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A Review of the Interaction of Sediment and Water Quality with Benthic Communities

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EXECUTIVE SUMMARY

Changes in benthic communities in bays and estuaries in response to eutrophication have occurred world-wide. General patterns of change include a shift in primary producers from large macrophytes, which are capable of nutrient storage and are more competitive at low ambient nutrient concentrations, towards ephemeral algae and phytoplankton which are more competitive at high nutrient loadings, and in the case of secondary producers, from large fauna towards small, opportunists, generally dominated by deposit-feeding polychaetes. Although these patterns are frequently described for marine systems in the literature, they have rarely been empirically linked to nutrient enrichment. This report reviews available evidence for empirical relationships between water - column and sediment pore-water quality and biological parameters for seagrasses, macroalgae, periphyton and benthic microalgae, benthic macrofauna and fish. The scope of this review is restricted to environments which are comparable to Port Phillip Bay.

In the case of seagrasses, there are no consistent links between nitrogen concentrations and either seagrass shoot density, biomass or production. Although seagrass shoot density can display a negative log-linear relationship with pore-water ammonium concentrations, relationships between other seagrass growth parameters and water and sediment nitrogen concentrations are not clear. In contrast, seagrass growth parameters show strong positive relationships to irradiance and hence negative relationships to light attenuation. Epiphytes have demonstrable negative effects on seagrass production by blocking light access to the leaves. Nutrients are more likely, therefore, to have indirect effects on seagrass growth by promoting epiphyte growth and/or water column turbidity, both of which would reduce light reaching the seagrass leaves.

For macroalgae, relationships between nitrogen concentrations and growth and production vary. At relatively coarse scales, the relationship between nitrogen concentrations and macroalgal biomass varies from highly positive to negative. Fine-scale laboratory studies provide equally variable results. Thus, although macroalgal biomass and production was expected to be positively related to nutrient concentration, processes such as luxury uptake and storage when nutrients are available, the use of stored nutrients for growth during periods of nutrient stress, and nutrient release during decomposition, confound this relationship. Macroalgal biomass and production are strongly related to irradiance, but this response is influenced by other factors, in particular seasonal differences in physiological conditioning.

For microalgae, relationships with nitrogen concentrations are not consistent. Periphytic microalgae, growing on seagrass leaves, have generally negative relationships with nitrogen concentration but this may reflect changes in habitat space provided by the host seagrass. Changes in benthic microalgae are generally not related to nitrogen concentration but are influenced by other factors such as light, temperature, tidal regime, wave exposure and sediment-type.

Relationships between macrofaunal density, biomass and production are not clear except at relatively coarse scales from data collected over long time periods. In addition, transitions between trophic or taxonomic groups in relation to nutrient concentrations are not evident from the data available. By contrast, macrofaunal

abundance is strongly related to water column oxygen concentrations. The effects of nutrients on macrofauna are hence likely to be indirect. They may initially stimulate macrofauna by providing more food resources, but cause long-term decline due to the decomposition of organic matter and subsequent anoxia in the water column.

Although positive relationships between primary production and fisheries yield have been described in the literature, direct empirical relationships between environmental nitrogen concentrations and fisheries yield have not been established. However, as for macrofauna, water column oxygen concentrations have direct and critical impacts on fish populations. Hence, the effects of nutrients on fish are likely to be indirect and related to processes which deplete water column oxygen levels, e.g. enhanced primary production with consequent increased organic loading to the benthic zone.

Benthic organisms have a variety of effects on their environment. For example, seagrasses influence water and sediment quality through the direct uptake of nutrients from the water column and sediments, by trapping suspended particles and by promotion of nitrification and denitrification in the sediments. Macroalgae may have direct effects on water column nutrient concentrations due to uptake during growth and release during decomposition. The decomposition of macroalgae can cause depletion of water column oxygen leading to anoxia, with resultant impacts on benthic fauna and on sediment nutrient flux. Microalgae are highly productive and oxygen generated from their photosynthesis can promote nitrification.

Benthic suspension-feeders, by filtering phytoplankton or suspended particles and hence reducing water turbidity, can have direct positive effects on benthic primary production. Conversely, suspension-feeders may have indirect negative effects on benthic primary production by promoting the recycling of nitrogen which is then available for phytoplankton, thus increasing water column turbidity. Infaunal deposit-feeders directly promote the flux of ammonium from the sediments by excretion and burrow irrigation and also aerate the sediments through bioturbation thereby promoting nitrification. Deposit-feeders may therefore have both positive and negative effects on the flux of ammonium from the sediments.

In conclusion, although general paradigms of community change in response to eutrophication are accepted in the literature, the demonstration of empirical links with changing environmental nutrient concentrations is difficult. This may be partially explained by the limitations of field studies in terms of their methodology, suite of parameters measured and the temporal and spatial scales over which the study was carried out. This may be further confounded by the effects of other environmental factors which have more direct influence over benthic communities or by the biological processes of organisms in structuring their environment. More rigorous testing of the paradigms is required.

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1. INTRODUCTION

1.1. Background

The Port Phillip Bay Environmental Study (PPBES) was commenced in 1992 with the objective of determining the environmental status of the Bay in relation to nutrients and toxicants, and providing a basis for the long-term management of point source and diffuse inputs. The study uses a systems approach to provide scientific information on the Bay which is fundamental to addressing the management issues that have been identified by the consortium group of Victorian agencies responsible for Bay management.

A major component of the study, which is crucial for coordinated management, is the development of a series of nutrient and toxicant budget models. These are being integrated with the physical processes of the Bay and ecosystem impacts are to be derived from these integrated models as a series of empirical relationships. The Study has avoided a totally process-based approach in favour of an empirical approach at higher trophic levels because of the complexity of higher trophic processes. Hence the model must draw on empirical or correlative relationships established in the Bay or other similar environments.

A knowledge of empirical relationships between the benthic communities of the Bay and water and sediment quality was seen as fundamental for the prediction of impacts on those communities if integrated models were to be used. Although there have been several reviews on the effects of nutrients on the marine environment (Pearson and Rosenberg, 1978; Nixon *et al*., 1986; Gray, 1992; Gabric and Bell, 1993; Goldberg, 1993) and toxicants (Reynoldson, 1987; Colodey and Wells, 1992; Goldberg, 1993) much of the information has been derived from qualitative comparisons rather than statistically sound quantitative data. Consequently there was a need to review available information selectively. In addition, due to the enormous literature, it was decided to concentrate the present review on nutrient-related impacts on the benthic communities given that PPBES results suggest that toxicants in the Bay cause less impact than nutrient loads.

The aim of this report is to review the available information on changes in benthic communities in response to water or sediment quality in temperate marine embayments. We also examine the converse, i.e. feedback relationships between the benthic community the sediment and the water column.

1.2. Scope

This review addresses benthic communities similar to those in Port Phillip Bay which have been identified by the PPBES Technical Group as either commercially important or ecologically significant and vulnerable. These communities include:

Seagrasses. These marine angiosperms stabilise inshore sediments (Fonseca *et al*., 1982), contribute to nutrient cycling (Hemminga *et al*., 1991), provide a habitat

for a diverse assemblage of algal epiphytes (Ducker *et al.*, 1977) and fauna (Howard *et al.*, 1989) and contribute to drift-weed which is considered a public nuisance when washed up as beach wrack on suburban beaches (Davies and Brown, 1986).

Macroalgae and microalgae. The macroalgae contribute to primary production (Moncreiff *et al.*, 1992), are a habitat for fauna (Edgar, 1983), and also contribute to beach wrack (Davies and Brown, 1986). Benthic microalgae contribute to primary production (Daehnick *et al.*, 1992), regulate nitrogen flux from the sediments (Sundbäck *et al.*, 1991), and are an important nutritional source for benthic deposit feeders (Murphy and Kremer, 1992).

Macroinvertebrates. These include benthic suspension-feeders and deposit-feeders. Suspension-feeders promote water clarity as they filter organic particles from the water column (Hatcher *et al.*, 1994; Asmus *et al.*, 1995). Deposit-feeders consume benthic organic material and may bioturbate or bioirrigate the sediment through their burrowing and feeding activities (Bird, 1994). Other benthic macroinvertebrates of particular importance, such as abalone which are commercially important, or introduced species, such as the polychaete worm *Sabella spallanzanii*, which may have detrimental effects on the natural ecology of the Bay, are included in this discussion.

Fish. These are included because they are commercially important and can represent an important feed-back link between eutrophication of coastal waters and human activities (Nicholson, 1992).

Benthic communities that are not included in the review include meiofauna and bacteria. Meiofauna have received relatively little attention in Port Phillip Bay or any other Australian waters even though their role in promoting nutrient cycling through predation of microscopic autotrophs (Kristensen, 1988), and contributing to benthic-pelagic coupling is well known (Bell *et al.*, 1988). Meiofauna have been used for monitoring the impacts of pollution (Bilyard, 1987; Warwick, 1993). Bacteria are important in nitrification and denitrification in sediments (Koike and Sørensen, 1988; Kristensen, 1988) but almost nothing is known of bacterial processes in Port Phillip Bay.

Finally, this review focuses on studies of areas with similar environmental conditions to Port Phillip Bay; i.e. shallow coastal waters or coastal embayments from warm to cold-temperate regions, typically between 25° to 55° of latitude. Freshwater and estuarine studies were not included. Data from studies carried out in waters deeper than 30m i.e. deeper than Port Phillip Bay, have not been included because depth is an important factor influencing benthic communities (Poore and Kudenov, 1978a; Edgar, 1983; Russo *et al.*, 1984), which sometimes masks the effects of nutrients (Gray *et al.*, 1988).

We have included tabled summaries of the literature reviewed to provide a quick and effective way of identifying studies of different communities. These tables also include literature which does not present empirical data but which provides important contributions to the discussion.

