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The Role of Suspension-feeding and Deposit-feeding Benthic Macroinvertebrates in Nutrient Cycling in Port Phillip Bay

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SUMMARY

This review documents biological variables of Port Phillip Bay macrobenthic suspension and deposit feeders that are critical to estimation of nutrient cycling in Port Phillip Bay. Biomass estimates are derived from Bay-wide macrobenthic species composition and abundance data collected during the period 1969-1973 (Poore *et al.*, 1975), and biomass data collected from three stations during the period 1973-1975 (Poore and Rainer, 1979). However, the Poore and Rainer (1979) data indicate that total macrobenthic biomass may vary by up to 100% between seasons and between years. Available data on spatial and temporal variation in macrobenthic biomass across Port Phillip Bay are limited. Since biomass is a critical determinant of nutrient-cycling variables, more reliable estimates of benthic biomass are urgently required.

Suspension feeders (mostly bivalve molluscs) are estimated to comprise half of the benthic macroinvertebrate biomass, and these animals are estimated to process a volume of water equivalent to Port Phillip Bay in about 16.5 days. Suspension feeders are estimated to be responsible for 15% of all organic matter ingested by benthic macroinvertebrates. However, since they have a greater assimilation efficiency than deposit feeders, they may account for 42% of total assimilation of organic material by Port Phillip Bay benthic macroinvertebrates.

Deposit feeders (mostly crustaceans, echinoids and polychaete worms) are estimated to make up about 35% of total macrobenthic biomass. In one year, these animals are estimated to process a volume of sediment equivalent to the top 13 mm of Port Phillip Bay sediments. These sediments contain a pool of organic matter that is estimated to be two orders of magnitude greater than the pool of particulate organic matter suspended in the water. If dissolved organic matter is taken into account, sediments contain one order of magnitude more organic matter than the water, but much of this dissolved material is probably not directly available to benthic macroinvertebrates. However, because deposit feeders process this organic matter at a slower rate and less efficiently than suspension feeders, deposit feeders account for about 85% of all organic matter ingested, but only about half of all organic matter actually assimilated by Port Phillip Bay benthic macroinvertebrates.

The rate at which Port Phillip Bay sediments are processed by deposit feeders is such that it is unlikely these sediments are a sink for nutrients unless feeding and bioturbation by deposit feeders causes organic matter to be buried at an inaccessible depth in the sediment, or in a refractory form. Studies of the feeding and burrowing activities of the two dominant deposit-feeding species (the echinoid *Echinocardium cordatum* and the crustacean *Neocallichirus limosa*) should enable this question to be addressed.

Estimates of nitrogen excretion from Port Phillip Bay benthic macroinvertebrates exceed the value estimated by Skyring *et al.* (1993). Since meiofauna and microflora (whose activities have not been included in this review) are likely to make similar contributions to benthic nitrogen excretion, it may be that total benthic biomass at the stations studied by Skyring *et al.* (1993) was significantly lower than the values estimated by us.

These data indirectly indicate that net annual secondary production by benthic deposit- and suspension-feeding macroinvertebrates is about 62,700 tonnes C, equivalent to a P:B ratio of 2.81. More direct measurements of secondary production are needed to confirm this estimate.

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1 Introduction

The macrobenthos is the community of organisms living on the sea floor, usually thought of as those bigger than 1 mm across. The fauna is numerous, diverse and active and plays a significant role in the passage of nutrients between sediments and its overlying water. Some species are predators and others herbivores, but most are either suspension feeders or deposit feeders.

Suspension feeders obtain their nutriment by trapping organic matter from the water with filters or mucus nets. Bivalve molluscs, tunicates and bryozoans are important suspension feeders, sometimes called filter feeders, as are some crustaceans and polychaetes. The organic matter is primarily living or dead phyto- and zooplankton and bacteria, resuspended benthic particles, and dissolved organic matter.

Deposit feeders ingest sediment which contains a small concentration of living and dead organic matter. Much of the organic matter in sediment is refractory (to individual species; it is unclear what percentage of organic matter is refractory to the community as a whole) so considerable amounts of sediment are processed in this way. The actual food source is organic matter itself, the interstitial meiofauna and the microflora attached to sediment particles.

Many species switch between deposit- and suspension-feeding but, because organic particles are often resuspended close to the sea floor, switching of feeding modes may not have much impact on the nature of their food. However, difficulty in determining the actual food source, living or dead, suspended or settled, has hindered the development of predictive and explanatory models of deposit-feeding (compared to, say, predator/herbivore systems).

Nevertheless, an appreciation of the scale of these processes is essential before anthropogenic effects from increased nutrients and pollutants on an ecosystem with limited exchange with the ocean, such as Port Phillip Bay, can be understood.

1.1 Aim of this review

Our aim is to identify those biological variables of Port Phillip Bay macrobenthic suspension and deposit feeders that are critical to estimation of nutrient cycling in Port Phillip Bay, and to make best estimates of Bay-wide quantities such as biomass, productivity and excretion on the basis of available information.

1.2 Scope

Our study is confined to the macrobenthos, that is the larger invertebrate animals of the benthos. We do not consider the smaller meiofauna, which may be more active than the macrofauna, nor the bacteria and other microflora except as a food source.

This review quantifies the role of deposit-feeding and suspension-feeding benthic invertebrates in sediment and water processing, nutrient cycling and secondary production in Port Phillip Bay. Quantifying the roles of both feeding types is vital for a better understanding of these processes in Port Phillip Bay.

The importance of benthic suspension feeders in Port Phillip Bay nutrient cycling was argued by Ward and Jernakoff (1993) who noted that benthic molluscs contribute a large fraction to the biomass of the Bay-wide fauna and that suspension-feeding molluscs may process a significant fraction of planktonic primary production. Estimates of biomass and clearance rates of suspension-feeding molluscs indicate a filtering time for the volume of Port Phillip Bay of 24 days (Poore and Rainer, 1974).

Scallops, which are suspension feeders, form a larger proportion of commercial fisheries catches in Port Phillip Bay than in other comparable temperate Australian locations. There is evidence that growth rates have increased over 20 years, possibly due in part to increased nutrient input to the Bay (Gwyther and McShane, 1988). However, increased growth rate is a frequent observation in exploited fisheries, and the scallop fishery has been operating in Port Phillip Bay for more than 20 years.

However, suspension feeders cannot be studied alone. *A priori*, deposit feeders may be more significant than suspension feeders in benthic nutrient cycling and secondary production. Of the molluscs dominating the benthic biomass, most are not suspension feeders. A notable example is the deposit-feeding bivalve *Theora lubrica* (= *T. fragilis*) which is the most common benthic invertebrate in the muddy environments that dominate Port Phillip Bay (Poore and Rainer, 1979).

All numerically important species in muddy environments are deposit feeders, and deposit feeders comprise "a major portion of the biomass" in these habitats (Poore and Rainer, 1979: 483). Muddy habitats constitute about 70% of the bottom area of Port Phillip Bay.

Most of the known nutrient pool in Port Phillip Bay is contained in sediments (only the upper 2 cm of sediments have been studied, and these contain 85% of P and 86% of N; based on data of Skyring *et al.* (1993). Deposit feeders typically process at least one body weight in sediment daily (Lopez and Levinton, 1987) and a more refined estimate of this rate of reworking of the sedimentary nutrient pool in Port Phillip Bay will therefore be important in estimating nutrient cycling in the Bay.

Many invertebrates can switch between deposit-feeding and suspension-feeding modes (Lopez and Levinton, 1987). Although local studies are lacking, switching of feeding modes has been demonstrated elsewhere in taxa which are significant components of the benthos of Port Phillip Bay: *Corophium* (Amphipoda; Meadows and Reid, 1966), Tellinidae (Mollusca; Pohlo, 1982) and Spionidae (Polychaeta; Taghon *et al.*, 1980; Dauer, 1983). Switching is often influenced by local environmental variables (current flow, concentration of suspended particles), so that a characterisation of feeding modes and efficiencies based on taxonomic composition of the community may by misleading.

Interactions between deposit- and suspension-feeding animals influence nutrient cycling and community structure. Suspension feeders remove particles from the water, adding to benthic deposits through biodeposition. Deposit feeders rework sediments and their activity results in a portion of the organic matter being resuspended in the water column.

1.3 Approach

Poore (1993) reviewed data on the soft-bottom macrobenthos of Port Phillip Bay and identified two Bay-wide quantitative studies completed in the 1970s. The first was a survey of the whole Bay which provided data on the density of hundreds of species at 86 stations (Poore *et al.*, 1975). Data on the biomass of only the molluscs were derived from this survey (Poore and Rainer, 1974). The second was a study of changes in numbers and biomass over three years at three sites on muddy habitats (Poore and Rainer, 1979).

These data are now held in computer databases at the Museum of Victoria and have been entered on the Port Phillip Bay Environmental Study Geographic Information System.

Published and unpublished data from these two sources were combined with data from the international literature on the biology of taxonomic and trophic groups identified as important in Port Phillip Bay to estimate Bay-wide distribution of biomass, feeding rates, secondary production and nutrient cycling.

A database of more than 600 references assembled in the course of this review is available to other participants of the Port Phillip Bay Environmental Study. The database is dominated by quantitative studies of temperate marine benthic taxa and communities.

2 Taxonomic and trophic composition of macrobenthos of Port Phillip Bay

2.1 Methods

Bay-wide biomass estimates for dominant trophic groups of benthic macroinvertebrates were obtained by combining biomass data originally collected by Poore and Rainer (1979) at three muddy stations with abundances at 86 stations collected in the Phase 1 study of Port Phillip Bay (Poore *et al.*, 1975).

