of the flagellate and ciliate compartments indicate further predator-prey interactions within these broad classes of organisms. In this model, production of phytoplankton smaller than 5 m is accessible to metazoa only after being 'repackaged' into larger protozoan cells. Reproduced from Sherr and Sherr (1991).

Using the upper and lower limits of the estimated feeding rates used in the above calculation, there is a range of 0.024-0.093 d^{-1} giving a clearance time somewhere between 11 and 42 days. It must be emphasised that the errors associated with such estimates are bound to be extremely large due to the large number of ecological parameters used in their calculation, many of which are, in themselves, crude approximations of the actual values. In addition many of these parameters, especially composition and abundance of zooplankton, are subject to temporal variation. For example, when the above calculation was performed using the composition and abundance data of Fancett (1988), a feeding rate of 0.17 or clearance of the Bay in only 6 d is obtained. In contrast data from Arnott (1974) resulted in an overall feeding rate of 0.022 or clearance of the Bay in 46 d. This wide variation was mainly due to the relatively high abundance of zooplankton in the study by Fancett (1988),and the fact that data on non-crustacea (particularly the important larvaceans) was not available in the report by Arnott (1974).

Broad estimates can also be made for feeding of microzooplankton using the abundance and composition of microzooplankton in the 50-100 μm range determined by Fancett (1988). Clearance rate for tintinnids was assumed to be in the mid range of values described previously (0.15 ml $individual^{-1}$ d^{-1}) and rates for *Acartia* nauplii and rotifers of about 0.5 ml $individual^{-1}$ d^{-1} were taken from White and Roman (1992). This latter rate was also assumed for bivalve larvae. The estimated clearance rate was 0.065 d^{-1}, or clearance of the Bay in 15 d, approximately equal to the estimate for mesozooplankton. Because only a narrow range of the microzooplankton was sampled, and very important groups such as oligotrichs were not included, it seems likely that the microzooplankton may have a greater impact on food populations than mesozooplankton.

10.2 Production

The value for production of *Acartia tranteri* in Western Port of 0.36 mg C m^{-3} d^{-1} (P:B = 0.10) (Kimmerer and McKinnon, 1987) may be representative of Port Phillip Bay. A P:B ratio of 0.1-0.2 is probably realistic, based on the typical values for temperate coastal waters presented by Conover (1979). Applying a P:B ratio of 0.15 d^{-1} to the biomass data of Fancett (1988) for zooplankton >150 μm, and assuming carbon is 40% of dry weight (Kimmerer and McKinnon, 1987), a value for production of 0.96-5.12 mg C m^{-3} d^{-1} is obtained.

10.3 Nutrient cycling rates

Direct measurements on size specific excretion rates of most zooplankton taxa in Port Phillip Bay are unavailable. Results of other studies indicate that nutrient cycling by zooplankton is highly variable, and may depend on body size (e.g. Uye *et al.*, 1990; James and Wilkinson, 1988), food abundance (Paffenhofer and Gardner, 1984) and season (Bamstedt, 1985). A first-order approximation of nutrient regeneration rates, based on an assimilation efficiency of 0.75 and a gross growth efficiency of 0.45, would be approximately 40% of assimilated nutrient. An alternative, assemblage level approach to estimating ammonium regeneration is described below.

11.0 ALTERNATIVE APPROACHES TO DETERMINING NUTRIENT FLUXES IN THE ZOOPLANKTON OF PORT PHILLIP BAY

The difficulty in estimating feeding parameters for individual zooplankton taxa increases dramatically for organisms in the micro-nanoplankton range, where assemblage level measurements are preferable. The high abundances and growth rates of these organisms allow the possibility of *in situ* incubation techniques.

11.1 Grazing

A simple, cost effective technique for measuring grazing in the microplankton, nanoplankton range is the so called 'dilution' method (Landry and Hassett, 1982). Requiring less manipulation and fewer assumptions than fractionation techniques (Capriulo and Carpenter, 1980), the method utilises increasing dilutions of the < 200 μm fraction of the natural plankton assemblage. Phytoplankton growth rate is determined at each dilution level, under the assumption that microplankton consume prey in direct proportion to prey density. A linear regression is fitted to the data, the negative slope is the coefficient of algal mortality, and the intercept is the estimated phytoplankton growth rate in the absence of grazing (Landry & Hassett, 1982; Gifford, 1988). Using this method, Gifford (1988) found that at certain times of year 100% of daily chlorophyll production was grazed by microplankton in Halifax Harbour. Grazing estimated by the dilution method also often exceeded phytoplankton growth in Chesapeake Bay (McManus and Ederington-Cantrell, 1992). Modifications to the method have been proposed by Gallegos (1989) and Evans and Paranjape (1992) to account for saturated feeding of grazers, with the result that the method is now a standard technique (Chavez *et al.*, 1991; Fahnenstiel *et al.*, 1991; Strom and Welschmeyer, 1991). The technique has been successfully applied to nanoplankton grazing on picoplanktonic algae (Campbell and Carpenter, 1986). Results of studies such as those described above indicate that microplankton grazing is typically more significant than mesoplankton grazing.