1.3. Treatment of data

A major problem in this review was to compare the results of different studies, carried out in different locations on different organisms and often using different scientific units and measures. Consequently, we have converted data to the same scientific units, where possible, so that the results of studies can be compared, particularly to derive empirical relationships. This was not possible for all studies but where possible nutrient data have been converted to µM concentrations. Seagrass data are restricted to the above-ground material, and seagrass biomass and production has been standardised to grams dry weight (DW) per m^2 and g DW m^{-2} y^{-1} respectively. Benthic macroalgae includes attached forms e.g. kelp, free-floating algal masses e.g. *Ulva* spp., and epiphytic forms attached to macrophytes, e.g. seagrass macro-epiphytes. The biomass of attached and free-floating macroalgae has been presented in this review as either tonnes wet weight (WW) or kg DW m^{-2} and growth rate as g WW d^{-1}. Epiphyte biomass and growth-rate has been presented as mg cm^{-2} of seagrass leaf and mg cm^{-2} of seagrass leaf day^{-1} respectively. Data on periphyton (microscopic epiphytes), inhabiting seagrass leaves have been treated as discreet from benthic microalgae, as these communities are exposed to different environmental conditions. Periphyton biomass and production has been presented as mg DW cm^{-2} of seagrass leaf and mg DW cm^{-2} seagrass day^{-1} respectively. Benthic microalgal production has been reported as mg C m^{-2} d^{-1}. Benthic macroinvertebrate biomass has been standardised as g Ash-Free Dry Weight (AFDW) per m^2 of seabed and production as g C m^{-2} y^{-1}. Where data could not be converted to a convenient, standardised unit it has been plotted separately.

Nutrient flux rates are reported in the literature in a variety of units, usually as grams or moles of nutrient flux per unit area per unit time. Only nitrogen fluxes are considered in this review. For ease of comparison, flux rates have been standardised and reported as g N m^{-2} y^{-1}.

The following sections discuss relationships between benthic communities and water and sediment quality parameters which are portrayed in the attached figures.

2. BENTHIC COMMUNITY RESPONSE TO WATER AND SEDIMENT QUALITY PARAMETERS

2.1. Patterns of benthic community change resulting from eutrophication

Four stages of change in benthic communities can be identified (Gray, 1992). Stage 1 involves an initial growth response and increase of primary and secondary producers. This is followed by a change in species composition viz. for primary producers generally towards ephemeral, opportunistic species; for fauna from large, slow-growing, long-lived species with low production:biomass (P:B) ratios towards smaller, fast-growing, short-lived species with high P:B ratios. In the third stage there are negative feed-back interactions between components of the community resulting in a loss of species and dominance by a few opportunistic species. The fourth or final stage is one of hypoxia, anoxia and mass death of the benthos, leaving just bacterial mats and perhaps a few hardy species.

Macrophyte dominated systems change towards phytoplankton dominated systems with increasing nutrient loads as nutrient limitation ceases and light attenuation increases (Valiela *et al*., 1992; Duarte, 1995). An increase in water column primary production increases light attenuation by the water column and promotes the organic enrichment of the sediments through sedimentation of suspended particles and detritus. Under healthy conditions the sediments support a diverse infauna which effects bioturbation. This in turn promotes nitrification in aerobic zones. Elsewhere in the sediments anaerobic conditions permit denitrification processes (Bird, 1994). As the organic load to the sediments increases the oxygen required to metabolise this organic matter becomes limiting (Pihl, 1992). Under extreme conditions, organic enrichment leads to hypoxia causing mobile fauna to leave the area. The redox potential discontinuity (RPD) marking the transition from aerobic to anaerobic sediment, which is normally located relatively deep in the sediments, moves towards the surface driving benthic infauna to the sediment surface (Nilsson and Rosenberg, 1994). As oxygen levels continue to decline, echinoderms, molluscs and crustaceans die (Baden, *et al*., 1990), and opportunistic polychaete worms, which are tolerant of low oxygen levels, dominate the system (Pearson and Rosenberg, 1978). Loss of the infauna leads to reduced bioturbation, reduction or cessation of nitrification and denitrification, and eventually sulphate reduction (Sloth *et al*., 1995).

In summary, eutrophication is characterised by a trend towards a loss of species diversity, excessive primary production by phytoplankton or free-floating macroalgae and a reduction in secondary production (Gray, 1992).

2.2. Critical environmental and ecological parameters and the spatial and temporal scales over which they operate:

This review attempts to identify empirical relationships between changes in benthic communities and changes in water or sediment quality in shallow water marine bays as a result of nutrient enrichment. In order to determine these relationships it is first important to identify those key nutrients which influence marine ecosystems and the spatial and temporal scales over which they operate. Secondly, it is important to identify other environmental parameters which influence benthic marine communities and determine whether nutrient enrichment influences these other parameters. Thirdly, it is important to identify the ecological parameters which are influenced by nutrients and the spatial and temporal scales over which they operate.

Unlike freshwater systems in which phosphorus is universally regarded as the critical limiting nutrient, much debate continues over which nutrient is limiting for primary production in marine systems (Howarth, 1988). Nitrogen is generally regarded as being the limiting nutrient (Howarth, 1988) and this is supported by a considerable volume of research carried out in field and mesocosm experiments (refer to Tables 1, 2 and 3). However, examples of phosphorus limitation (Powell *et al*., 1989; Peckol *et al*., 1994) and even silicon limitation (Doering *et al*., 1989) of primary production have also been observed in systems where nitrogen has been supplied to excess. In Port Phillip Bay, nitrogen is widely considered to be the limiting nutrient for all algae and seagrasses (Brown, 1988,Builthuis *et al* ,1992). Hence we have focused on the effects of nitrogen enrichment on marine benthic communities.

It is important to identify what measures of nitrogen availability should be used as the basis for empirical relationships with benthic community change. Hinga *et al*., (1995) reviewed empirical relationships between nitrogen concentrations and loading versus phytoplankton abundance in marine systems and concluded that neither concentration nor loading adequately represented the nitrogen available to the system. For example, instantaneous measures of nitrogen concentration may be inversely proportional to phytoplankton abundance due to rapid uptake during blooms or release during decomposition (Hinga *et al*., 1995). Such inverse relationships have also been observed between sediment pore-water nitrogen concentrations and seagrass shoot density (Short, 1983b), and between water column nitrogen concentrations and macroalgal biomass (Sfriso *et al*., 1992). The capacity of macroalgae for luxury uptake of nutrients when nutrient concentrations are high (Mann *et al*., 1982) with subsequent utilisation for growth under conditions of nutrient stress (Hanisak, 1983) further complicate these relationships.

In addition, processes in the sediment, such as primary production by benthic microalgae and bioturbation by infaunal macrofauna, influence sediment-water column nitrogen flux rates. This causes the nitrogen concentrations and nitrogen flux rates in these habitats to vary over short spatial (for example, within and between animal burrows; Aller, 1982) and temporal (diel; Wiltshire, 1992) scales. These points illustrate the inherent problems associated with matching instantaneous measures of nutrient concentration with ecological measures such as abundance or biomass which integrate environmental conditions over longer time periods. Hinga *et al*., (1995) conclude that where nitrogen concentrations are to be used as a basis for empirical relationships, long-term averages should be used.

Hinga *et al*., (1995) also demonstrate that the relationship between loadings and nitrogen availability is not only influenced by the rate at which nitrogen may be re-mineralised and consumed but also by hydrodynamic forces such as water residence times and mixing. These authors conclude that in shallow, well mixed systems with relatively short residence times, nitrogen concentrations are likely to be proportional to loadings. Conversely, in systems with longer residence times, nitrogen loadings and concentrations are unlikely to be related because of uptake and remineralisation or denitrification within the sediments. This has been demonstrated by mesocosm experiments which showed only a 3.5x increase in primary production and 1.5x increase in secondary production with a 32x increase in nutrient loading, with much of the added nitrogen being lost from the system through denitrification within the sediments (Oviatt *et al*., 1986).

Mesocosm studies (Doering *et al*., 1989; Sullivan *et al*., 1991; Oviatt *et al*., 1993), and field studies (Hopkinson and Wetzel, 1982; Graneli and Sundbäck, 1985; Reay *et al*., 1995) have both demonstrated the important influence of nutrient cycling in sediments on the fate of nitrogen in marine ecosystems and the consequent availability of nitrogen to the ecosystem. So, how particular marine ecosystems respond to increased nitrogen loadings is likely to vary between locations depending on site-specific hydrodynamic forces, sediment characteristics and the composition of local benthic communities.

Relationships between nitrogen concentrations or loadings and changes in benthic communities may also be confounded or masked by other environmental factors.. For example, irradiance (PAR) is a critical limiting factor for benthic autotrophs. The theoretical relationships between nutrients, irradiance and the abundance of autotrophs have been reviewed by Duarte (1995) and Harlin (1995). These authors suggest that at low nitrogen concentrations when nitrogen is limiting, seagrasses or benthic macroalgae will predominate because these macrophytes are able to store and use nutrients efficiently and receive adequate light. Increasing nutrient concentrations favour production by phytoplankton or free-floating, ephemeral macroalgae, which decrease light penetration in the water column and cause light limitation to benthic plants. Thus, a shift occurs from benthic, perennial macrophytes to phytoplankton and ephemeral algae in the water column.

Instantaneous measures of irradiance, or factors which influence light penetration e.g. water column chlorophyll *a*, particulate organic matter (POM) or turbidity, are likely to be as variable as nutrient concentrations. On the other hand, measurements of the abundance, biomass, production or depth distribution of benthic plants over longer time periods integrate such changes. For example, seagrasses require high levels of irradiance so that their shoot density and biomass decline rapidly i.e. on time-scales of months, in low light conditions (Bulthuis, 1983; Gordon *et al*., 1994; Fitzpatrick and Kirkman, 1995).