Unpublished raw data, the basis of the Poore and Rainer (1979) paper, were used to obtain estimates of the individual biomass (ash-free dry weight - AFDW) for all Port Phillip Bay invertebrates. Trophic status of each species was obtained from Poore and Rainer (1974), Brusca and Brusca (1990) and Fauchald and Jumars (1979). Poore (1993) provided a hierarchical classification based on analysis of Phase 1 data, and this classification of benthic communities was used to recognise two strata approximately reflecting a division into muddy and sandy sediments. The distribution of stations from the Phase 1 study closely reflects the relative areas of the two strata in the Bay: 70% of the area comprises muddy sediments, 30% sand. A map showing the results of the hierarchical analysis of benthic communities at the 86 regularly-spaced stations has been published by Poore (1993: Figure 1). Abundances were obtained from the product of densities of individuals per tenth-m2 in the Bay-wide survey data (Poore *et al.*, 1975) for muddy and sandy strata separately. The estimated biomass in each strata was then summed for feeding groups in all taxa to obtain biomass values presented in Table 1.
Data drawn from the literature on feeding rates and other processes were converted where necessary to standard units, "ash-free dry weight of feeder" (AFDW). Other abbreviations used are WW = wet weight; DW = dry weight; C = carbon; V = volume (mm^3). All rates are given per day.

For all taxa:

AFDW = 0.88 x DW	(Cammen, 1980a)

For annelids:

AFDW = 0.17 x WW	(Cammen, 1980a)
AFDW = 2.17 x C	(Nichols, 1975)
AFDW mg = 0.15 x V mm^3 - 0.002	(Forbes and Lopez, 1987; Cammen, 1980a)

For crustaceans:

AFDW = 0.15 x WW	(Lie, 1968)

For molluscs (including shell):

AFDW = 0.07 x WW	(Cammen, 1980a)

For holothurians:

DW = 0.14 x WW	(Bakus, 1968)

2.2 Results

Table 1 provides Port Phillip Bay-wide abundance and biomass estimates for all taxonomic and trophic groups. Molluscs (36%), Crustacea (29%), Annelida (16%) and Echinodermata (14%) contributed the vast majority of biomass. (The majority of annelids were species of polychaetes, and are listed as such in following tables.) The dominant species in terms of biomass are listed in Table 2. Dominating the biomass, despite being restricted to a few estuarine localities, was the suspension-feeding bivalve *Notospisula trigonella*. Other dominant species were widely distributed in Port Phillip Bay, and were headed by two deposit-feeding species, the echinoid *Echinocardium cordatum* and the thalassinidean crustacean *Neocallichirus limosa* (previously known as *Callianassa limosa*). Both of these species were widespread and abundant on muddy sediments in Port Phillip Bay. The ten dominant species accounted for an estimated 57% of the total macrobenthic biomass in Port Phillip Bay.

By trophic group, irrespective of taxonomic classification, suspension feeders accounted for 49% of total macrobenthic biomass in Port Phillip Bay and deposit feeders contributed a further 35% (Table 3). Some species were difficult to categorise by trophic group, thus the category "deposit or suspension" appears in Table 1. Half of each biomass quantities for these composite categories has been added to the separate "deposit" and "suspension" categories for calculations, commencing with Table 5.

Ten taxonomic-trophic groups, hereafter described as feeding groups, accounted for 87% of the total macrobenthic biomass in Port Phillip Bay but were unequally distributed between the two dominant sedimentary regimes (Table 4). Muddy environments comprise 70% of the total area of 1950 km2 of Port Phillip Bay and sandy sediments the remainder.

Table 1. Calculated abundance and estimated biomass of Port Phillip Bay invertebrates by taxonomic feeding groups. (Subtotals are for all feeding groups of each taxon)

	FEEDING TYPE	No. species	Individuals per m^2	Bay-wide biomass AFDW (g)	% of Baywide biomass
Bryozoa	suspension	3	1.24	1.09e+09	2.13
Chordata	suspension	9	3.41	8.31e+08	1.63
Cnidaria	deposit	1	6.55	1.14e+07	0.02
	predator	13	4.66	8.08e+06	0.02
	SUBTOTAL	14	11.21	1.94e+07	0.04
Crustacea	deposit	161	831.29	8.72e+09	17.08
	parasite	1	0.15	8.67e+05	0.00
	predator	4	2.20	2.31e+07	0.05
	scavenger	45	51.70	1.93e+09	3.78
	suspension	29	265.07	4.10e+09	8.04
	SUBTOTAL	240	1150.42	1.48e+10	28.95
Echinodermata	deposit	3	40.73	4.68e+09	9.16
	deposit or suspension	11	8.99	1.89e+09	3.70
	grazer	2	1.19	9.71e+07	0.19
	predator	4	0.96	3.36e+08	0.66
	SUBTOTAL	20	51.87	7.00e+09	13.71
Echiura	deposit	1	0.21	1.29e+08	0.25
Mollusca	deposit	10	852.11	1.69e+09	3.32
	grazer	23	58.21	5.43e+08	1.06
	predator	19	13.60	1.27e+08	0.25
	scavenger	3	12.98	1.21e+08	0.24
	suspension	44	268.54	1.57e+10	30.83
	SUBTOTAL	99	1205.43	1.82e+10	35.69
Nematoda	deposit	22	73.16	3.57e+07	0.07
	predator	1	6.40	3.12e+06	0.01
	SUBTOTAL	23	79.57	3.88e+07	0.08
Nemertea	predator	12	17.09	8.55e+08	1.68
Phoronida	suspension	3	47.97	2.71e+07	0.05
Platyhelminthes	predator	3	0.11	4.92e+05	0.00
Polychaeta	deposit	134	579.33	2.56e+09	5.02
	deposit or suspension	13	64.71	1.07e+08	0.21
	predator	81	182.85	2.02e+09	3.96
	suspension	10	33.64	3.33e+09	6.53
	SUBTOTAL	238	860.52	8.03e+09	15.72
Porifera	suspension	6	0.27	3.95e+05	0.00
Priapula	predator or deposit	1	0.15	6.75e+05	0.00
Pycnogonida	predator	5	1.22	2.03e+06	0.00
Sipunculoidea	deposit	3	0.92	2.00e+06	0.00
All Phyla	TOTAL	680	3431.61	5.11e+10	100

Table 2. Ten dominant (by biomass) species of benthic macroinvertebrates in Port Phillip Bay.

Taxon	**Trophic group**	**Estimated proportion of total biomass**
Notospisula trigonella (Mollusca)	suspension	17%
Echinocardium cordatum (Echinodermata)	deposit	8%
Neocallichirus limosa (Crustacea)	deposit	7%
Chioneryx cardiodes (Mollusca)	suspension	6%
Theora lubrica (Mollusca)	deposit	5%
Dimorphostylis cottoni (Crustacea)	suspension	4%
Phyllochaetopterus socialis (Polychaeta)	deposit	4%
Fulvia tenuicostata (Mollusca)	suspension	2%
Mytilus edulis (Mollusca)	suspension	2%
Mysella sp. 2 (Mollusca)	suspension	2%
TOTAL		57%

Table 3 Estimated numbers of species and of individuals and total biomass for Port Phillip Bay benthic macroinvertebrate feeding groups (across all sediments)

Trophic group	**no. of spp.**	**% of total spp.**	**abundance (individ.m^{-2})**	**% of total abundance**	**biomass AFDW (g)**	**% of total biomass**
Suspension or deposit	24	3.53	70.70	2.14	2.00e+09	3.90
Suspension	104	15.29	620.14	18.04	2.51e+10	49.12
Scavenger	51	7.50	71.94	2.00	2.05e+09	4.01
Predator	143	21.03	180.93	5.26	4.07e+09	7.98
Parasite	1	0.15	0.15	0.00	3.04e+05	0.00
Grazer	25	3.68	59.35	1.73	6.40e+08	1.25
Deposit	332	48.82	2407.67	70.03	1.78e+10	34.88
TOTAL	680	100.00	3431.61	100.00	5.11e+10	100.00

Together, suspension and deposit feeders comprised 98% of the total biomass on muddy environments but only 75% on sandy environments. Other feeding groups, especially predators, were more abundant on sandy sediments.

Deposit feeders comprised about 41% of the total macrobenthic biomass at muddy stations, but were less important on sandy sediments (30%) which have lower organic content. Suspension-feeding molluscs are the single most important taxonomic-trophic group on muddy sediments, where they comprise about 42% of the total macrobenthic biomass. The most important group on sandy sediments were deposit-feeding crustaceans, which make up about 22% of the total macrobenthic biomass.

2.3 Sources of error and variability

The accuracy of these calculations based on extrapolation to generate Port Phillip Bay-wide estimates of total biomass can be tested by comparison with Poore and Rainer's (1974: Table 3, p. 392) estimate of total biomass of suspension-feeding molluscs in Port Phillip Bay: 1.90×10^{10} g AFDW. Our estimate is 1.57×10^{10} g AFDW. The discrepancy is likely to be due to unequal size-class distribution across all sediment types in Port Phillip Bay. This conclusion is supported by the close agreement between estimates of mean biomass.individual^{-1} for molluscs in the central basin of Port Phillip Bay. Poore and Rainer (1974) estimated 4.43 mg AFDW.individual^{-1}, compared with 4.78 mg AFDW.individual^{-1} calculated from unpublished Poore and Rainer (1979) data. No data are available for comparison of other trophic groups. Muddy sediments tend to be dominated by smaller size-classes than occur in better-sorted sediments. If this is generally true, the biomass extrapolations that we have made will underestimate the Port Phillip Bay biomass for all feeding groups. This source of error will be most apparent in those groups that prefer sandy to muddy sediments, such as suspension feeders. Since individual specimen weights were not recorded in the Poore and Rainer (1979) data, standard deviations cannot be calculated. In the absence of a direct estimate of sample variance, the 20% difference between our estimate and the Poore and Rainer (1974) value is an estimate of the level of uncertainty resulting from inadequate knowledge of size-class distribution of the fauna.