Other methods of investigating microplankton grazing have been reviewed by Gifford (1988). Methods for investigating *in situ* nanoplanktonic grazing on picoplanktonic algae include the use of prokaryotic (Campbell and Carpenter, 1986; Fahnenstiel *et al.*, 1991) and eukaryotic (Caron *et al.*, 1991) inhibitors, filtration (Kuosa, 1991; Weisse and Scheffel-Möser, 1991) and tracer techniques (Fahnenstiel *et al.*, 1991).

The measurement of grazing of mesozooplankton assemblages *in situ* is also possible using a variety of techniques. Natural assemblages of mesozooplankton and phytoplankton can be incubated *in situ* after radiolabelling phytoplankton with ^{14}C or ^{3}H forms of methylamine (Roman and Rublee, 1981; Roman *et al.*, 1990; White and Roman, 1991). Clearance and ingestion rates are calculated using activities of grazers per unit weight and particulates per unit volume of medium. The ^{3}H form has the advantage of incorporation in phytoplankton in both light and dark, but the disadvantage of take up by heterotrophic bacteria (White and Roman, 1991). White and Roman (1992) used this method to estimate grazing by micro and mesoplankton and also subdivided the analysis further to investigate dominant grazing taxa individually. Garcia-Pamanes *et al.* (1991) measured daily grazing rates of zooplankton in an upwelling area using ^{14}C incubation and found wide variation on a daily scale.

An alternative *in situ* method for determining mesoplankton grazing rates is to use the gut fluorescence method (Wang and Conover, 1986; Perissinotto, 1992). The chlorophyll contained within guts of zooplankters is determined from fluorescence of pigments. The gut evacuation rate is determined, usually from decline of pigments in the guts of starved animals. These parameters are then combined to estimate ingestion rate. Gut clearance for starving animals is initially similar to continuously feeding animals but becomes relatively slower over time (Kiørboe and Tiselius, 1987). To overcome this problem, instead of transferring to filtered seawater, animals can be transferred to a solution of inert particles (Perissinotto, 1992). Pigment destruction in the gut may lead to a 10 to 30% underestimation of grazing rate (Kiørboe and Tiselius, 1987). Pigment degradation in the gut can be affected by a number of factors including ingestion rate, feeding history and digestive aclimation (Penry and Frost, 1991; Mayzaud and Razouls, 1992) which will influence the accuracy of grazing rate estimates. Bautista and Harris (1992) size fractioned phytoplankton and mesozooplankton and found greatest grazing impact on the larger phytoplankton fraction. Using this method Bautista *et al.* (1992) found higher grazing rates on a diatom bloom than a *Phaeocystis* bloom.

11.2 Nutrient regeneration

Nutrient regeneration, particularly for the smaller size ranges of plankton, are typically addressed *in situ* at the assemblage level using tracer experiments (Harrison, 1978; Gilbert, 1982). An elegant technique has been developed whereby ammonium uptake by phytoplankton and regeneration by zooplankton can be measured simultaneously using the ^{15}N dilution technique (Lehman, 1980; Gilbert, 1982). The plankton assemblage is incubated in $^{15}NH_4^+$ and the uptake of ^{15}N in the particulate fraction is measured concurrently with the dilution of $^{15}NH_4^+$ in the medium due to zooplankton excretion (Gilbert, 1982). Dugdale and Wilkerson (1986) have provided some experimental considerations for the improvement of this technique. The plankton assemblage can be size fractionated for analysis (Gilbert, 1982). Gilbert (1982) found that NH_4^+ uptake and remineralisation was in balance, and that the small fractions (<10 μm) were most important for regeneration. Harrison *et al.* (1983) also found that a large proportion of NH_4^+ regeneration was derived from the smallest size fractions of plankton. Size fractionated measurements have been found to show different patterns of NH_4^+ regeneration when compared with the total assemblage, perhaps due to a non-linear function of zooplankton density and/or multiple trophic interactions (Gilbert *et al.*, 1992). This method is now a standard technique.