Similarly, the depth distribution of benthic macrophytes provides an integrated measure of water column transparency (Kautsky *et al*., 1986; Lumb, 1989) and may show changes on scales of years to decades. Kautsky *et al*., (1986) discovered a retreat in the depth distribution of the macroalga *Fucus vesiculosus* from 11.5m to 8.5m over a 50 year period. In this way, light, nitrogen and benthic macrophyte abundance relationships may be established empirically.

In contrast, light does not appear to have the same level of influence over benthic microalgae as it does over benthic macrophytes which may be related to the former's lower light requirements (Cahoon *et al*., 1993). Field studies have shown that factors such as temperature, tide height, wave energy and sediment-type have greater influence on benthic microalgal communities (Davis and MacIntire, 1983; Shaffer, 1988).

Mesocosm studies have provided equivocal results relating benthic diatom abundance to increasing nutrient concentrations (Doering *et al*., 1989; Sundbäck and Snoejs, 1991). Benthic microalgae inhabit highly dynamic environments (Shaffer and Sullivan, 1988), are highly variable over short spatial (Beardall and Light, 1994) and temporal (Shaffer, 1988) scales so that relationships between nitrogen enrichment and benthic microalgal abundance, biomass or production are likely to be difficult to establish. Comparisons between average nitrogen concentrations and benthic microalgal abundances over long time scales, or along environmental gradients are probably required to identify relationships between nitrogen availability and change in benthic microalgal communities.

The response of secondary producers to nutrient enrichment is influenced, in part, by food availability (bottom-up control) and predation (top-down control) (Flothman and Werner, 1992; Sarda *et al*., 1992; Posey *et al*., 1995). Food availability is influenced by which subset of the autotrophic community responds to nutrient enrichment. For example, whereas increased diatom production has resulted in higher levels of secondary production (Doering *et al*., 1989), increased production by blue-green algae has not (Flothman and Werner, 1992). Predation regulates benthic macrofaunal abundance and influences the degree to which benthic secondary producers may respond to increased food availability (Oviatt *et al*., 1993; Posey *et al*., 1995). Thus, direct, empirical relationships between nitrogen enrichment and changes in the abundance, biomass or production of secondary producers are likely to be difficult to establish due to the confounding of these bottom-up and top-down controls.

Links between nitrogen enrichment and changes in fish abundance, biomass or production are difficult to detect due to the large scales of variability of these measures (Kerr and Ryder, 1992). Although changes in species composition (De Jonge and Raaphorst, 1995; Koivisto and Blomquist, 1988; Hansson and Rudstam, 1990; Isaksson and Pihl, 1992) and community size structure (Koivisto and Blomquist, 1988) have been recorded over time scales ranging from years to decades, empirical relationships with nitrogen enrichment have not been satisfactorily established (Nixon, 1986; Hansson and Rudstam, 1990; De Jonge and Raaphorst, 1995). Long-term spatially tied sampling of fish communities and physico-chemical parameters is probably required in order to establish any such relationships.

Although direct effects of nitrogen enrichment on benthic macrofauna and fish communities may be difficult to establish, nitrogen effects on other water and sediment quality parameters may affect these taxa indirectly. For example, the increase in rate of supply of organic matter from primary producers as a result of nitrogen enrichment increases the biological oxygen demand of benthic communities and in extreme circumstances can cause hypoxia and anoxia and general ecosystem dystrophy (Viaroli *et al*., 1992). Benthic macrofauna and fish are sensitive to water column and sediment oxygen concentrations and decline rapidly in response to hypoxia and anoxia. A 90%

loss of benthic fauna in four days has been reported (Stachowitsch, 1992). Sensitivity to hypoxia varies between species (Dauer *et al*., 1992; Desprez *et al*., 1992), with fish being particularly sensitive (Baden *et al*., 1990). Large, relatively long-lived species such as echinoderms, are more sensitive to hypoxia than small, short-lived species like deposit-feeding polychaete worms (Pearson and Rosenberg, 1978). Changes in the abundance, biomass, species richness, community size-structure and feeding guilds have been observed along gradients of organic enrichment over spatial scales of hundreds of metres (Poore and Rainer, 1974; 1979; Pearson and Stanley, 1979; Weston, 1990). Hence environmental parameters such as oxygen concentration (or surrogate measures like redox potential or redox potential discontinuities), may provide a more stable basis for identifying relationships between nitrogen enrichment and changes in benthic faunal communities.

In summary, neither nitrogen concentration nor nitrogen loading truly reflect nitrogen availability to, or effect on, marine ecosystems. Long-term averages probably provide a better basis than instantaneous concentrations for establishing empirical relationships with benthic community changes. Nitrogen loadings are influenced by local hydrodynamic forces, sediment characteristics and benthic community composition which can confound empirical relationships with benthic community change, particularly in terms of cross-system comparisons. Nitrogen enrichment influences other environmental parameters which have more direct influences on benthic communities, e.g. irradiance for benthic autotrophs or oxygen levels for benthic fauna. Therefore, critical parameters such as irradiance or oxygen levels may provide more stable bases from which to derive empirical relationships between changes in water and sediment quality and benthic communities.

2.3. Seagrasses

Seagrasses obtain nutrients from both the water column and the sediments (Hillman *et al*., 1989). We have therefore examined the empirical relationships of seagrass shoot density, biomass and production with water column and sediment nitrogen concentrations. A synopsis of the literature reviewed in this section is provided in Table 1.

Seagrass degradation and loss in relation to pollution has been widely documented (Den Hartog and Polderman, 1975; Larkum, 1976; Nienhuis, 1983; Cambridge and McComb, 1984; Cambridge *et al*., 1986; Neverauskas, 1987; Geisen *et al*., 1990; Larkum and West, 1990; Walker and McComb, 1992), yet relatively few studies have quantified a link between nitrogen enrichment and rates of seagrass decline.

Figures 1a, 1b and 1c indicate that, based on the available empirical data, there seems no relationship between seagrass shoot density and water column dissolved inorganic nitrogen (DIN), ammonium (NH_4), or nitrate + nitrite (NO_3/NO_2). Similarly, Hillman *et al*., (1991) found no correlation between shoot density and nitrogen concentrations in seagrass beds from Princess Royal Harbour, Oyster Harbour or King George Sound, Albany, Western Australia.

Bulthuis *et al* (1992) could find no relationship between shoot density and pore-water DIN (Figure 2a). However, Short (1983a) detected a strong negative relationship between shoot density and pore-water NH_4 concentration (Figure 2b), and ascribed this to uptake of nitrogen by *Zostera marina* with consequent rapid depletion of nitrogen in the sediments. Shoot densities recorded in this study went up to 10 000 m^{-2} and therefore represent a high nitrogen demand, which may explain the strong relationship observed.

In terms of seagrass above-ground biomass, when data from different studies were pooled, there appeared to be a negative relationship between shoot biomass and water column DIN (Figure 3a) and NO_3/NO_2 (Figure 3c) but no relationship with NH_4 (Figure 3b). Seagrass biomass /water column nitrogen relationships were not consistent between the studies and only data from Hillman *et al*., (1991) showed a consistent, negative, non-linear relationship between biomass and DIN, NH_4 and NO_3/NO_2. These differences may reflect differences in seagrass species. For example, high water column NO_3 concentration caused a decline in the biomass of *Zostera marina* whereas NO_3 stimulated the production of *Halodule wrightii* (Burkeholder *et al*,1994). There appeared to be no relationship between seagrass biomass and pore-water DIN (Figure 4a) or pore-water NH_4 (Figure 4b).

No relationship has been demonstrated between seagrass shoot production and water column DIN, NH_4 and NO_3/NO_2 (Figures 5a, 5b and 5c). The data from Pedersen and Borum (1993) indicated a higher level of seagrass production at given nitrogen concentrations than that reported in the other studies which must be related to site-, time- or species-specific factors. However, excluding their data, there appeared to be a consistent negative relationship between seagrass production and water column DIN, NH_4 and NO_3. The relationship was particularly evident in the data set of Hillman *et al*., (1991), the largest data set presented in Figures 5a to 5c.

The relationship between pore-water NH_4 concentration and shoot production appeared variable, particularly at low concentrations (Figure 6). In a study of seagrass transplant growth, Kenworthy and Fonseca (1992) found that NH_4 enrichment of the sediments promoted the vegetative growth of *Z. marina* and *H. wrightii*, but did not improve the long-term survival of these seagrasses Data relating shoot production to pore-water DIN or NO_3/NO_2 were not available.

In summary, clear, direct and consistent relationships between water and sediment nitrogen concentrations and seagrass growth were not evident from the range of studies reviewed. Moriarty and Boon (1989) reviewed nutrient processes in seagrass meadows and concluded that the relationship between seagrass growth parameters and sediment nitrogen concentrations depended on the nitrogen demand of the seagrass versus rates of availability, either through external supply or internal recycling. Hemminga *et al*., (1991) reviewed nitrogen gains and losses in seagrass meadows and concluded that seagrasses are open systems, experiencing imbalances between gains and losses through time which may explain temporal variations in seagrass biomass. In this context, seagrasses may be considered variously as a source or sink for nitrogen depending on the relative scales of these gain and loss processes. It is therefore, not surprising that stronger relationships between water or sediment nitrogen concentrations were not observed.

Clearer relationships between seagrass shoot density, biomass and production and water and sediment nitrogen concentrations would have been expected if nitrogen was limiting to seagrass growth. Several studies have identified nitrogen limitation in seagrass meadows (Bulthuis and Woelkerling, 1981, 1983a, Short, 1983a, b, 1987; Powell *et al.*, 1989; Bulthuis *et al.*, 1992; Van Lent *et al.*, 1995), whereas others suggest that nitrogen limitation is rare (Zimmerman *et al.*, 1987; Pedersen and Borum, 1993) or that phosphorus is limiting (Short, 1987; Powell, *et al.*, 1989). Moreover, changes in benthic macrophytes in relation to eutrophication are not gradual but appear to occur in steps which do not directly parallel increased nutrient loadings (Duarte, 1995).