Another source of uncertainty in biomass estimates is temporal variation. Poore and Rainer (1979) recorded wide fluctuations in abundance of several species, and noted that inter-annual effects were more important than seasonal variation. Further analysis of data collected by Poore and Rainer reinforces this conclusion, as demonstrated by the following examples. Average seasonal biomass (g AFDW.m^{-2}) across all stations over 3 years are: 6.89 (summer); 11.24 (autumn); 7.62 (winter) and 12.61 (spring). The low summer value compared with autumn and spring biomass indicates that seasonal variation in macrobenthic biomass in Port Phillip Bay may be at least 40%. Even greater variability is indicated by inter-annual comparison of total macrobenthic biomass at all three stations for all four seasons: 1973 biomass was 6.37; 1974 biomass was 8.00 and in 1975 biomass was more than double that recorded in 1973 - 14.91 (g AFDW. m^{-2}). Similar variation for different trophic groups can be demonstrated. For example, at station PPBES 940 biomass of suspension feeders on separate sampling occasions varied from 0 to 93.6 g AFDW. m^{-2}. Although such variation is due in part to patchy distribution of large species such as the ascidian *Pyura stolonifera*, the evidence of large-scale variation in total biomass presented above suggests that wide variation in total macrobenthic biomass occurs in Port Phillip Bay from year to year.

Our calculations, based on the best available data, indicate that uncertainty exists even for the most straightforward values such as total biomass. Care should therefore be taken in extrapolating from these values to productivity and other rates (next sections).

2.4 Comparisons and use of biomass estimates

The average macrobenthic biomass for Port Phillip Bay of about 25 g AFDW.m^{-2} is at the high end of the range of values for subtidal marine benthic faunas summarised by Kennish (1990), which are in the range 8-26 g AFDW.m^{-2}. Many of these studies were of benthos retained on a 0.5 mm mesh. Given that the Port Phillip Bay data were collected using a 1.0 mm mesh sieve, biomass is exceptionally high.

Biomass estimates for ten feeding groups (Table 4) were used to estimate rates of nutrient cycling in Port Phillip Bay. Given the present incomplete knowledge of the biology of Port Phillip Bay benthic invertebrate species, we believe that feeding group is the most realistic scale for further calculations. Subsequent estimates depend on drawing on rates from the literature; no rate measurements for Port Phillip Bay benthos have ever been made.

Differences between the two feeding modes have led workers to measure feeding rates and productivity in different ways. In both cases some measure of the amount of material handled is made (sediment ingested or water filtered), combined with a concentration of organic matter, assimilation rate and excretion rate to give a measure of productivity. The following sections deal with each of these steps in turn and estimate values for Port Phillip Bay.

3 Feeding and clearance rates of deposit and suspension feeders

3.1 Experimental methods and sources of error

Rates of deposit feeding are estimated from measurement of ingestion or egestion or of gut volume and turnover time. Ingestion rates can be obtained only by subtraction from a measured sediment/food supply. Many such experimental studies use artificial food. Where comparisons have been made feeding rate on natural sediments normally exceeds that on artificial foods (Taghon, 1988). Gut volume and turnover time measurements rely on approximations of gut architecture and ontogeny that may often be invalid, especially for juveniles (Penry and Jumars, 1990). Turnover may be measured with starved animals (in which case feeding rates will be overestimated due to starvation effects) or may be measured using coloured, radioactive or magnetic markers (Lopez *et al*., 1989; Lopez and Elmgren, 1989; Jumars and Self, 1986; Grémare *et al.*, 1991). A statistical design developed by Jumars and Self (1986) involving preparation of "calibration curves" for individual specimens reduced variance, but even without such calibration the error in these methods appears to be less than the variability due to environmental factors.

The most frequently-used method of obtaining feeding rates for deposit feeders is measurement of egested sediment. Egestion rate measurements underestimate ingestion rates by the product of assimilation efficiency and organic matter content of sediment (Cammen, 1980a). For most marine environments organic matter content is less than 10% and errors due to failing to account for assimilation efficiency are insignificant.

Values of egestion rates were compiled from the literature and means were calculated for taxonomic groups. When multiplied by the total biomass of deposit feeding groups an estimate of the weight of sediment ingested by all deposit feeders was obtained.

Rates of suspension feeding are usually derived using one of two methods. In one method individuals (or at least the inlet siphon) are contained in a vessel which allows the current to be directly measured. The other method that is commonly used involves measuring the rate at which a known concentration of food particles is removed from a volume of water. Optical measurement of water clarity is often used to establish the concentration of food particles in the water. There is little criticism of either technique in the literature, and experimental errors appear to be insignificant compared with variability due to environmental conditions.

Table 4 Distribution of biomass for 10 dominant benthic macroinvertebrate feeding groups across the two major Port Phillip Bay sediment types.

Feeding group	Sandy sediments		Muddy sediments		PPB totals	
	AFDW ($g \times 10^9$)	% of sandy biomass	AFDW ($g \times 10^9$)	% of muddy biomass	AFDW ($g \times 10^9$)	% of PPB biomass
Polychaeta						
deposit	1.0	5.2	1.5	4.9	2.6	5.1
suspension	1.4	7.4	1.9	6.0	3.3	6.6
Bryozoa						
suspension	0	0	1.1	3.5	1.1	2.1
Ascidiacea						
suspension	0.4	2.3	0.4	1.2	0.8	1.6
Crustacea						
deposit	4.2	21.5	4.4	14.1	8.7	17.1
suspension	3.1	15.7	1.0	3.2	4.1	8.0
Echinodermata						
deposit	0.0	0.0	4.7	14.8	4.7	11.0
deposit or suspension	1.0	5.7	0.9	2.9	1.9	1.8
Mollusca						
deposit	0.0	0.0	1.7	5.4	1.7	3.3
suspension	3.4	17.3	13.1	41.6	15.7	30.8
TOTAL	14.6	74.5	30.7	97.6	44.6	87.3

Values of suspension-feeding rates were compiled from the literature and means were calculated for taxonomic groups as was done for deposit feeders. When multiplied by the total biomass of suspension feeding groups an estimate of rate of water filtration by macrobenthos and a Bay turn-over time were obtained.

3.2 Published values and variability of feeding rates

Deposit feeders. Appendix 1 summarises feeding rates for several marine deposit feeders (measured as ingestion or egestion rate). Values have been converted to standard units (g DW sediment.gAFDW feeder^{-1}.d^{-1}) where necessary. Per gram, bivalve molluscs have the lowest deposit-feeding rates and polychaetes the highest.

Deposit-feeding rates may vary as much between populations of a single species as across phyla. For example, measurements from two studies within populations of the polychaetes *Abarenicola pacifica* and of *Thoracophelia mucronata* varied by an order of magnitude (Appendix 1). The methods used do not appear to be faulty, and this variation must be taken as indicative of different environmental conditions and/or genetic differences between populations.

Numerous experimental studies of single species have demonstrated positive correlation between ingestion rate and organic content of sediment (Kemp, 1986; Taghon and Jumars, 1984; Hummel, 1985). Typically, ingestion rate varies by a factor of between 2 and 5 for variations of organic content that might be expected in natural sediments. However, other studies have shown an inverse relationship between organic content of food and feeding rate (Gordon, 1966; Kudenov, 1982).

Some of these contradictory results can be explained by the quality of food offered. Positive associations between ingestion rate and organic content tend to result from studies using food of low organic content (<1%) or poor nutritive quality, whereas inverse relationships may occur at rich food levels (Lopez and Levinton, 1987; Cammen, 1989). This conclusion implies that realistic nutrient cycling models for Port Phillip Bay should be verified using feeding rate data collected in the field, or in laboratory conditions that closely replicate nutrient quality and quantity of Port Phillip Bay sediments. Laboratory studies indicate that nitrogen content of sediments determines nutritive quality (below a limiting threshold), and that nitrogen content of sedimenting material usually found in coastal systems is limiting for a typical deposit feeding population (Tenore, 1981). Other factors that may be responsible for variation in feeding rate include reproductive activity (Grémare and Amouroux, 1990), current flow and sediment transport (Warner and Woodley, 1975; Levinton, 1991) and diurnal influences (Lopez and Elmgren, 1989; Coulon and Jangoux, 1993). However, studies which have measured multiple factors (Tenore, 1977; Christensen and Kanneworff, 1985; Thompson and Nichols, 1988) and recent reviews (Cammen, 1980a, 1989; Lopez and Levinton, 1987) show convincingly that concentration and quality of organic matter in sediment (rather than temperature or salinity) are the major environmental factors determining feeding rates of deposit-feeding marine invertebrates.

Feeding rates of deposit feeders also vary with body size, but the relationship is not linear. Feeding rates scale with body volume to the power 0.7, closely paralleling scaling of gut surface area with volume (to the power 0.77) (Cammen, 1980a; Forbes and Lopez, 1987). This relationship appears to reflect metabolic and physiological constraints on gut function (Forbes and Lopez, 1987) and holds true across phyla, with the unaccountable exception of bivalve gastropods, which have lower feeding rates than predicted (Cammen, 1980a).

Suspension feeders. Appendix 2 summarises feeding rates for marine suspension feeders (measured as filtration or clearance rate). Values have been converted to standard units ($l.gAFDW^{-1}.d^{-1}$) where necessary and values which appeared to be unrepresentative were omitted from subsequent calculations. Per gram, annelid worms have the highest mean filtration rate, about double that of molluscs. Ascidians such as the genus *Pyura* (the dominant ascidian genus in Port Phillip Bay) filter at slower rates. We have not been able to locate estimates of water filtering rates for relevant suspension-feeding bryozoans, crustaceans (mostly ostracods and amphipods in Port Phillip Bay) and echinoderms (mostly ophiuroids). The mechanics of suspension-feeding in these groups, which use net-like structures to sweep particles from the water, is most similar to feeding in suspension-feeding polychaetes, so water filtering rate for polychaetes has been applied to crustacean and echinoderm suspension feeders hereafter. The filtering rate of ascidians has been applied to bryozoans also.

Filtering rates calculated by early workers were highly variable as no account was taken of variation due to size. The filtering rates given in Appendix 2 have been linearly corrected for size (weight) but because filtering rate is geometrically related to body weight (Klumpp, 1984; Bayne and Newell, 1983) some error still exists. To properly calculate the filtering rate of Port Phillip Bay suspension-feeding benthos would require biomass estimates across size classes. *Doering et al*. (1986) calculated that size accounts for 31% of variability in measurements of filtering rate and temperature another 10%.