An alternative *in situ* measure of ammonium excretion was used by King (1984) to estimate zooplankton (>153 μm) ammonium excretion rates off Massachusetts using measurements of glutamate dehydrogenase (GDH) activity. GDH is a key enzyme associated with ammonium excretion. A previously determined value for the GDH activity:excretion ratio of 16.8 was used for the conversion from GDH activity to excretion rate. Estimates for 5 stations ranged from 1.03 to 2.87 mg-at N $m^{-2}d^{-1}$ over a spatial scale of several hundred kilometres. It was estimated that this nitrogen source could supply 20-40% of phytoplankton requirements. This method, however, has not been widely used.

12.0 RECOMMENDATIONS

1. Functional relationships are available for grazing by most genera occurring in Port Phillip Bay, although relationships are lacking for two potentially very important taxa, the larvaceans and raptorially feeding cladocerans. All laboratory estimates are affected by a variety of variables and application to the field situation will be subject to large errors. Application of literature estimates would need to be accompanied by extensive field sampling to determine taxonomic and size composition, and seasonal and spatial variation in abundance. In general, the results would be imprecise and the field sampling would be expensive. Therefore this approach cannot be recommended.

2. A better, more cost efficient approach may be to carry out dilution experiments to determine microplankton grazing at the assemblage level. This could be done in conjunction with *in situ* assemblage level estimates of mesozooplankton grazing using radiolabelling or gut fluorescence. Radiolabelling may be preferable because it is subject to less errors and is logistically simpler. It is, however, a more manipulative technique, usually requiring concentration of grazers. *In situ* measurements of grazing should be carried out concurrently with phytoplankton production estimates. A possible extension would be to carry out ^{15}N uptake and regeneration experiments, although these are logistically and analytically more complex.

3. Quantification of the abundance and biomass of smaller heterotrophs, including bacteria, in relation to phytoplankton and larger zooplankton would be highly desirable, particularly given that concentrations of dissolved organic nitrogen in Port Phillip Bay are thought to be relatively high.

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Table 1. Tabulated synopsis of feeding and ingestion rates for zooplankton taxa occurring in Port Phillip Bay

Reference	Species	Description	F (ml body C^{-1} d^{-1})	I (μg C μg body C^{-1} d^{-1})	Ct (μg C l^{-1})	Cc (μg C l^{-1})	Specific ingestion (d^{-1})	Comment
Kimmerer and McKinnon (1989)	*Paracalanus indicus*	Lab. study, radiotracer method	0.8–5	–	–	–	–	PPB animals, one food [ ].
Checkley (1980)	*P. parvus*	Lab. study, multiple food types	30*	2.1*	Not apparent	47	1.5–3.6	Useful and detailed study. Effect of food [ ], C:N ratio & species.
Paffenhofer (1982)	*Paracalanus sp.*	Lab. study, different sized food	3–30	–	Not apparent	–	–	Larger cells depleted before small. No affect of [ ] or F.
Paffenhofer (1984a,b)	*Paracalanus sp.*	Lab. study , different sized food, single vs. mixed food	–	–	–	–	0.5–2	Rigorous and detailed study. Weight specific ingestion rates given for different food and developmental stages.
Kimmerer and McKinnon (1989)	*Acartia tranteri*	Lab. study, Radiotracer method	0.4–1	–	–	–	–	Western Port Bay samples, one food [ ].
Ambler (1986)	*Paracalanus sp.*	Ingestion functions derived from Paffennofer Studies	–	1.7*	–	–	–	I max increased with developmental stages. Useful for modelling.

* maximum

Table 1. Tabulated synopsis of feeding and ingestion rates for zooplankton taxa occurring in Port Phillip Bay

Table 1 (Cont'd.)

Reference	Species	Description	F (ml body C^{-1} d^{-1})	I (µg C µg body C^{-1} d^{-1})	Ct (µg C l^{-1})	Cc (µg C l^{-1})	Specific ingestion (d^{-1})	Comment
Kirøboe *et al.* (1985)	*A.tonsa*	Lab. study, single food species	0.6–8*	0.28*	–	–	1.8	Useful study, functional relationships given.
Berggreen (1988)	*A. tonsa*	Lab study, multiple phytoplankton species	–	–	–	–	1.2	F increased with developmental stage.
Stottrup & Jensen (1990)	*A. tonsa*	Lab. study, multiple phytoplankton species	0.4–3.2*	0.5*	–	90	3	Fmax varied with phytoplankton species.
White & Roman (1992)	*A. tonsa* *A. hudsonica*	Field study, radiotracer method	0.36–2.56 0.05–0.38	0.58–2.8 0.11–1.79	–	–	–	Weight specific F&I decreased with developmental stage.
Durbin & Durbin (1992)	*A. hudsonica*	Lab. study, effect of T° on feeding on one phytoplankton species	3.3–6*	–	9–20	170–230	.44–.93	Rigorous study. F and specific ingestion increased with temperature.
Reeve & Walter (1977)	*A. tonsa*	Lab. study, 3 phytoplankton species	2*		7–18	350	–	Also conducted experiments using natural particle assemblages.