In contrast, the importance of light requirements for seagrass survival has been well established (Bulthuis, 1983; Silberstein *et al.*, 1986; Neverauskas, 1988; Duarte, 1991, Gordon *et al.*, 1994; Fitzpatrick and Kirkman, 1995) and seagrasses are known to have the highest requirements (generally between 5 and 20% of surface irradiance)for photosynthetically active radiation (PAR) of all aquatic macrophytes : Bulthuis, 1983; Silberstein *et al.*, 1986; Dennison *et al.*, 1992). Photosynthesis-Irradiance curves for *Posidonia sinuosa* and *Amphibolis antarctica* (Figure 7) demonstrate the positive relationship between seagrass production and irradiance (Walker *et al.*, 1994).

Light reduction experiments have been carried out in seagrass meadows to demonstrate the light dependence of seagrasses *in situ* (Bulthuis, 1983; Neverauskas, 1988; Gordon *et al.*, 1994; Fitzpatrick and Kirkman, 1995). Figure 8 shows the results of a shading study carried out by Bulthuis (1983) on the seagrass *Heterozostera tasmanica*. Shoots which received between 2 to 9% of surface PAR died back completely after 4 to 8 months respectively, whereas when receiving greater than 25% of surface PAR, seagrass viability was maintained. Other studies of shading effects on seagrasses, carried out elsewhere, have yielded similar results. In South Australian *Posidonia* meadows, Neverauskas (1988) detected a rapid decline in seagrass shoot density and biomass under a 50% light reduction regime, after an initial lag-time of 6 months. In Western Australian *Posidonia sinuosa* meadows, Gordon *et al.*, (1994), found that seagrass shoot density and production declined by 80 to 99% from that of unshaded seagrasses over a 148 day period. In long-term shading studies, Gordon *et al.*, (1994) further found that shoot density and production were reduced by 90% after 307 days, and by > 92% after 393 days. Similarly in a shaded *Posidonia australis* meadow in New South Wales, Fitzpatrick and Kirkman (1995) found that seagrass shoot density declined from 340 m^{-2} to 80 m^{-2} after 3 months, and thereafter remained at between 10 to 60 shoots m^{-2}, even 17 months after the removal of the shading. Seagrass shoot densities in the control plots were between 270 to 340 m^{-2} throughout the study period.

Epiphyte growth on seagrass leaves has been implicated in seagrass decline (Cambridge *et al.*, 1986; Silberstein *et al.*, 1986; Tomasko and Lapointe, 1991) and Burt *et al.*, (1995), measured a strong positive relationship between the biomass of periphyton on seagrass leaves and light attenuation at the leaf surface (Figure 9). Bulthuis and Woelkerling (1983b) found that light attenuation increased linearly with epiphyte biomass and that epiphytes could accumulate fast enough to cause shading of seagrass leaves. Silberstein *et al.*, (1986) measured a strong negative relationship between seagrass production and the degree of shading caused by epiphytes inhabiting the seagrass leaves (Figure 10) whilst Sand-Jensen (1977) observed that epiphytes reduced seagrass photosynthesis by up to 31%. Borum (1985) and Tomasko and

Lapointe (1991) found that seagrass epiphyte biomass was strongly linked to water column nitrogen concentrations In this way, nutrients may influence seagrasses indirectly by promoting either phytoplankton or epiphyte growth which then attenuate light (Wetzel and Neckles,1986).

So, although seagrass degradation in relation to anthropogenic pollution has been widely reported in the literature, these effects have not been adequately quantified, and clear empirical relationships between nutrient loadings and seagrass decline have not been observed. Studies of seagrass-nutrient interactions have demonstrated conflicting results ranging from nitrogen limitation, to no nutrient limitation or phosphorus limitation so that site- and species-specific differences in nutrient demand of seagrasses and nutrient availability may be responsible. The capacity of seagrass epiphytes and periphyton to attenuate light before reaching the seagrass leaves and for epiphytes and periphyton to respond rapidly when nutrients and light are available have also been demonstrated. Thus, measuring relationships between nutrients, epiphytes and light attenuation may be more important than direct observations of nutrient-seagrass relationships when trying to determine the likely effects of eutrophication on seagrasses.

2.4. Macroalgae

In this review, macroalgae refers to macroscopic plant forms which may either be attached to hard substrates, free-floating or epiphytic on seagrasses. Unlike seagrasses, macroalgae are confined to obtaining their nutrients from the water column. Thus, only relationships with water column nutrients are presented here. A synopsis of the literature is provided in Table 2.

Ephemeral types of macroalgae can respond rapidly to nutrient enrichment of the water column (Duarte, 1995; Pedersen, 1995), and their distribution is influenced by environmental nutrient concentrations (McGlathery, 1992). Massive blooms of algae such as *Ulva* spp., *Cladophora* spp., and *Enteromorpha* spp., are a commonly reported symptom of eutrophication (Lapointe and O'Connell, 1989; Piriou and Menesguen, 1992; Sfriso *et al*., 1992; Valiela *et al*., 1992; Viaroli *et al*., 1992). However, few studies have demonstrated a clear, direct link between such blooms and nutrient enrichment of the water column probably because macroalgae act as sources or sinks for nutrients (Hanisak, 1983), and are highly influenced by other parameters, such as irradiance and temperature (Lobban *et al*., 1985; Lüning, 1990). For example, Lapointe and O'Connell (1989) report that, although massive *Cladophora* blooms had occurred over a 20 year period in Harrington Sound, Bermuda, USA, no studies had conclusively linked these blooms to nutrient enrichment.

In contrast, in the Bay of Saint-Briuec, northern Brittany, France, Piriou and Ménesguen (1992) demonstrated a strong, positive relationship between the maximum biomass of floating wracks of *Ulva* (tons WW) and total nitrogen loadings (kg d^{-1}) which occurred in June of 1986, 1988 and 1989 (Figure 11). These data are from a single study over a three year time-frame but suggest that measurements of mean Total N loadings to a marine system may provide a reasonable basis from which macroalgal community responses to eutrophication can be determined and evaluated.

Figure 12a shows a negative, non-linear relationship between macroalgal biomass and water column DIN, in four bays in the northern Adriatic Sea (after Sfriso *et al.*, 1992. Each data set is based on a monthly sampling regime over a fifteen month period. When the data from each bay were averaged within seasons, the negative, log-linear relationship between biomass and DIN was more evident and appeared to be consistent within each bay (Figure 12b). When seasonal differences were highlighted by averaging across bays, the negative, log-linear relationship was still apparent (Figure 12c). These negative relationships may be indicative of water-column nitrogen depletion through uptake by macroalgae (Sfriso *et al.*, 1992; Viaroli *et al.*, 1992; Valiela *et al.*, 1992; Peckol *et al.*, 1994) and will be discussed in detail in the subsequent section on feed-back influences of macroalgae on water-column and sediment quality parameters.

In laboratory studies of epiphytic macroalgal growth, Walker *et al.*, (1994) found no relationship between algal biomass and either water column DIN, NH_4 or NO_3 (Figures 13a, 13b and 13c respectively) and this appeared to be consistent between seasons (Figures 13b and 13c) and between batch and continuous culture experiments (Figures 13a and 13c). Similarly, epiphyte growth rates did not show any relationship with water column NH_4 or NO_3 concentrations (Figures 14a and 14b). However, the nitrogen concentrations supplied in these experiments represented a small range (2 to 4.5 µM DIN; 1 to 2.5 µM NH_4; 0.5 to 2.5 µM NO_3). Additionally, these experiments were run over a relatively short time-frame (35 days for batch cultures, 55 days for continuous culture), so their application to a field situation is limited.

Unlike the study by Walker *et al.*, (1994) on seagrass epiphytes, Schramm *et al.*, (1988), detected a clear relationship between the wet weight growth-rates of the macroalgae *Fucus vesiculosus* and *Phycodrys rubens* and water-column DIN (Figure 15).

The response of macroalgae to nutrient enrichment is variable but change in community structure from dominance by perennial macrophytes to dominance by ephemeral, opportunistic algae is a commonly reported symptom of eutrophication (Gray, 1992; Duarte, 1995). Seagrasses and perennial macroalgae are good competitors at low nutrient concentrations because they have lower nutrient requirements than ephemeral algae (Duarte, 1995; and see review of C:N:P ratios of aquatic plants by Duarte, 1992), are able to store and efficiently recycle nutrients and, in the case of seagrasses, have access to sediment nutrient pools. As nutrient concentrations increase, fast-growing macroalgae and phytoplankton are more competitive because they capture and use light more efficiently (Harlin, 1975; Duarte, 1995).

Pedersen (1995) compared the growth responses of a seagrass (*Zostera marina*), a perennial macroalga (*Fucus*), two ephemeral macroalgae (*Ulva* and *Chaetomorpha*) and phytoplankton to nitrogen (NH_4) enrichment (Figure 16). The seagrass and perennial macroalga showed no response to nitrogen enrichment whereas the growth of ephemeral macroalgae and phytoplankton were stimulated by higher concentrations. In Rhode Island Lagoon, USA, experimental enrichment of NH_4 in seagrass beds stimulated the growth of *Ulva* and *Enteromorpha* (Harlin and Thorne-Miller, 1981) and in Waquoit Bay, USA, seagrasses have been replaced by macroalgae such as *Ulva*, *Cladophora*, *Enteromorpha* and *Gracilaria* as nutrient levels in the bay have increased (Horne *et al.*, 1994). In contrast, Fong *et al.* (1993) report that

phytoplankton and free-floating macroalgae were out-competed for nutrients, by benthic macro- and microalgae as nutrient concentrations increased (nitrogen from 1.2 µM to 77 µM and phosphorus from 0.01 µM to 5 µM). The form of the nutrients was not stated nor the individual effects of N and P.