Most workers have calculated filtering rates under controlled conditions in the laboratory using monocultures of algae or bacteria or natural seston. Under these conditions, suspension-feeding ascidians have recorded higher gonad weights than under natural conditions (Klumpp, 1984) suggesting that the laboratory conditions may bear little resemblance to natural conditions. The relationship between laboratory and field conditions is unclear, but it is likely that the laboratory rates represent optimal rates under ideal conditions and not natural rates (Doering *et al*., 1986). Few workers have studied rhythms in filtration rates, but Klumpp (1984) found no discernible pattern in the variation in filtration rate of the tunicate *Pyura stolonifera*.

Variation in filtering rate within taxa is generally much less than the variation between taxa. This represents a real difference that may be due to differences in average body size between taxa, the efficiency of their filtering apparatus, or ability to generate feeding currents. Filtering rates for taxa that can both deposit and suspension feed were considerably lower than rates for dedicated suspension feeders. These lower values have not been included in further calculations.

3.3 Estimated Port Phillip Bay-wide sediment and water turnover rates

Multiplication of biomass (Table 4) and sediment egestion rates (calculated from Appendix 1) or water filtration rates (calculated from Appendix 2) gave values of total sediment or water turnover rates.

Table 5 presents estimates of the rate of sediment processing by the major macrofaunal deposit-feeding groups in Port Phillip Bay. Polychaetes accounted for about 44% of total sediment processed by deposit-feeding benthic macroinvertebrates in Port Phillip Bay. The dominance of this group was due to a rate of sediment processing per unit biomass about three times higher than for echinoderms and six times higher than for crustaceans. The total amount of sediment processed by these animals in one year is estimated at 3.2×10^7 tonnes, or about 66% of the top 2 cm of sediments in Port Phillip Bay (assuming an average sediment density of 1.24 $g.cm^{-3}$; A. Longmore, pers. comm.). Thus, complete turnover of the top 2 cm of sediments by deposit-feeding macrobenthos is estimated to occur in about 1.5 years. This does not indicate the level of sediment processing; many species operate at much greater depth. It seems from the spatial and temporal variability in our estimates of total biomass that uncertainty in estimating sediment turnover is at least 60%.

Table 6 presents estimates of the rate of water clearance by suspension-feeding macrobenthos in Port Phillip Bay. Bivalve molluscs account for about 46% of total water volume filtered by suspension-feeding benthic macroinvertebrates. These estimates of filtering indicate that the subtidal water volume of Port Phillip Bay will be filtered in about 16.5 days, or about 22 times per year. This is close to the estimate due to molluscs alone (24 days) by Poore and Rainer (1974). The difference is due to refined estimates of filtering rates based on a wider literature survey in this review. (Of course, these estimates assume that the waters of Port Phillip Bay are perfectly mixed and equally accessible to suspension feeders.)

Table 5 Estimated rate of sediment processing by deposit-feeding macrofauna in Port Phillip Bay

Deposit-feeding group	**Total AFDW ($g \times 10^9$)**	**Sediment ingestion rate: mean (range) (gDW sed. gAFDW $feeder^{-1}$. day^{-1})**	**Weight of sediment ingested (tonnesDWsed. $year^{-1}10^7$)**	**% of total PPB sediment turnover**
Crustacea	8.72	2.3 (0.4-6.5)	0.7	22
Echinodermata	5.63	5	1.0	31
Mollusca	1.69	1.7 (0.1-4.8)	0.1	3
Polychaeta	2.56	15.3 (4.5-34.1)	1.4	44
TOTAL	18.60		3.2	100

3.4 An important species ignored

There are no quantitative data available for feeding rates of temperate deposit-feeding echinoderms, and the sediment processing rate of *Echinocardium cordatum*, which dominates the Port Phillip Bay benthos, is unknown. Qualitative descriptions of feeding in *E. cordatum* (from a population in Normandy, France; De Ridder, 1982) indicated that the gut may take up to 23 hours to fill and that faecal pellets are held in the caecum for long periods (only 1 of 19 animals studied defecated in a 83 hour period). These food passage times are almost twice the values estimated for a tropical holothurian (Bakus, 1968) and may indicate a relatively slow feeding rate for *E. cordatum*, perhaps compensated for by higher assimilation efficiency, which generally increases as gut passage time increases (Kofoed *et al.*, 1989). Another northern hemisphere population of *E. cordatum* has been studied by Buchanan (1966), who reported a declining rate of secondary production with increasing age, but provided no quantitative data on feeding rates. A quantitative study of feeding and assimilation rates in *Echinocardium cordatum* would enable these predictions to be tested, and would provide more accurate data on which to base estimates of nutrient cycling in Port Phillip Bay. In the absence of quantitative data, published feeding rate values for holothurians have been used to estimate sediment processing in Port Phillip Bay by *E. cordatum*.

Table 6 Estimated rate of water filtering by suspension-feeding macrofauna in Port Phillip Bay, using feeding rate data summarised from Appendix 2.

Suspension-feeding group	**Total AFDW ($g \times 10^9$)**	**Water filtering rate ($l.gAFDW^{-1}.day^{-1}$)**	**Volume of water filtered ($l.day^{-1} \times 10^{10}$)**	**Proportion of total water filtered (%)**
Ascidiacea	0.8	18.1	1.5	1
Bryozoa	1.1	18.1	2.0	1
Crustacea	4.1	94.3	38.7	25
Echinodermata	1.0	94.3	9.0	6
Mollusca	15.7	45.7	71.7	46
Polychaeta	3.3	94.3	31.4	20
TOTAL	26.0		154.2	100

4 Assimilation efficiency of deposit and suspension feeders

Assimilation efficiency is the ratio between the amount of organic material absorbed by an animal for growth, respiration, reproduction etc. and the amount entering the gut.

4.1 Experimental methods and sources of error

Assimilation efficiency may be determined by direct measurements of organic content of foregut and faeces (and pseudofaeces; non-assimilated pellets produced by suspension feeders). If efficiency is determined by comparison of faeces with sediment concentrations of organic material and selective feeding occurs, measurement will fail to distinguish selective feeding and assimilation efficiency and the latter will be overestimated. Radioactive tracers are also employed to measure uptake of labelled carbon from the sediment. However, recycling of tracer and non-feeding transfer of tracer mean that these methods also may overestimate absorption efficiencies, perhaps by as much as a factor of two (Yingst, 1976).

Measures of assimilation efficiency provide a lower limit on estimates of the fraction of the organic matter that is biologically available to individual species. However, it is not clear how much overlap there is between species in food requirements. The fraction of the total organic matter that is collectively available to the benthic community is thus unknown (despite a considerable research focus on the problem; Lopez *et al.*, 1989, Cheng *et al.*, 1993, and references therein). Conceivably, in a community of more than 200 species, a high percentage of the organic matter could be biologically available even though individual species might have low assimilation efficiencies.

Even the chemical composition of sedimentary organic matter is poorly known (A. Longmore, pers. comm.), although Mayer (1989) has suggested that the non-refractory material is mostly polymeric, probably polysaccharides and protein.

Methods for estimating the biologically available fraction of sedimentary organic matter, in addition to those methods used to estimate assimilation efficiencies (see above), include more biologically informative approaches. Enzymatic assay procedures that mimic hydrolytic processes thought to occur in animal guts have been used to estimate non-refractory content (Mayer, 1989; George, 1964). More direct still are bioassay methods which use species abundance and biomass as a measure of biologically available organic matter (Cheng *et al.*, 1993). Such single-species bioassay studies have led us to propose what may be a novel method for assessing the refractory content of sedimentary organic matter in Port Phillip Bay (see recommendations, below).

4.2 Published values

Assimilation efficiencies for deposit feeders are mostly in the range 5-50%, but high values have generally been recorded in laboratory studies under optimum conditions (Appendix 3). Mayer (1989) also estimated that between 5 and 30% of organic matter in sediments was available to deposit feeders. However, even values recorded for organisms in natural sediments may exceed 50% (Jacobsen, 1967). Mean values were calculated to estimate Bay-wide assimilation rates. Assimilation efficiencies for suspension feeders are higher than for deposit feeders, and are mostly in the range 10-70% (Appendix 4). As with deposit feeders, high values are often recorded in laboratory studies in ideal conditions. For this reason, high values have been omitted before calculation of mean values for Port Phillip Bay feeding groups (Table 7).

4.3 Sources of variability in assimilation efficiency

Factors responsible for variability in assimilation efficiency of both deposit and suspension feeders are not well understood.

There appears to be no correlation between assimilation efficiencies of deposit feeders and organic content of sediment. Values exceeding 30% have been recorded in sediments of unusually high (32%) and low (<1%) organic content (Whitlach, 1974; Jacobsen, 1967). It is likely that nutritional quality of the organic fraction is more important (Yingst, 1976). For some taxa, assimilation efficiency increases during the growing season (Hummel, 1985) or in surface rather than deeper sediments (Lopez and Elmgren, 1989), but it is not clear if this effect is due to variation in temperature or food quality or quantity. Since absorption is a time-dependent process, and since larger animals tend to have longer gut-residence times, assimilation efficiency might be expected to increase with body size (Kofoed *et al.*, 1989); however, no data are available to test this hypothesis.

Studies of assimilation efficiency in suspension feeders, however, have identified quality and quantity of organic matter as the major determinant of assimilation efficiency. A great deal of variability in assimilation efficiency can be accounted for by variation in food quality. Both molluscs and ascidians have much higher assimilation efficiencies when fed on algae than when fed on seston or natural particles (Appendix 4). However, values recorded for animals feeding on seston or detritus may better reflect the assimilation efficiencies of suspension feeders in Port Phillip Bay. Variation may also occur due to concentration of organic matter: Morais and Fiala-Medioni (1985) found assimilation efficiency in the ascidian *Phallusia mammillata* increased with organic content and fell to zero at concentrations of organic matter below 5-10%. Seasonal variations in assimilation efficiency appear to be due to variation in food quality (Morais and Fiala-Medioni, 1985).