Table 1. (Cont'd.)

* maximum

Table 1 (Cont'd.)

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Reference	Species	Description	F (ml body C^{-1} d^{-1})	I (µg C µg body C^{-1} d^{-1})	Ct (µg C l^{-1})	Cc (µg C l^{-1})	Specific ingestion (d^{-1})	Comment
Stoeker & Sanders (1985)	*A. tonsa*	Lab. study, feeding on tintinnid and dinoflagellate	35–87.1 (tintinnid) 0–40* (dinoflagellate)	–	–	–	–	Study shows preferential feeding on microzooplankton.
Lampitt & Gamble (1982)	*Oithona nana*	Lab. study, multiple food species	0.48–4.5*	0.004–0.37*	–	–	.04–.42*	Maximum rates when food was *Acartia clausi* nauplii.
Landry & Fagerness (1988)	*O. spinirostrus*	Lab. study	56.3*	–	–	–	–	Food was nauplii of *Calanus pacificus*.
White & Roman (1992)	*O. colcarva*	Field study, radio tracer method	4.7	1.42	–	–	–	Feeding on natural prey assemblage.
Paffenhofer & Orcutt (1986)	*Penilia avivostrus*	Lab. study, one phytoplankton species, range of [ ]	3.3–11*^{Y}	–	–	–	0.8–2.5	Detailed and useful study. Maximum weight specific F & I decreased with increasing body weight.
Alldredge (1981)	*Olkopleura dioica*	Clearance rate determined *in situ* using plastic beads	42*	–	–	–	–	Significant impact on particulates.

* maximum
*^{Y} N based.

Table 2. Tabulated synopsis of excretion rates for zooplankton taxa occurring in Port Phillip Bay

Reference	Species	Description	Excretion rate	Specific excretion (N based) d^{-1}	Comment
Kiørboe et al. (1985)	*Acartia tonsa*	Lab. study, varying food [ ]	38–188 μg NH_4^+–N μg body N^{-1} d^{-1}	–	Useful study. Excretion increased with food [ ] to a plateau.
Checkley *et al.* (1992)	*Acartia spp.*	Excretion of freshly collected animals	53–245 μg NH_4^+–N μg body N^{-1} d^{-1}	0.12	*in situ* estimate, similar to above.
Gorsky *et al.* (1987)	*Oikopleura dioica*	Lab. study, effects of T^o and body size	2.4×10^{-3}–4.32×10^{-2} μg NH_4 μg wt^{-1} d^{-1} 4.2×10^{-4}–9.4×10^{-3} μg PO_4 μg wt^{-1} d^{-1}	–	Excretion rate affected by T^o. Weight specific excretion decreased with increasing body size.

Table 2. Tabulated synopsis of excretion rates for zooplankton taxa occurring in Port Phillip Bay

Table 3. **Tabulated synopsis of growth efficiencies for zooplankton taxa occurring in Port Phillip Bay.**

Table 3. Tabulated synopsis of growth efficiencies for zooplankton taxa occurring in Port Phillip Bay.

Reference	Species	Description	Gross growth efficiency (GGE)	Net growth efficiency (NGE)	Comment
Checkley (1980)	*Paracalanus parvus*	Lab. study on egg production efficiency	0.37 (N) 0.15–0.41 (C)	–	Detailed study, GGE in terms of C varied with C:N ratio of food.
Kiørboe *et al* (1985)	*Acartia tonsa*	Lab. study, estimates from egg production	0.39–0.49 (C) 0.4–0.49 (N)	0.6–0.76 (C) 0.5–0.65 (N)	Useful study, GGE decreased and NGE increased with increasing food [ ].
Berggreen *et al* (1988)	*Acartia tonsa*	Lab. study, estimation from juvenile growth	0.44 (C)	–	Estimate for C very similar to Kiorboe et al (above).
Stottrup & Jensen (1990)	*Acartia tonsa*	Lab study, estimates from egg production, multiple food species	0.33 (C)* 0.40 (N)	–	Estimate varied with algal species.
Paffenhoffer & Orcutt (1986)	*Penilia avivostrus*	Lab. study, two food [ ]	0.4–0.74 (N)	–	Efficiencies decreased with increasing age.