In Port Phillip Bay, macroalgal communities in relatively high nutrient environments, i.e. near sewage outfalls, are characterised by a dominance of ephemeral species. Brown *et al.*, (1980), and Axelrad *et al*., (1981) found that macrophyte communities at nitrogen enriched sites near the Werribee sewage treatment plant in Port Phillip Bay were dominated by *Ulva* and *Cladophora* spp., whereas large brown algae such as *Ecklonia radiata* or *Sargassum* spp., which were important zone-forming algae at other sites, were absent. This may, however, be a function of the availability of suitable substrata for the larger algae or distance from recruitment sites. In their review of macroalgal communities in Port Phillip Bay, Light and Woelkerling (1992) concluded that substrate suitability, light attenuation, water depth, wind, currents and sediment transport, rather than nutrient availability, were the main factors structuring benthic macroalgal communities.

As with seagrasses, light is an important requirement for benthic macroalgae and the depth distribution of algae has been used as a monitoring tool to detect long-term changes in water turbidity (Kautsky *et al*., 1986; Lumb, 1989). Strong positive relationships between irradiance and epiphyte biomass and production (Figures 17a and 17b respectively), were observed in culture experiments carried out over two seasons and four water temperatures by Walker *et al*., (1994). These positive relationships were evident in both summer and winter and suggest that algal responses to irradiance were more strongly influenced by seasonal factors e.g. physiological pre-conditioning (Hanisak, 1983), than by temperature effects alone. For example, in the study by Walker *et al*., (1994), algal biomass and production were always higher in summer than in winter, whereas temperature effects were inconsistent within each season.

The lack of consistent trends between the fine-scale studies of Schramm *et al*., (1988), Fong et al, (1993), Walker *et al*., (1994) and Pedersen (1995) indicate that to quantify the responses of macroalgal communities to eutrophication requires holistic study of the interactions between nutrients, light, temperature and taxonomic differences, taking into consideration physiological influences related to growth history of the algae. We know of no example which examines this suite of variables within a single study, using algae which have been acclimated to controlled laboratory conditions for a sufficient period of time to overcome artefacts related to their growth history.

Although coarse-scale studies of bay-wide nutrient loadings and macroalgal biomass or production may yield more consistent relationships the time-frame for such studies may be unacceptably long. In addition, the magnitude of change occurring before a relationship can be detected may be unacceptably high, by which time irreversible and detrimental change may already be present. The use of macroalgal tissue nutrient concentrations for monitoring long-term changes in water-column nutrient concentrations (Lyngby, 1990), or long-term changes in macroalgal depth distribution for monitoring changes in water turbidity (Lumb, 1989), may be more efficient and effective tools for detecting eutrophication.

2.5. Microalgae

Microalgae in this review include forms which grow as periphytes on hard substrates or on seagrasses and other macrophytes, or which may occur within the sediments. In this review, two groups are of particular interest: the microscopic algae which occur on seagrass leaves, here termed periphyton, and the microalgae which occur in the sediments, here termed benthic microalgae. Although there may be considerable overlap in species composition between these two groups (J. Nielsen, personal observation), there are considerable differences in the light and nutrient levels and physical disturbance experienced by these groups. A synopsis of the literature is provided in Table 3.

2.6. Periphyton

Figures 18a, 18b and 18c show strong negative relationships between periphyton biomass and water column DIN, NH_4 and NO_3/NO_2 respectively (after Hillman *et al*., 1991). However, care must be taken with the interpretation of these biomass data as they follow a similar pattern to that of seagrass shoot density when plotted against water column nutrients and may reflect the availability of seagrass as a living space rather than a direct relationship with nutrients. In contrast, Borum (1985) found that ambient nutrient concentrations had a greater influence on periphyton biomass than on phytoplankton and that variations in periphyton biomass were positively correlated with water column nutrient concentrations.

Coleman and Burkholder (1994) found that nutrients stimulated an increase in periphyton biomass which was dominated by cyanobacteria. In a subsequent study they found that whilst primary production was comparable between enriched and ambient nutrient treatments, enrichment caused a community shift from dominance by crustose red algae and dinoflagellates to dominance by the diatom *Cocconeis placentula*. However, Neckles *et al*., (1994) studying the interactive effects of nutrients and grazing on seagrass periphyton found that diatoms did not respond to nutrient enrichment but were controlled by grazing, whereas cyanobacteria were stimulated by nutrient additions and were not grazed. This suggests that under nutrient enriched conditions, a community shift from diatoms to cyanobacteria may occur. This could potentially lead to changes in faunal communities, e.g. from grazers towards detritivores, as cyanobacteria are less attractive than diatoms as food items for grazers (Neckles *et al*., 1994; Widbom and Frithsen, 1995).

2.7. Benthic microalgae

Although few studies on benthic microalgae have been carried out in Port Phillip Bay, data on their production, which is high compared with other marine areas, suggest that benthic microalgae are potentially very important in the Bay.

Sundbäck and Snoejs (1991) studied the effects of nutrient enrichment on benthic microalgae and found that increased nutrient concentrations stimulated the production

of diatoms, filamentous cyanobacteria and flagellates. However, there were no differences in community structure or direction of community succession between enriched or non-enriched treatments. In this study, silicon was never limiting so that diatoms were never outcompeted by other algae.

A variety of studies have reported that other factors than nutrients are important in structuring benthic microalgal communities. For example, Sundbäck and Jonsson (1988) concluded that benthic microalgae may benefit from nutrient enrichment during the early phases of eutrophication but decline as water turbidity increases following increased phytoplankton growth. Masini (1990) found that nutrient concentrations accounted for differences in benthic microalgal biomass between marine systems but that light availability influenced abundance within systems. Beardall and Light (1994) concluded that benthic microalgal biomass and production in Port Phillip Bay, were influenced by irradiance, water temperature, depth and sediment-type in addition to nutrient availability.

Figure 19 shows the relationship between microalgal production and irradiance found in two laboratory studies (Davis and MacIntire, 1983; Masini, 1987), and a field study (Shaffer and Sullivan, 1988). The results of the laboratory incubations show a clear and consistent trend of increasing production to an asymptote with increasing irradiance, whereas the field data show variable rates of production across the range of irradiance levels. Figure 20 shows the relationship between benthic microalgal production and phytoplankton production in the field (Axelrad *et al*., 1981; Cahoon and Cooke, 1992; Moncreiff *et al*., 1992; Cahoon *et al*., 1993), indicating that either water column primary production does not inhibit benthic primary production or that pelagic and benthic production are coupled. The study by Axelrad *et al*., (1981) was aimed at identifying the effects of the effluents from the Werribee Treatment Complex on benthic communities in Port Phillip Bay. In this study, across the range of sites sampled, phytoplankton did not appear to affect benthic microalgal production.

Light does not appear to have the same level of influence on benthic microalgal communities as it does on other marine plants. For example, Cahoon *et al*., (1993) reported that benthic microalgae can maintain a high production even at irradiances less than 1% of water-surface PAR. Shaffer and Sullivan, (1988), examining field data collected every two days over a thirty day period, found a poor relationship between microalgal biomass and ambient light levels.

Other studies have shown that environmental factors which are unrelated to nutrient conditions may have important influences over benthic microalgal communities. For example, Rasmussen *et al*., (1983) found that benthic microalgal production had a linear relationship with water temperature over a range of 5 to 30°C. Daehnick *et al*., (1992) reported that water temperature, tidal range and light were the best predictors for hourly production rates on benthic microalgae within seagrass meadows. On the other hand, Colijn and De Jonge (1984) found that benthic microalgal production and assimilation was correlated with tidal height but not with temperature or irradiance. Sabbe (1993) reported that the organic content of marine sediments was an important predictor of epipelic diatoms. Plante *et al*., (1986), Fielding *et al*., (1988), and Delgado (1989) reported that exposure to high wave energy has major impacts on microalgal resuspension and distribution within the sediments thus influencing their production and spatial distribution. Thus, benthic microalgae are influenced by complex

interactions between sediment-type, hydrodynamic forces and seasonal influences (Davis and MacIntire, 1983; Shaffer, 1988).

Hence, although some studies have demonstrated a direct link between nitrogen enrichment and production by benthic microalgae, the majority of studies have identified other factors to be of greater significance in influencing benthic microalgal communities. These factors include light, water temperature, water depth, tidal fluctuations, sediment-type and wave energy. Factors influencing benthic microalgal communities are complex and direct relationships between microalgal biomass or production and nitrogen concentrations are unlikely to be clearcut.

2.8. Benthic Macrofauna

In Port Phillip Bay, 70% of the area of the Bay consists of relatively deep, muddy, unvegetated sediments (Wilson *et al*., 1993), and components of the macrofauna inhabiting these sediments have been recognised for their important role in bioturbation of the sediments (Bird, 1994), contributions to nutrient cycling (Wilson *et al*., 1993), and commercial fisheries (Nicholson, 1992). This review, therefore, focuses on the macrofauna which inhabit these types of sediments. We focused on suspension and deposit feeders as these dominate the macrofauna in Port Phillip Bay, representing approximately 42% and 35% of the macrofaunal biomass respectively, and together accounting for 75% and 92% of the biomass in sandy and muddy habitats respectively (Wilson *et al*., 1993). We discuss these groups separately in the text and plot data individually in the figures. Otherwise the term macrofauna refers to the entire macrofaunal community including other feeding-groups such as grazers, predators and scavengers. A synopsis of the literature reviewed in reference to this section is provided in Table 4.