Competition between individuals of the same or different species may alter filtering rates or assimilation efficiencies. It is well known that suspension-feeding organisms can significantly deplete suspended materials on a local scale and effect growth rates (Peterson and Black, 1991; and references therein), but the impact of density on efficiency has not been studied.

4.4 Port Phillip Bay-wide estimates of assimilation efficiency and masses of material absorbed by macrobenthos

The mass of material cycled and processed by macrobenthos in Port Phillip Bay can be estimated from values of total biomass for different feeding groups (Table 4), organic content of sediments (for deposit feeders) or in the water (for suspension feeders), feeding rates (Tables 5 and 6) and assimilation efficiencies (Appendices 3 and 4, summarised in Table 7). Organic content of the top 2 cm of sediment is estimated at 1.94×10^6 tonnes which is 4% of the total sediment weight of 4.84×10^7 given a density of 1.24 $g.cm^{-3}$ (A. Longmore, pers. comm.). The amount of organic matter in Port Phillip Bay water is estimated at 1.08×10^5 tonnes (twice the TOC quantity of 54,073 tonnes given by Skyring *et al.*, 1993). Recent analyses of Port Phillip Bay show that the fraction of the TOC that is particulate, and therefore potentially available to suspension feeders, is 12.6% (A. Longmore, pers. comm.). Although it is likely that some dissolved organic matter is also taken up by suspension feeders, most studies have only quantified feeding rates on particulate matter. We have therefore based calculations on the estimated particulate organic content (1.36×10^4 tonnes), although this probably underestimates, by an unknown amount, the quantity of organic matter processed by suspension feeders.

The results of these calculations for all feeding groups are presented in Table 7. Deposit-feeding polychaetes (35%) and echinoderms (25%) account for the highest proportion of organic matter processed per year. Collectively, deposit feeders are estimated to account for 85% of all organic matter processed by benthic macroinvertebrates in Port Phillip Bay. Although the pool of particulate organic matter assumed to be available to deposit feeders is two orders of magnitude larger than that available to suspension feeders, the clearance rate for this organic matter is much faster for suspension feeders (22 times per year) than for deposit feeders (0.66 times per year).

In terms of organic matter assimilated, there is less difference between deposit feeders (estimated to assimilate 58% of organic matter) and suspension feeders (42%).

Table 7 Estimates of assimilation efficiency and masses of material processed by 9 dominant macrobenthic feeding groups in Port Phillip Bay. Quantity of organic matter processed per year is derived from Tables 5 and 6. Assimilation efficiency estimates are summarised from Appendices 3 and 4.

Feeding group	**Total biomass (gAFDW x10^9)**	**Organic matter processed.year^{-1} (tonnes x 10^3)**	**Proportion of total organics processed (%)**	**Assimilation efficiency (%)**	**Organic matter assimilated (tonnes x10^3.year^{-1})**	**Proportion of total organics assimilated (%)**
Ascidiacea						
suspension	0.83	3.0	< 1	40	1.2	< 1
Bryozoa						
suspension	1.09	3.9	< 1	30	1.2	< 1
Crustacea						
deposit	8.72	290.0	18	20	58.0	18
suspension	4.1	76.6	5	30	23.0	7
Echinodermata						
deposit	5.63	400.0	25	20	80.0	25
suspension	0.95	17.6	1	30	5.3	2
Mollusca						
deposit	1.69	40.0	3	30	12.0	4
suspension	15.7	142.0	9	60	85.2	27
Polychaeta						
deposit	2.56	560.0	35	6	33.6	11
suspension	3.30	62.1	4	30	18.7	6
TOTAL	44.57	1595.2	100		318.2	100

5 Excretion products and rates of deposit and suspension feeders

5.1 Published values and variability in excretion rates and products

Our discussion of excretion concentrates on the fate of nitrogen. Most marine invertebrates for which data are available are ammonotelic, that is, they excrete nitrogenous waste as ammonia (Campbell, 1970). Bivalve molluscs can eliminate between 5 and 50% of total nitrogen excretion in the form of amino acids, but this phenomenon is highly seasonal and is usually associated with periods of starvation and/or gametogenesis. At these times catabolism of protein provides a reserve energy supply (Bayne and Scullard, 1977). Excretion of total nitrogen (ammonia and amino acids) by the bivalve mollusc *Mytilus edulis* declined as a result of starvation in summer and autumn, but increased with winter starvation; excretion rates were highest in summer and lowest in winter (Bayne and Scullard, 1977). The same authors also showed that rates of ammonia excretion increased with temperature. Starvation in echinoderms also resulted in an increased rate of excretion of ammonia but not amino acid due to catabolism of tissue (Stickle, 1988; Diehl and Lawrence, 1979; Davoult *et al.*, 1991). Studies of molluscs (Duerr, 1968; Bayne and Scullard, 1977), polychaetes (Emerson, 1969; Hult, 1969; O'Malley and Terwilliger, 1975) and crustaceans (Emerson, 1969; Nelson *et al.*, 1977) confirm that taxa which dominate Port Phillip Bay macrobenthos excrete 90% or more of total nitrogen as ammonia. However, echinoderms have been shown to excrete significant quantities of urea (16 of 22 species studied excrete at least 10% of total nitrogen as urea; Stickle, 1988). Among echinoderms, echinoids (which are dominant in terms of Port Phillip Bay biomass) have the lowest proportion of urea excreted (less than 5% of total nitrogen), but only two species in a single genus have been studied (Stickle, 1988). The rate of urea excretion in echinoderms is apparently independent of nutritional status (Diehl and Lawrence, 1979), but the polychaete *Pista pacifica*, which is normally ammonotelic, will excrete 10% of nitrogen as urea when starved (O'Malley and Terwilliger, 1975). Related phyla of deuterostomes (i.e., ascidians, in the context of Port Phillip Bay benthos), might be expected also to excrete urea, but those ascidians that have been studied excrete up to 95% of non-protein nitrogen as ammonia (Campbell, 1970). Nelson *et al.* (1977) demonstrated an inverse relationship between ammonia excretion rate and body weight in the shrimp *Macrobrachium rosenbergii*. However, Duerr (1968) showed a positive logarithmic relationship between ammonia excretion rate and body weight for molluscs. No other workers appear to have investigated possible correlations between ammonia excretion rate and body weight.

Comparative studies of echinoderms (Diehl and Lawrence, 1979; Stickle, 1988) and molluscs (Duerr, 1968; Emerson, 1969) have failed to demonstrate any relationship between ammonia excretion rate and trophic status or phylogenetic relatedness. However, the data summarised in Table 8 indicate that crustaceans and polychaetes excrete nitrogen at approximately twice the rate per unit biomass as molluscs and echinoderms. These data also indicate that, for molluscs at least, nitrogen excretion rate does not depend on trophic status.

Quantitative data on ammonia excretion rates in several species are summarised in Appendix 5. Values range considerably, from 0.1 to 1.8 $mgN.gAFDW^{-1}.d^{-1}$, and are summarised by feeding groups in Table 8.

5.2 Estimated flux of nitrogen to Port Phillip Bay from benthic macroinvertebrates

The product of total biomass of benthic macroinvertebrates for Port Phillip Bay (Table 1) by mean values of nitrogen excreted for major feeding groups from Appendix 5 gives a value of about 15,430 tonnes as the estimated quantity of nitrogen excreted by benthic macroinvertebrates in Port Phillip Bay per annum (Table 8). This value exceeds the estimate of total annual inorganic nitrogen flux (11,800 tonnes) from sediments given by Skyring *et al.*, 1993 (p. 37), based on measurements on incubated Port Phillip Bay sediment cores.. (For our estimate, feeding groups for which no excretion rate estimates were available were assigned the mean of values recorded for the four major phyla: 0.85 mg $N.gAFDW^{-1}.day^{-1}$.) Our estimate of total nitrogen excretion is based on macrofauna alone. As discussed in section 7.3 (below), smaller components of the benthos (meiofauna and microflora) would be expected to make a similar or greater contribution to benthic nitrogen excretion to that of benthic macroinvertebrates. It is surprising, therefore, that our estimate for benthic macroinvertebrates alone exceeds the value estimated by Skyring *et al.* (1993). The discrepancy is likely to be due to fluctuations in total benthic biomass and/or to effects of the experimental cores of Skyring *et al.*, which may disrupt activities and nitrogen excretion of benthic animals.

As discussed above, nitrogen excretion rates are also likely to vary with nutritional status, and, depending on the taxon, may either increase or decrease during periods of low food quality or quantity. We have insufficient information to estimate this source of variability in Port Phillip Bay.

Crustacea make the largest single contribution (about 46%) to macrobenthic nitrogen excretion. The discrepancy between the relative assimilation rates of molluscs as a whole (56%) and crustaceans (20%), reported in Table 7, may be partly explained by the higher relative excretion rate of crustaceans. Molluscs (22%) and polychaetes (21%) also make major contributions to the nitrogen excretion load from benthic macroinvertebrates.

Table 8 Estimates of total nitrogen excretion loads for dominant taxa of Port Phillip Bay benthic macroinvertebrates. Total N excretion rate data summarised from Appendix 5.

Taxon	**Biomass ($gAFDW \times 10^9$)**	**N excretion rate ($mgN.gAFDW^{-1}.day^{-1}$)**	**Total N excreted ($tonnes.year^{-1}$)**
Ascidiacea	0.8	0.85	248
Bryozoa	1.09	0.85	338
Crustacea	14.8	1.3	7,022
Echinodermata	7.0	0.5	1,277
Mollusca	18.2	0.5	3,321
Polychaeta	8.03	1.1	3,224
TOTAL			15,432

6 Benthic net production by deposit and suspension feeders

6.1 Experimental methods

Net production is the sum of growth and reproductive effort, that is, what is left after excretion and respiration are taken away from assimilated organic material. The ratio between net annual production and standing biomass is the production:biomass (P:B) ratio. Two methods are frequently used in studies of net production of benthic communities. Net production can be calculated by following distinct cohorts through time (Waters, 1979) and estimating production from differences in biomass resulting from growth of cohorts (Maslin and Pattee, 1989; Loo and Rosenberg, 1989). Other methods ignore growth and instead consider the fate of biomass in an ecosystem, principally by measuring inputs to and outputs from the system (Dame and Dankers, 1988; for a general introduction to secondary production see Crisp, 1984).