Increased nutrient loads have been associated with reduction in biomass and species richness and changes in community composition and size-structure (Gray, 1992). Pearson and Rosenberg (1978) reviewed community succession in relation to organic enrichment of the sediments and found that effects could be detected around the source of enrichment and that but were more diffuse with increasing distance from the source. They reported that sediments in the vicinity of the source are devoid of fauna, but that an increase in abundance and richness occurs with increasing distance from the source. Maximum abundance and richness are found at a transition zone, or ecotone, which is composed of a mix of short-lived opportunists and long-lived ‘equilibrium’ species. On the polluted side of the ecotone point, opportunistic species dominate whereas on the unpolluted side, equilibrium species dominate. Pearson and Rosenberg (1978) also reported that capitellid, nereid and spionid polychaetes are typical early colonisers of enriched sediments, but that deposit-feeding amphipods e.g. *Corophium* spp., and bivalves, e.g. *Macoma balthica* and *Mya arenaria*, may also be early colonisers.

Observations of benthic faunal communities around the Werribee waste-water treatment plant by Poore and Kudenov (1976) and Axelrad *et al*., (1981) showed the above pattern of community change described by Pearson and Rosenberg (1978). These studies found that communities in the vicinity of the treatment plant were

dominated by deposit-feeding polychaetes and amphipods, but that this influence of the outfall was exerted only for a few hundred metres. Although these general patterns may be easily recognised and have been observed in a variety of field and experimental studies, their relationship to nutrient loadings have not been well quantified (Gray, 1992).

No relationship could be detected in Port Phillip Bay between water-column total nitrogen (TN) or dissolved inorganic nitrogen (DIN) concentrations and the abundance of macrofauna (Figure 21a, Poore and Rainer, 1974, 1979). When data from Bogdanos and Satsmadjis (1992), collected in the Messolonghi Lagoon, Greece, were averaged within seasons, no patterns of abundance in relation to water column DIN could be observed (Figure 22a). However, there did seem to be a decline in the number of species with increasing water column DIN (Figure 22b), particularly in winter and spring when the highest DIN concentrations were recorded.

When biomass levels of benthic molluscs in Port Phillip Bay, divided into feeding guilds, were plotted against water column TN on a logarithmic scale (Figure 23), there appeared to be no convincing trend. Figure 23 also shows that infaunal suspension-feeders dominated the biomass across the range of TN concentrations and that surface deposit-feeders appeared to decline with increasing TN concentration.

Nutrient enrichment may promote secondary production in some cases though. For example, Beukema and Cadée (1986) reported that the growth rate and reproductive success of the deposit-feeding bivalve *Macoma balthica* increased over a fifteen year period during a concomitant increase in nutrient loading. Macroinvertebrate biomass and production data from the Dutch Wadden Sea, collected over a fifteen year period (1970-1984), were matched with data on nutrient loading of the Rhine River (Nienhuis, 1992) collected over the same time period. It is important to note that only between 6 to 20% of the Rhine River flows into the Dutch Wadden Sea which also receives inputs from other sources. Thus the nutrient loadings of the Rhine River serve only as an indicator of the typical increases in nutrient loadings entering these coastal areas during this period. Macrofauna biomass showed a positive relationship with TN, DIN and NO_3 (Figures 24a, 24b and 24c, respectively), but a negative relationship with NH_4 loadings (Figure 24d). Macrofaunal production showed a similar relationship (Figures 25a, 25b, 25c and 25d for TN, DIN, NO_3 and NH_4 respectively. There is also evidence from Port Phillip Bay that the growth rates of abalone are higher near the WTC drain, where nitrogen levels are higher than elsewhere in the Bay (Gwyther, 1990).

Although Figures 24a to 24d and 25a to 25d do not provide a strictly quantitative relationship between inputs to a system and changes within the system, they are important in demonstrating a measurable increase in biomass and production of benthic fauna with increased nitrogen loadings from anthropogenic sources. Such data is surprisingly sparse in the literature. This may be because of limitations of the research in that most studies either occur over relatively small spatial and temporal scales or do not collect a full suite of environmental data. Small scale spatial and temporal variability may mask these apparent relationships, but long-term, system-wide observations resulting in mean annual estimates of nutrient concentrations and biological parameters, may provide better evidence of the relationship between nutrient enrichment of coastal waters and changes in macrofaunal communities. Alternatively, the lack of quantified relationships may be related to the diffuse nature of the

associations or the complex pathways through which nitrogen is cycled in marine systems. For example, in a mesocosm study, Oviatt *et al*., (1986) found that a 32x increase in nitrogen loading stimulated only a 3.5 x increase in primary production and a 1.5x increase in secondary production, with denitrification being responsible for the fate of most of the additional nitrogen. Flothman and Werner (1992) found that nutrient enrichment resulted in higher primary production, dominated by the cyanobacteria *Merismopedia* sp., but that secondary production was not enhanced because *Merismopedia* was not a suitable food resource for higher trophic groups. Nixon *et al*., (1986) suggest that the association between nutrient loading and secondary production is difficult to detect as the macrofauna represent a small component of the nutrient budget in marine systems and only a relatively small fraction of the nutrient increment gets transferred to higher trophic levels.

Other biotic and abiotic factors also influence the strength of these associations. Gray *et al*., (1988) reported that water depth had controlling influences on benthic community structure in two Norwegian Fjords, and that this masked effects which could be attributed to pollution. Grant and Thorpe (1991) demonstrated that high water turbidity affected the feeding-rate of suspension-feeding bivalves and that long-term exposure to high turbidity caused bivalve mortality. The studies of Poore and Rainer (1974) and Bogdanos and Satsmadjis (1992) showed that sediment physical properties were the major controlling influences over infaunal communities, and Poore and Rainer (1974) could find no relationships between the infauna and physico-chemical characteristics of the overlying water column. Oviatt *et al*., (1986) and Widbom and Frithsen (1995) suggested that competition for space in the sediments within mesocosm enclosures limits the capacity for benthic macrofauna to exploit additional food resources made available through nutrient enrichment.

Gray (1992) emphasises that the critical effects of eutrophication are experienced when water column oxygen concentrations become depleted as total community respiration increases due to increased organic loads to the sediments. Increased nutrient loadings are generally associated with increased episodes of hypoxia or anoxia, particularly in stratified waters, with subsequent detrimental effects on the fauna (Baden *et al*., 1990; Schaffner *et al*., 1992). Hypoxia may cause local extinction of benthic populations (Gaston and Edds, 1994), reduced growth rates of benthic fauna (Forbes and Lopez, 1990; Forbes *et al*., 1994) and changes in benthic communities (Pearson and Rosenberg, 1978; De Zwann et al., 1992; Josefson and Jensen, 1992; Stachowitsch, 1992). Rosenberg *et al*., (1983) reported oxygen concentrations of 1.0 mg l^{-1} as being a threshold level of hypoxia. Nilsson and Rosenberg (1994) found that mild hypoxia, when oxygen concentrations reached 1.0 mg O_2 l^{-1}, caused fauna to emerge from their burrows, and under severe hypoxia, at oxygen concentrations of 0.5 mg O_2 l^{-1}, resulted in a reduced number of species and individuals. Stachowitsch (1992) showed that the loss of benthic fauna during anoxia can be rapid, e.g. 90% loss of biomass in four days, and recovery may take many years. He found no recovery of some pre-anoxia taxa even after six years.

Figure 26a shows a clear positive relationship between water column oxygen concentrations and macrofaunal abundance. Different macrofaunal groups have different tolerances to hypoxia and Figure 26b shows the responses of different faunal groups to water column oxygen levels. Overall, polychaetes were the most abundant group across the range of oxygen levels observed and did not decline in abundance

with declining oxygen concentrations. Bivalves were found only at higher oxygen levels and the abundance of other fauna tended to decrease at lower oxygen levels.

Polychaetes are generally recognised as having a relatively high tolerance to hypoxia and rapidly colonise or dominate organically enriched environments (Pearson and Rosenberg, 1978; Gray, 1992). Dauer *et al*., (1992) found that hypoxia caused a decline in long-lived molluscs and maldanid polychaetes but increased the abundance of opportunistic polychaetes. 'Head-down' deposit-feeding polychaetes such as *Clymemella torquata*, feed at depths of 10-20 cm into the sediment and have a high tolerance for hypoxia and even the hydrogen-sulphide concentrations experienced at these depths (Fuller, 1994). Desprez *et al*., (1992) found that the polychaete *Pygospio elegans* was more tolerant to anoxia and recovered more quickly after anoxia than did the bivalve *Cerastoderma edule*. The deposit-feeding bivalve *Theora fragilis* had a high tolerance to hypoxia (tested at 1.3 to 1.4 mg O_2 l^{-1}; Tamai, 1993), but not to hydrogen sulphide (Tamai, 1994). Ueda *et al*., (1994) did not detect any influence of water column oxygen concentrations on the abundance of *Theora lubrica* over the range of concentrations from 4 to 11 mg O_2 l^{-1}.

The results of Tamai (1993, 1994) and Ueda *et al*., (1994) for *Theora* spp., are of particular relevance to Port Phillip Bay, as *Theora lubrica* is a dominant member of the macrobenthos in the Bay. In contrast, the bivalve *Abra alba* and the urchin *Echinocardium cordatum* are sensitive to hypoxic conditions (Gray, 1992; Nilsson and Rosenberg, 1994). Baden *et al*., (1990) observed that oxygen tensions of 10% saturation were critical for lobsters, e.g. *Nephrops norvegicus*, urchins e.g., *Echinocardium cordatum*, ophiuroids e.g. *Ophiura albida* and *Amphiura filiformis* and molluscs e.g. *Abra alba*. Thus, increased nutrient loads may have important indirect effects on benthic macrofauna by increasing the organic load to the sediments thus promoting oxygen consumption by increasing heterotrophic processes and benthic respiration. This may lead to hypoxia or anoxia which may have a range of effects on the benthic macrofauna depending on macrofaunal community composition and their resistance to hypoxia and the frequency, duration and intensity of hypoxic events.

If oxygen levels decline in response to nutrient enrichment then oxygen-nitrogen relationships may be useful in identifying when critical periods of hypoxia or anoxia are likely to occur. For example, Lapointe and Clark (1992) detected significant negative relationships between water column dissolved oxygen concentrations and NH_4, NO_3, total dissolved nitrogen (TDN), soluble reactive phosphate (SRP), total dissolved phosphate (TDP), particulate nitrogen (PN), particulate phosphorus (PP) and chlorophyll *a*. In Port Phillip Bay, water column oxygen levels are high and have been consistently measured at concentrations exceeding 80% saturation (MMBW and FWD, 1973; Brown and Davies, 1991). Not surprisingly therefore, over the range of nitrogen concentrations measured in the Bay, there appear to be no relationships between TN, DIN, NO_3 and NH_4 and water column oxygen levels (Figures 27a, 27b, 27c and 27d respectively). However, other physical and chemical processes in the Bay would tend to confound such relationships.

Thus, although patterns of community change from dominance by large, long-lived, equilibrium species towards small, short-lived opportunists in the vicinity of sewage outfalls has been documented in a wide range of geographical locations, few studies empirically relate these changes to changes in nutrient concentrations. In many studies

of benthic macrofaunal communities, a complementary suite of environmental data including nutrient concentrations are either not measured or are not presented. In addition, most studies are carried out over relatively short temporal scales and do not supply the kind of long-term information which may be required to identify these relationships. In addition, given the erratic nature of the relationships between environmental nutrient concentrations and benthic primary producers, the links between nutrient concentrations and secondary producers are likely to be diffuse.

2.9. Fish

Fish are a valued attribute within the Bay and could be affected by eutrophication in ways that reduce palatability, change abundance or species composition or present a health threat (Nicholson, 1992). A synopsis of the literature is provided in Table 5.

Data on water -column nitrogen concentrations and fish biomass data, collected during the 1968-1971 Port Phillip Bay Study (MMBW and FWD, 1973) and averaged across the Bay within sampling periods, showed no relationships between fish biomass and either TN, DIN, NH_4 or NO_3/NO_2 (Figures 28a, 28b, 28c and 28d respectively). Conversely, Nixon *et al*., (1986) observed a positive relationship between fisheries yield and net primary production from estuarine and coastal marine systems (Figure 29; based on Figure 19 of Nixon *et al*., 1986; data drawn from 35 studies). Presumably, if positive relationships between nitrogen loadings and primary production can be observed e.g. Boynton *et al*., 1982, then direct links between fisheries yield and nitrogen loadings should also be observed. In a mesocosm study, Keller *et al*., (1990) did in fact observe an increased growth rate of *Brevoortia tyrannus* under nutrient enriched conditions. Hansson and Rudstam (1990) reported that fish catches in the Baltic Sea had increased by an order of magnitude over a fifty year period (to present), but related this mainly to increased fishing effort and perhaps eutrophication. Elsewhere, empirical links between increased nutrient loadings and increased production of higher trophic groups have not been widely documented (Nixon *et al*., 1986). The high mobility of fish and large scales of spatial and temporal variability typically associated with measures of fish abundance, growth rates and yield levels (Kerr and Ryder, 1992) make these type of comparisons problematic.

On the other hand, eutrophication is commonly associated with changes in fish species or size-distribution (Koivisto and Blomqvist, 1988; Hansson and Rudstam, 1990; Lee *et al*., 1991; Isaksson and Pihl, 1992; Pihl, 1992) and a general decline in biomass and species diversity (Baden *et al*., 1990; Pihl, 1992; Reise, 1994). Gwyther (1990) and Nicholson (1992) have reviewed commercial fisheries in Port Phillip Bay and the possible effects of nutrient enrichment on these fisheries. Finfish abundance and diversity were found to decline near the WTC drain (Brown and Negiliski, 1976, cited in Gwyther, 1990). Brown (1977, cited in Gwyther, 1990), found that flathead catches were lower near the WTC drain but this probably reflected a preference for deeper waters. Gwyther (1990) concludes that just as the effects of the WTC drain on the biota such as bacteria, microalgae macroalgae, macrobenthos, phytoplankton and zooplankton are not detectable beyond 500m from the drain, it is unlikely that impacts on commercially important fish species would be detected in Port Phillip Bay.

Similarly, Gray *et al*., (1992) studied fish larvae in effluent plumes and non-impacted sites along the coast near metropolitan Sydney. Although they found some evidence of interactions between the nutrient plumes and fish larval distribution, these interactions were difficult to isolate due to relatively large scales of spatial and temporal heterogeneity.

The input of nutrients into Port Phillip Bay could, of course, affect fisheries indirectly through a change in suitable benthic habitats. Seagrass decline occurs through smothering by excessive epiphytic growth (Silberstein *et al*., 1986) and anecdotal evidence of a decline in fisheries with a loss of seagrass have been reported (Klumpp and Nichols, 1983). However, Edgar *et al.,* (1993) researched the impacts of a loss of seagrass (*H. tasmanica* and *Z. muelleri*) on commercial fisheries in Western Port Bay, Victoria.

Overall, they found fish production was highly correlated with seagrass biomass and the production of small epifaunal crustaceans. Additionally, they found that epifaunal production was considerably higher in vegetated habitats, with a loss of approximately 2500 tonnes of epifauna annually as the result of seagrass loss. However, despite this considerable loss of material, direct links between seagrass loss and a loss of commercial fish species could only be demonstrated for two fish species: the six spined leatherjacket (*Meuschenia freycineti*) and the blue rock whiting (*Haletta semifasciata*). Most fish losses were of non-commercial species such as weed-fish, pipe-fish and soldier-fish, whereas losses of higher-order fish predators were difficult to quantify because larger fish fed from pelagic sources over a wide area. Additionally, Edgar *et al*., (1993) found that the seagrass meadows were not such important nursery areas as has been reported in the literature (Lenanton, 1982; Pollard, 1984). It is likely that the seagrass meadows of Port Phillip Bay perform similar ecological functions as those of Western Port, and a loss of seagrasses would result in the loss of feeding grounds for adult fish rather than of nursery areas for juvenile fish.

As with benthic macroinvertebrates, hypoxia causes immediate problems for fish species. Breitburg (1992) demonstrated that hypoxia in Chesapeake Bay influenced the spatial distribution and population structure of demersal fish whose juveniles were less tolerant of but less able to migrate from hypoxic waters so that they experienced mass mortality. After the abatement of hypoxia, fish rapidly recolonised previously hypoxic zones. Abandonment occurred at 0.36 mg O_2 l^{-1} and death at 0.24 mg O_2 l^{-1} giving fish a low escape margin between abandoning their shelters and dying. Baden *et al*., (1990) reported declines in fish catches in response to hypoxia in bottom waters of the south-east Kattegat. Figure 30 shows the relationship between fish biomass and water column oxygen concentration reported by Pihl (1992) for the south-east Kattegat. Clearly, water column oxygen depletion as a result of eutrophication can have a major impact on demersal fisheries but oxygen levels in Port Phillip Bay never approach danger point.

In conclusion, although positive relationships between primary production fisheries yield have been observed, direct empirical relationships between nitrogen concentration and fisheries yield have not been established. More subtle changes in fish communities such as changes in species composition and a shift towards smaller size-distributions have been observed but their relationship with nitrogen enrichment have not been quantified. The effects of nutrients on fisheries are likely to be indirect

and may either promote productivity by providing more food resources, or reduce productivity by depleting water column oxygen concentrations through the decomposition of organic matter. Because of the indirect nature of these relationships, they are likely to be diffuse and difficult to detect. In contrast, clear, direct impacts of water column oxygen concentration were detected. Thus, elucidating the relationships between nitrogen and oxygen concentrations and between oxygen concentrations and fish community parameters may be of greater value in determining the effects of nitrogen enrichment on benthic fish communities.

3. FEED-BACK EFFECTS OF BENTHIC COMMUNITIES ON WATER AND SEDIMENT QUALITY

The preceding chapter discussed the effects of changes in water and sediment quality on benthic communities. The aim of this chapter is to review how benthic organisms affect water and sediment quality. These effects, here termed feed-back effects, can have important influences on the fate of nutrients in the marine environment and on how marine ecosystems respond to eutrophication. The focus of this chapter is on feed-back effects on nitrogen although other environmental parameters are discussed where they have important direct or indirect influences on nitrogen cycling.

The discussion is limited to the effects of seagrasses, macroalgae, benthic microalgae and macrofauna although it is recognised that bacteria can have significant impacts on nutrient cycling through nitrification and denitrification. Given the diffuse nature of the relationship between nitrogen and fish identified in the preceding chapter and the added complexity of this relationship caused by fish harvesting (Nixon *et al*., 1986), the effects of fish on water and sediment quality are not discussed further.

Nutrient flux values have been converted to standard units of g N m^{-2} y^{-1} to compare between studies and between groups of organisms. Positive flux values refer to a net efflux from the sediments whereas negative values refer to a net influx i.e. uptake within the sediments.

3.1. Seagrasses

Seagrasses may influence sediment and water quality directly through uptake or release of nutrients, release of organic matter, loss of leaf material or by promoting sedimentation (Hemminga *et al*., 1991), or indirectly through oxygenating the sediments, therefore promoting nitrification-denitrification processes (Moriarty and Boon, 1989).

With as much as 60-80% of their biomass in the sediment (Moriarty and Boon, 1989), and their capacity to absorb nutrients from both the sediment and water column (Hillman *et al*., 1989), seagrasses can have major impacts on sediment and water column nutrient concentrations. Seagrasses may promote the removal of nitrogen from the sediments through direct uptake. For example, Short (1983a) observed a strong, negative, logarithmic relationship between *Zostera marina* shoot-density and pore-water NH_4 concentrations because NH_4 was rapidly depleted during seagrass growth (Figure 2b). However, gross production was extremely high due to the high density of these meadows (to 10 000 shoots m^{-2})and the nitrogen demand exhibited here, relative to the size of the sediment nutrient pool, may not be typical of seagrass systems elsewhere (Moriarty and Boon, 1989).