6.2 Published values and sources of variability in P:B ratios

Appendix 6 summarises P:B ratios for marine deposit and suspension feeders respectively. Values cited for deposit-feeding polychaetes are in the range 0.68-3.0. These values come from studies of intertidal populations; there are no values for subtidal polychaete species. (Subtidal populations typically have lower values for secondary production; Kennish, 1990.) P:B ratios for suspension-feeding molluscs are generally in the range of 1 to 5.

Useful values of P:B ratios are mostly from suspension-feeding molluscs. An exception is the bivalve *Theora lubrica* for which a P:B ratio of between 3.4 and 3.93 was calculated in the Sea of Japan (Mukai, 1974). This is probably the same species, recorded as *T. fragilis,* which is so common in Port Phillip Bay. Most studies of production in bivalve molluscs have measured growth of soft tissue only, not reproduction or production of the shell and byssal threads (Maslin and Pattee, 1989; Schaffee and Conan, 1984). Shell and byssal thread production may represent a substantial fraction of annual production (Bayne *et al.*, 1988) and may account for a 10-21% increase in P:B ratio (Maslin and Patte, 1989).

Production also varies according to the life stage of the species in question. Loo and Rosenberg (1989) found a pronounced difference in P:B ratios of two species of bivalves between first year recruits and older individuals, possibly due to the energy cost of reproduction on the older individuals. Thus, successful recruitment may result in a significant increase in production. Temperate communities usually show substantial seasonal variations in production which are closely related to variation in metabolic rate (Kautsky and Evans, 1987). Therefore, production estimates calculated over periods shorter than one year may be biased; most of the data in Appendix 6 are annual measurements.

6.3 Port Phillip Bay-wide estimates of secondary production

Estimation of production for Port Phillip Bay benthos by rigorous methods would require measurement of growth and mortality of each age class (Rigler and Downing, 1984). P:B ratios vary too greatly (Appendix 6) to be applied directly to Port Phillip Bay. The most important variable in determination of P:B is the mortality experienced by the population, however, both growth and mortality curves are required for accurate estimation of P:B for a given population (Allen, 1971). These data are not available for any elements of the benthos of Port Phillip Bay.

However, a coarse estimate of secondary production by suspension- and deposit-feeding macroinvertebrates can be obtained by subtracting the quantity of C excreted from the quantity assimilated. If the C:N ratio is assumed to be 100:16, the value in Table 8 for total N excreted is equivalent to 96,450 tonnes C per year respired. From Table 7, total C assimilated is about 159,150 tonnes per year (half of the quantity of total organic matter). Thus, net annual production by benthic suspension and deposit feeders is estimated at 62,700 tonnes C, which is equivalent to a P:B ratio of 2.81 (using the biomass figure from Figure 4 and based on the assumption that 50% of organic matter is carbon). More accurate estimates of secondary production and of spatial and temporal variability in secondary production for Port Phillip Bay can only be made by direct measurement.

Ecosystem wide P:B ratios have been calculated for macrobenthos of a few estuaries and bays (Appendix 7). Values are greater, 1 or more, in estuaries which may suffer organic enrichment, than in non-enriched marine systems where the ratio is about half as much. The P:B ratio value of 2.81 for benthic macroinvertebrates in Port Phillip Bay is at the top end of the range compared with values from other studies (Appendix 7).

7 Factors influencing nutrient cycling in benthic communities

The rate of nutrient cycling in benthic communities is influenced by many factors, some more tangible and measurable than others. Temperature, salinity, sedimentology, water circulation, depth and the rate and kind of nutrient inputs may have predictable effects, at least qualitatively if not quantitatively. The effects of species composition and size distribution are less tractable. Three biological phenomena are given special consideration here: bioturbation, competitive interactions and the contribution of the smaller biota.

7.1 Bioturbation

Surface marine sediments are not stable environments and there is often considerable movement close to the water-sediment interface. Water currents are an obvious disturbance. When currents are high, particles are sorted and fine silts and clays winnowed away. But even in quieter environments the activity of burrowing macrofauna has a significant effect on sediment structure by disturbing its vertical profile. Material is translocated continuously between levels during feeding, burrowing and tube construction. Burrow and faecal pellet formation alters the biogeochemical properties of the sediment by creating a mosaic of microenvironments rather than a vertically stratified distribution. New reactive substrates such as mucus may be introduced into the sediment and mechanical disturbance may influence microbial activity (Aller, 1982). This topic has been the subject of considerable biological and geological research (*e.g.*, Cadée, 1976; Rhoads and Boyer, 1982; Suchanek, 1983).

Benthic macroinvertebrates stimulate microbial decomposition of organic matter by changing the surface area of organic detritus, by grazing and thus maintaining microbial populations at the highly productive phase of their life cycle, by irrigation of burrows, and by capturing resuspended organic material.

Much of Port Phillip Bay has muddy sediments which are typically rather impervious to unaided nutrient diffusion. Mobile organisms are particularly important here in that they increase the water flux in these sediments by the action of burrowing and reworking.

Both of the dominant infaunal species of Port Phillip Bay belong to taxa known to be active burrowers. The echinoid, *Echinocardium cordatum*, moves through sediment close to the surface at speeds of up to 2 $cm.hr^{-1}$ and at depths of about equal to the depth of the test of the animal (about 2 cm) (Buchanan, 1966). *Echinocardium cordatum* feeds on particles which fall down a respiratory funnel connected with the sediment surface, but may also collect surface material using the tube feet (Buchanan, 1966; De Ridder, 1982). Although this species occurs world-wide in muddy sediments little appears to be known of its feeding rate. Its activity is probably like that of a plough.

Much more is known about callianassid shrimps, the family to which *Neocallichirus limosa* belongs. (This species was previously in the genus *Callianassa*.) Callianassids build permanent burrows deep into the sediment. Three major ecological types have been identified (Suchanek, 1983): filter/suspension feeders, deposit/detritus feeders, and seagrass/algae harvesters.

Callianassids in Port Phillip Bay are probably deposit/detritus feeders but this is not certain. Most research on callianassids has been done in tropical reef lagoons where sediments are much coarser than in Port Phillip Bay or in seagrass beds (Suchanek, 1983). In these environments up to 12 $kg.m^{-2}.d^{-1}$ of sediment can be moved during burrow construction and feeding. Their activity stimulates decomposition of organic material and may stimulate benthic microfloral production. Murphy and Kremer (1992) concluded that the rate of NH_4 production from burrows was about 10% of the total flowing from the sediment. They and others have noted that callianassids selectively process finer particles from the native sediment and accumulate coarser particles at depth. The results from this tropical work cannot be extrapolated to Port Phillip Bay populations.

Stamhuis (1992), working with a northern temperate species, *C. subterranea*, in a muddy environment, found that its diet was only sediment, that it selected for particles less than 30 μm in size and with twice the organic content of the habitat. Rowden and Jones (1992) discovered that the sediment processing rate was highly variable and depended on season and size of individual. Their estimates of turnover were five times those of Witbaard and Duineveld (1989) for the same species, that is, turning over the equivalent of the top 15 mm of sediment annually.

The three species of Callianassidae in Port Phillip Bay discriminate between sediment types: *Neocallichirus limosa* is confined to muddy habitats where it dominated the fauna consistently over three years (Poore, 1975; Poore and Rainer, 1979); *Callianassa arenosa* and *C. ceramica* occur on sandy sediments, the latter at shallower depths. *N. limosa* is numerically the most important in Port Phillip Bay; it is a small species (30 mm long) occurring at higher densities and favouring muddy environments like *C. subterranea*. Only very general statements about its ecology can be made; nothing quantitative is known. Nothing is known of the biology of the other species either. Anecdotal evidence from video film taken during a study of the effect of scallop dredging on benthos in Port Phillip Bay suggests that callianassids can rapidly transform a flattened bottom profile by burrowing (G. Parry, pers. comm.)

Many species of polychaetes are also burrowers and their "conveyor belt" feeding, transporting material from the surface to depth, must influence the ability of the benthos to process nutrients.

7.2 Interactions within the macrobenthos

This review, and most of the studies cited here, treat individual benthic macroinvertebrates as living in ideal conditions, unaffected by neighbouring animals. Of course, this is not realistic, and benthic animals are constantly interacting with other animals, which may be competing for food or other resources, or may be potential predators or prey.

These dynamic effects are probably a major reason why measurements of feeding and assimilation rates in the field are usually less than those recorded in laboratory conditions. Macrobenthic animals in natural conditions mostly process nutrients at sub-optimum levels. Therefore, rates of nutrient processing in Port Phillip Bay may be less than those estimates made here. Measurements of critical quantities in the field will be required to determine if this is so.

7.3 The smaller biota: meiofauna and microflora

Comprehensive treatment of the interstitial meiofauna is beyond the scope of this review but the likely importance of meiofauna in nutrient cycling in Port Phillip Bay should be noted. Nutrient cycling and secondary production by meiofauna have rarely been measured, but biomass (Rudnick *et al.*, 1985) and secondary production (Warwick *et al.*, 1979) may equal or exceed values recorded for macrobenthos. Greater productivity of smaller individuals combined with far greater numbers explain this.

Meiofauna may also play a role in structuring communities. Larvae and juveniles of macrofaunal species recruit into the benthos in the same size range as adult meiofauna and meiofaunal abundances have been shown to be inversely correlated with recruitment success of deposit feeders and positively correlated with recruitment of predatory syllid polychaetes (Watzin, 1983). Competition has also been demonstrated between meiofauna and adult *Capitella* worms (Alongi and Tenore, 1985). Thus, meiofaunal abundances may influence the trophic structure of benthic macrofaunal communities.

Treatment of protozoans and bacteria, the microflora living on the surface of organic and inorganic particles, is also beyond the scope of this review, but it has been suggested that microbial breakdown of detritus and faecal pellets may release nutrients that would otherwise be unavailable to macrobenthic deposit feeders (Lopez and Levinton, 1987). Microbial carbon has been shown to provide up to 25% of total requirements in individual deposit-feeding species (Cammen, 1980b), although a review of laboratory studies indicates that microbial carbon is usually makes up a lower percentage of total energy requirements (Lopez and Levinton, 1987).

8 The relevance of the estimates to Port Phillip Bay today

8.1 Port Phillip Bay - then and now

The estimates of abundance, biomass and community structure for Port Phillip Bay benthic macroinvertebrates used in this review are derived from material collected during the period 1969-1975 (Poore *et al.*, 1975; Poore and Rainer, 1979). Since that time there have been no quantitative studies which would enable long-term changes in the benthos to be detected across Port Phillip Bay. However, several more narrowly-focussed studies provide some information about long-term changes in species composition of the benthic communities. A study of the effects of scallop dredges in southern Port Phillip Bay has found that while the thalassinidean crustacean *Neocallichirus limosa* remains a dominant member of the benthos, a species of sabellid polychaete that appears to have been rare or absent 20 years ago is now widespread and numerically important (D. Currie, pers. comm.). Another species in the same family of polychaetes, *Sabella spallanzanii*, is now a conspicuous member of the macrobenthic community in Corio Bay (Carey and Watson, 1992). *S. spallanzanii* probably dominates the macrobenthic biomass in Corio Bay now, but was unknown in Port Phillip Bay 10 years ago; it is a Mediterranean species and is likely to be a recent accidental introduction. *S. spallanzanii* is a filter feeder and the effect of this large and abundant species on community and trophic structure is likely to be substantial.

There is little other information on long-term trends in community structure in Port Phillip Bay macrobenthos. The information presented above represents a very incomplete resampling of Port Phillip Bay benthos but indicates that substantial changes have occurred since 1973. Detecting these changes will depend heavily on sampling design, but also on careful taxonomic study and on maintaining a representative voucher collection (the identity of *S. spallanzanii* was only determined by consultation with specialists in the US and in Wales and removed any possibility that the species was confused with another large sabellid occurring on reefs and pier piles in Port Phillip Bay).

8.2 Recommendations for nutrient studies and monitoring

1 All estimates of nutrient cycling in the macrobenthos depend crucially on accurate measurements of densities and biomass. This review has demonstrated wide seasonal and inter-annual variations in density and biomass, and has documented significant variation between major taxonomic-feeding groups in feeding and excretion rates and assimilation efficiency. Therefore, future benthic monitoring studies must measure temporal and spatial variation in abundance and biomass for all major taxonomic and trophic components of the benthic macrofauna. Sufficient data on biomass of individual specimens should also be collected to allow standard errors to be calculated.

2 Significant changes in community structure appear to be occurring in Port Phillip Bay. The best-documented example is the suspension feeding polychaete *Sabella spallanzanii*, which appears to be a recent introduction to Port Phillip Bay and is now a conspicuous component of the benthic community in Corio Bay. Future studies will need to monitor changes of this nature and estimate their influence on community structure and nutrient cycling in Port Phillip Bay. A sampling design for monitoring community structure in Port Phillip Bay is in progress (task E5.1).

3 The role of meiofauna and microflora in nutrient cycling is likely to be of the same order as the macrofauna. More accurate estimates or measurements of the role of these elements of the benthic community may also be required in Port Phillip Bay.

4 The quality of organic matter in the sediment or water and the quantity of that organic matter that is available to benthic suspension and deposit feeders are quantities for which only the coarsest of estimates are available. Many of the literature values used to estimate these quantities in this review are based on studies of idealised or optimum conditions and are likely to overestimate feeding rates and assimilation efficiencies in nature. Estimating the biologically-available fraction of organic matter could be achieved by laboratory study of a microcosm of Port Phillip Bay benthic community, with sedimentary organic matter labelled with a tracer isotope. However, maintaining a benthic microcosm that was indicative of conditions in the field may prove to be a major technical problem. We suggest a more direct approach using a field experiment. A site such as one of the outfalls as Werribee would be required where organic input to the benthos could be regulated. Organic inputs from such an outfall can be assumed to be in sufficient quantity that food is not limiting for the benthic community. Input from the outfall would then be stopped, and changes in community and trophic structure, biomass, benthic N and CO_2 production, and organic content of sediments monitored. If inputs could be minimised for a sufficient time at a level at which food is limiting, organic matter may approach a value which would be a true estimate of the refractory content of the sediments. It would be important to monitor the chemistry of sediments in as much detail as possible, since differential loss of organic compounds in the sediment might be able to be correlated with loss of trophic-taxonomic groups from the community, perhaps allowing testable inferences about the composition of the refractory material. It appears that such an experiment would be novel, as well as being technically demanding. However, if successful, the experiment would make an important contribution to the international literature on the ecology of marine sediments.

5 Among widespread species which dominate the macrobenthic biomass in Port Phillip Bay, two deposit-feeding species, the echinoid *Echinocardium cordatum* and the thalassinidean crustacean *Neocallichirus limosa* are deserving of further study. Processing of the top 2 cm of sediments in Port Phillip Bay is estimated to occur every 1.5 years. Since the sedimentation rate of about 3 $mm.year^{-1}$ (away from major input sources; Batley, 1993) is much less than the volume processed annually, it is unlikely that Port Phillip Bay sediments are a sink for nutrients unless feeding and bioturbation by deposit feeders causes organic matter to be buried at an inaccessible depth in the sediment or in a refractory form. Study of feeding and burrowing activities of the two dominant deposit-feeding species should enable this question to be addressed.

6 Nitrogen excretion rates in marine invertebrates are dependent on nutritional status (i.e. organic content of the sediments and water) and possibly body weight; these parameters must be known more accurately if benthic nitrogen flux is to be estimated more accurately.

7 These data indirectly indicate that net annual secondary production by benthic deposit- and suspension-feeding macroinvertebrates is about 62,700 tonnes C, equivalent to a P:B ratio of 2.81. More direct measurement of secondary production in the field is needed to confirm this estimate.

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Appendix 1 Feeding and egestion rates for deposit-feeding marine invertebrates

Species	**Rate** gDWsed. $gAFDW^{-1}.d^{-1}$	**Reference; % organic matter in food; Comments**
Annelida		
Abarenicola pacifica	118.1	Taghon (1988); value for natural sediment
Abarenicola pacifica	10.2	Hobson (1967); 1.2%
Abarenicola claparedi	28.11	Hobson (1967); 0.4%
Arenicola grubii	13.3	Kisseleva and Vityuk (1970); 2.2%
Arenicola marina	4.5	Jacobsen (1967); 0.64%
Axiothella rubricincta	11.4-34.1	Kudenov (1982)
Capitella capitata	9.1-11.4	Forbes (1984)
Scoloplos sp.	51-136	D.Rice, unpublished, cited in Lopez and Levinton (1987)
Pectinaria gouldii	23.7	Gordon (1966); 0.7%
Thoracophelia mucronata	6.5	Fox *et al.* (1948); 1%
Thoracophelia mucronata	0.8	Kemp (1986); 0.03%
Crustacea		
Hyalella azteca	1.54	Hargrave (1972); 50%
Ilyoplax pusilla	6.5	Ono (1965); 4.2%
Scopimera globosa	0.9	Ono (1965); 23.6%
Macropthalmus japonicus	2.0	Ono (1965); 2.1%
Orchestia grillus	0.4	Lopez (1976); 88%
Echinodermata		
Holothuria tubulosa	4.5-5.3	Coulon and Jangoux (1993)
Mollusca		
Hydrobia neglecta	3.2	Hylleberg (1975); 18%
Hydrobia ventrosa	4.8	Hylleberg (1975); 17%
Hydrobia ulvae	0.8	Hylleberg (1975); 13%
Macoma balthica	1.0	Bubnova (1972); 20%
Portlandica arctica	0.2	Bubnova (1972); 8.8%
Scrobicularia plana	0.13	Hughes (1969, 1970); 3.4%

Appendix 2 Filtering rates for suspension-feeding marine invertebrates

Species	**Rate ($l.gAFDW^{-1}.d^{-1}$)**	**Reference; Comments**
Annelida		
Chaetopterus variopedatus	88.1	Riisgard (1989); algae
Hydroides norvegica	19.2	Dales (1957); graphite
Lanice conchilega	3.6-28.2	Buhr (1976); algae
Myxicola infundibulum	2.2-11.4	Dales (1957) and Shumway *et al.* (1988); (graphite-algae respectively)
Nereis diversicolor	5.7	Riisgard (1991); occasional suspension filter
Pomatoceros triqueter	20.4-29.8	Klockner (1978); algae
Sabella penicillus	8.0	Dales (1957); graphite
S. penicillus	444.7	Riisgard and Ivarsson (1990); algae
Salmacina dysteri	42.4	Dales (1957); graphite
Schizobranchia insignis	7.1	Dales (1961); graphite
Spirorbis borealis	19.6	Dales (1957); graphite
Ascidiacea		
Ascidiella aspersa	54.5-112.8	Randlov and Riisgard (1979)
Ciona intestinalis	74.8-157.1	Robbins (1983) and Fiala-Medioni (1974)
Clavelina lepadiformis	52.3-134.3	Fiala-Medioni (1974)
Halocynthia papillosa	134.3	Fiala-Medioni (1974)
Microcosmus sabatieri	145.7	Fiala-Medioni (1974)
Phallusia mamillata	89.7	Fiala-Medioni (1974)
Pyura stolonifera	10.2-26.0	Klumpp (1984)
Styela clava	27.9-121.6	Holmes (1973)
Steylla plicata	185.0	Fiala-Medioni (1974)
Mollusca		
Arctica islandica	71.9	Winter (1969)
Argopecten irradians	4.2-9.6	Cahalan *et al.* (1989); juveniles
Cerastoderma edule	31.89	Ali (1970)
Hiatella artica	7.47	Ali (1970)
Macoma balthica	1.1-3.5	Harvey and Luoma (1984); bacteria; occasional suspension feeder
M. nasuta	1.48	Harvey and Luoma (1984); bacteria; occasional suspension feeder
Modiolus modiolus	62.4	Winter (1969)
Mya arenaria	38.9	Allen (1962)
Mytilus californianus	39.4-52.8	Jorgensen (1943)
M. edulis	113.1-185.1	Haranghy (1942)
Ostrea edulis	10.1	Allen (1962)
Scrobicularia plana	111.8	Hughes (1969)
Venus mercenaria	79.2	Coughlan and Ansell (1964)
V. striatula	23.1	Allen (1962)

Appendix 3 Assimilation efficiencies for deposit-feeding marine invertebrates

Species	**Assimilation efficiency (% organics absorbed)**	**Reference; Organic or carbon measured; % organic content of sediment**
Annelida		
Nereis succinea	10.5	Cammen (1980b)
Cirriformia tentaculata	7.9	George (1964)
Capitella capitata	38	Forbes (1984)
Pectinaria gouldii	30	Whitlach (1974); organic; 32%
Pectinaria gouldii	50	Gordon (1966)
Glycera dibranchiata	34-41	Adams and Angelovic (1970)
Eupolymnia nebulosa	4.7-5.1	Grémare *et al.* (1991)
Euzonus mucronata	0.76-1.72	Kemp (1986); carbon; 0.7%
Arenicola marina	29-66	Jacobsen (1967); organic
Crustacea		
Pontoporeia, 2 spp	28-40	Lopez and Elmgren (1989); carbon
Echinodermata		
Holothuria difficilis	40	Bakus (1968); organic
Parastichopus parvimensis	17	Yingst (1976); carbon; 6-14%
Mollusca		
Macoma balthica	35-56	Hummel (1985); chlorophyl absorption
Abra alba	1.9-5.4	Grémare *et al.* (1991)
Hydrobia ventrosa	34	Kofoed (1975)
Hydrobia totteni	29	Lopez and Cheng (1983)

Appendix 4 Assimilation rates for benthic suspension-feeding marine invertebrates (% absorption)

Species	**Assimilation Efficiency (%)**	**Reference; comments**
Annelida		
Ampharete acutifrans	30	Warwick *et al.* (1979)
Nephtys hombergi	30	Warwick *et al.* (1979)
Nereis diversicolor	86	Riisgard (1991); algae
Ascidiacea		
Pavlova (M*onochrysis) lutheri*	70-90	Fiala-Medioni (1973, 1974, 1978)
Phallusia mamillata	45 (summer) 75 (winter)	Morais and Fiala-Medioni (1985); 19% OM in seston
Pyura praeputialis	75±10 (algae) 34+13 (seston)	Goddard and Hoggett (1982)
Pyura stolonifera	34	Seiderer and Newell (1985); seston
P. stolonifera	40	Klumpp (1984); kelp fragments
Styela plicata	33	Fisher (1976); 19% OM in seston
Other ascidians	73-93	Fiala-Medioni (1973, 1974); algae
Mollusca		
Aulacomya ater	50	Stuart *et al.* (1982); kelp fragments
Cardium edule	65	Warwick *et al.* (1979)
C. edule (adults)	62.5-72.4	Loo and Rosenberg (1989); natural seawater
C. edule (recently settled)	60-61.2	Loo and Rosenberg (1989); natural seawater
Choromytilus meridionalis	40	Griffiths (1980)
Mercenaria mercenaria	32	Doering *et al.* (1986); mesocosm-natural food
Mya arenaria	75	Warwick *et al.* (1979)
Mya arenaria (1 year old)	62.8-68.5	Loo and Rosenberg (1989); natural sea water
M. arenaria (recently settled)	60-63.6	Loo and Rosenberg (1989); natural sea water
Mytilus edulis	50-64	Bayne *et al.* (1989); variable organic matter of seston
Mytilus edulis	38	Bayne and Widdows (1978); at 19% OM in seston
Placopecten magellanicus	72-88 (algae) 29-50 (seston)	Cranford and Grant (1990)
Venus verrucosa	85-90 (Lactobacillus)11-20 (*E.coli*)	Charles *et al.* (1992); feed on different bacteria
Clams	21-22 (seston) 82 (algae)	Bricelj and Malouf (1984)

Appendix 5 Total nitrogen excretion rates for marine invertebrates (deposit-feeders or herbivores unless marked otherwise).

Species	**Total N excreted mgN.gAFDW^{-1}.day.$^{-1}$**	**Reference**
Polychaeta		
*Nephtys caeca**	1.8	Emerson (1969)
Pista pacifica	0.3	O'Malley and Terwilliger (1975)
Crustacea		
Macrobrachium rosenbergi	0.5-1.6	Nelson *et al.* (1977)
Pagurus sp.	1.2	Emerson (1969)
Callianassa sp.	1.6	Murphy and Kremer (1992)
Mollusca		
Mytilus edulis (suspension)	0.3-0.8	Bayne and Scullard (1977)
Macoma inconspicua	0.1	Emerson (1969)
Thais emarginata (carnivore)	0.9	Emerson (1969)
Thais lamellosa (carnivore)	0.4	Emerson (1969)
Thais lamellosa (carnivore)	0.1	Duerr (1968)
Thais lima (carnivore)	0.1	Duerr (1968)
Fusitriton oregonensis (carnivore)	0.3	Duerr (1968)
Littorina sitkana	0.9	Duerr (1968)
Littorina sitkana	0.1	Emerson (1969)
Acmaea scutum	1.2	Emerson (1969)
Acmaea scutum	0.6	Duerr (1968)
Acmaea digitalis	0.1	Duerr (1968)
Calliostoma ligatum	1.2	Duerr (1968)
Echinodermata		
Crinoidea	0.96	Stickle (1988)
Ophiuroidea	0.45 (0.09-0.96)	Stickle (1988)
Asteriodea	0.43 (0.13-1.08)	Stickle (1988)
Luida clathrata	0.2-0.3	Ellington and Lawrence (1974)
Luida clathrata	0.1-0.3	Diehl and Lawrence (1979)
Echinoidea	0.43 (0.22-0.65)	Stickle (1988)
Strongylocentrotus droebachiensis	0.1	Emerson (1969)
Holothuroidea	0.42 (0.14-0.50)	Stickle (1988)
Eupentacta quinquesemita	0.3	Emerson (1969)

* *Nephtys caeca* may be a deposit feeder or a carnivore (Fauchald and Jumars, 1979).

Appendix 6 Secondary production ratios

Species	P:B	Reference
Annelida		
Ampharete acutifrans	5.46	Warwick *et al.* (1979); field-0.5mm
Arenicola (Deposit)	2.27	Asmus and Asmus (1991); temperate intertidal
Ceratonereis erythraeensis (Deposit)	2.94	Dorsey (1981); Werribee Farm
Euzonus mucronata (Deposit)	1.73	Kemp (1986); 0.42mm Low OM, sandy beach
Nephtys hombergi	0.86	Warwick *et al.* (1979); field-0.5mm
Nereis diversicolor (D/S)	3.0	Chambers and Milne (1975)
N.diversicolor (D/S)	2.5	Heip and Herman (1979)
N. succinea (Deposit)	2.0	Kay and Brodfield (1973)
Nereis spp (Deposit)	O.68	Asmus and Asmus (1991); temperate intertidal
Mollusca		
Abra alba	1.7-2.9	Dauvin (1986)
A. ovata	2.4-2.1	Guelorget and Mazoyer-Magere (1982)
Arthritica semen	3.9-4.1	Wells and Threlfall (1982)
Cardium edule	0.42	Warwick *et al.* (1979); field-0.5mm
C. edule (adults)	0.7	Loo and Rosenberg (1989)
C. edule (recently settled)	4.6	Loo and Rosenberg (1989)
C. edule	2.2-21	Möller and Rosenberg (1983)
C. gibba	4.2±1.7	Jensen (1991)
Corbula trigora (Tropical)	1.9-3.8	Maslin and Pattee (1989); excluding shell
Corbula trigora (Tropical)	2.1-4.6	Maslin and Pattee (1989); including shell
Macoma balthia	0.6-2	Bachelet (1982)
M. balthica	2.1	Chambers and Milne (1975)
M. balthica	1.5	Burke and Mann (1974)
Mercenaria mercenaria	2	Doering *et al.* (1986); mesocosm
Mya arenaria	0.48	Warwick *et al.* (1979); field-0.5mm
M. arenaria (1 year old)	2.8	Loo and Rosenberg (1989)
M. arenaria (recently settled)	8.3	Loo and Rosenberg (1989)
Mytilus arenia	2-13.5	Möller and Rosenberg (1983)
M. edulis	1.76	Kautsky and Evans (1987)
Nucula papluta	3.51	Mukai (1974)
N. turida	0.6	Davis and Wilson (1985)
Pillucina neglecta	3.98	Mukai (1974)
Tellina fabula	1.6	Salzwedel (1980)
Theora lubrica	3.40-3.93	Mukai (1974)
Venus ovata	1.1-2.1	Dauvin (1985)
Veremolope micra	3.13-3.17	Mukai (1974)

Appendix 7 Production:Biomass ratios from other estuarine studies

Location	**P:B ratio**	**Reference; comment**
Lynher Estuary, UK	1.01	Warwick *et al.* (1979); 0.5mm
Grays Reef, USA	0.52	Hopkinson *et al.* (1991)
Long Island Sound	0.62	Sanders *et al.* (1962)
Kiel Bight, Germany	0.68	Arntz and Brunswig (1975; cited in Wolff, 1983)
Tamar Estuary, UK	1.02	Warwick and Price (1975); intertidal
Southhampton Water, UK	1.18-1.39	Hibbert (1976); intertidal
Grevelinger Estuary, Netherlands	2.42-2.76	Wolff and De Wolff (1977)