Seagrasses can promote nitrogen flux from the sediment above that of unvegetated sediments. For example, Short (1983a) measured a release of NH_4 due to diffusion of 88 µmol N m^{-2} h^{-1} (10.79 g N m^{-2} y^{-1}), compared with a release from seagrass covered sediment of 138 µmol m^{-2} h^{-1} (16.9 g N m^{-2} y^{-1}). These rates were low compared with

the observations of Iizumi *et al*., (1982) who detected NH_4 release rates from seagrass meadows of 116.8 to 186.15 g N m^{-2} y^{-1}. In a tropical Australian environment, Boon (1986) reported that NH_4 release to the water column was 14x higher from a seagrass meadow than from adjacent unvegetated sites. In contrast, in a temperate Australian system, Bulthuis *et al*., (1984) detected no differences in the release of NH_4 from seagrass covered mudflats compared with unvegetated mudflats. In the same study, Bulthuis *et al*., (1984) detected a lower efflux of suspended solids, phosphorus and silicates from the seagrass meadow than that from the bare mudflats. Thus, the influence of seagrasses on nutrient flux appear to be variable and site and species specific.

Seagrasses may also promote nitrification and denitrification. Seagrass roots release organic exudates and oxygen and therefore provide a suitable environment for nitrifying bacteria (Moriarty and Boon, 1989). Nitrification rates have been estimated at between 1 to 2 g N m^{-2} y^{-1} (Iizumi *et al*., 1982; Kaspar, 1983), and denitrification rates of 0.11 to 1.1 g N m^{-2} y^{-1} (Iizumi *et al*., (1980) and 0.44 to 2.2 g N m^{-2} y^{-1} (Kaspar, 1983). However, sediments within seagrass meadows are generally anoxic environments and the reduction of nitrate to ammonium (ammonification) is a major path of nutrient cycling (Moriarty and Boon, 1989). Thus, nitrification and denitrification is low compared with non-seagrass environments, e.g. up to 235 g N m^{-2} y^{-1} and 97 g N m^{-2} y^{-1} for nitrification and denitrification respectively, in unvegetated sediments (Koike and Sørensen, 1988).

Seagrasses may increase the total nitrogen load to the system through nitrogen fixation. Hemminga *et al*., (1991) provide rates of nitrogen fixation from a variety of sources of between 0 to 55 g N m^{-2} y^{-1} (generally between 0 to 2 g N m^{-2} y^{-1}; see Hemminga *et al*., 1991, for more detail). In Marmion Lagoon, Western Australia, Crossland (1988) estimated that nitrogen fixation by seagrass was 0.25 and 0.015 g N m^{-2} y^{-1}, by *Amphibolis antarctica* and *Posidonia sinuosa* meadows respectively. Estimates of the importance of nitrogen fixation to plant nutrition vary from 5 to 10% of requirements (Kirkman *et al*., 1991) to 50% (Moriarty and Boon, 1989).

Sedimentation is another important source of nitrogen loading to the sediments and settled particles can include sediment, phytoplankton and detritus (Hemminga *et al*., 1991). The wave attenuation effects of seagrasses have been well established (Fonseca *et al*., 1982), and meadows in high velocity areas may be sources of autochthonous detritus whereas meadows in low velocity areas may be sinks (Fonseca *et al*., 1983). Almasi *et al*., (1987) provide empirical data on deposition rates of material in *Thalassia* meadows of 67.1 and 21.6 kg m^{-2} y^{-1}, in summer and winter respectively, compared with 41.2 and 20.3 kg m^{-2} y^{-1} for bare sand areas, and 73.6 and 24.6 kg m^{-2} y^{-1} for artificial *Thalassia* structures. Hemminga *et al*., (1991), estimated that sedimentation could account for an input of 60 g N m^{-2} y^{-1} to the sediments, based on the work of Harlin *et al*., (1982), and that sinking of phytoplankton onto sediments within seagrass meadows could contribute between 7-45 g N m^{-2} y^{-1}, based on the work of Kenworthy and Thayer (1984).

Seagrasses have other important effects such as the provision of living space for suspension- or deposit-feeders and grazers. Brenchley (1982) reported that the roots and rhizomes of seagrasses reduced the mobility of a variety of burrowing species including polychaetes (*Arenicola pacifica, A. claparedii*), callianassid crustaceans

(*Callianassa californiensis*, *Upogebia pugettensis*), bivalve molluscs (*Macoma nasuta*, *Clinocardium nuttalli*), echinoids (*Dendraster excentricus*) and holothuroids (*Leptosynapta clarkii*). Consequently, bioturbation by infauna is likely to be limited in seagrass meadows and Phillipart and Dijkema (1995) found that sediment working and faecal production of the infaunal polychaete *Arenicola marina* was considerably lower within seagrass meadows than in adjacent unvegetated areas. The influence of bioturbation on sediment processes is discussed in detail later in this review.

3.2. Macroalgae

Macroalgae can have a major influence on water column nutrient concentrations, either through the uptake of nutrients during growth or their release during decomposition, acting alternately as nutrient sources or sinks (Hanisak, 1983). Fluctuations in water column nutrient concentrations in relation to patterns of macroalgal growth and decomposition, i.e. due to source/sink processes, have also been observed across large spatial scales (Piriou and Ménesguen, 1992; Sfriso *et al*., 1992; Viaroli *et al*., 1992; Peckol *et al*., 1994).

Macroalgal nutrient uptake and release has the capacity to influence water column nitrogen concentrations on a bay-wide scale. For example, in the Lagoon of Venice, Sfriso *et al*., (1992) concluded that macroalgal biomass (primarily *Ulva* spp.,) was correlated with seasonal sediment and water column nitrogen concentrations. In this study, nitrogen depletion of the water column, from 30-90 µM to 2-7 µM, occurred in spring due to macroalgal growth. Subsequent nitrogen enrichment of the sediments, from 1.2 mg N g^{-1} sediment to 3.1 mg N g^{-1} sediment, occurred in late summer due to macroalgal deposition and decomposition. Piriou and Ménesguen (1992) related cyclical variations in nitrogen concentrations in the water column to fluctuations in *Ulva* biomass. Similarly, in Waquoit Bay, *Cladophora vagabunda* and *Gracilaria tikvahiae* were able remove substantial quantities of nutrients from the water column and were considered to be responsible for low water column concentrations in summer (Peckol *et al*., 1994).

The influence of macroalgae on water column nutrients may be facilitated by their capacity for luxury uptake and storage depending on ambient nutrient concentrations (Hanisak, 1983). In Kiel Bight, Schramm *et al*., (1988) found that tissue nutrient concentrations were higher in macroalgal tissues than in the surrounding water column, with nitrogen saturation occurring in winter and limitation in summer. Mann *et al*., (1982) reported that the alga *Laminaria longicruris* stored nitrate to 28 000 times ambient concentration in winter. This was then available for growth during summer. In Port Phillip Bay, Brown *et al*., (1980) found that macroalgae growing near the Werribee Treatment Plant had higher tissue nitrogen concentrations than those further offshore, which were considered nutrient limited. Given the dynamic relationship between water column and algal tissue nutrient concentrations, Lyngby (1990) and Fong *et al*., (1994) suggest that monitoring macroalgal tissue nutrient concentrations may be a useful tool for detecting long-term trends in water column nutrient levels and availability.

The influence of macroalgae on water column nutrients can be mediated by environmental factors. For example, in controlled experimental conditions, Peckol *et al*., (1994) found that the growth of *Cladophora vagabunda* and *Gracilaria tikvahiae* under nutrient enriched conditions was not related to tissue nutrient concentrations but was regulated by water temperature and irradiance. Hanisak (1993) studied temperature effects on nitrogen release during the decomposition of *Gracilaria verrucosa* and *Ulva lactuca*. Release rates of nitrogen during decomposition were 5.91 and 6.37 g N m^{-2} for *Gracilaria* and *Ulva* respectively and the rate of decomposition increased with increasing temperature. These results suggest that nutrient uptake and release processes of macroalgae are likely to be strongly influenced by factors such as temperature and light which vary seasonally.

Macroalgae may influence water and sediment nutrient concentrations indirectly by influencing water column oxygen concentrations. Macroalgal respiration or decomposition can deplete water column oxygen concentrations and lead to hypoxia and anoxia (Sfriso *et al*., 1992; Viaroli *et al*., 1992). For example, Sfriso *et al*., (1992) found that macroalgal decomposition led to anoxic episodes in the Lagoon of Venice. This resulted in the rapid reduction of nitrate within the sediments and the concurrent release of phosphate which subsequently contributed to phytoplankton blooms. A similar pattern of nitrate consumption and phosphorus release was observed by Viaroli *et al*., (1992) in the northern Adriatic Sea following water column oxygen depletion during *Ulva* decomposition. In Waquoit Bay, United States, Valiela *et al*., (1992) found that macroalgal growth and respiration controlled water column oxygen profiles and that nocturnal respiration accounted for most of the oxygen depletion during this time. During overcast periods, low irradiance levels led to higher algal respiration rates and subsequent deoxygenation of the water column (Valiela *et al*., 1992). Thus, based on the strong relationships between faunal abundance and water column oxygen levels identified in the previous chapter, macroalgae may have detrimental impacts on benthic communities through decomposition and the resulting depletion of oxygen in the water column.

Additionally, macroalgae may influence other benthic organisms by changing the quality of the habitat. Viaroli *et al*., (1992) observed that the increased load of organic material to the sediments as a result of macroalgal blooms, stimulated an increase in the abundance of grazers and deposit-feeders. In contrast, Valiela *et al*., (1992) reported very clear declines in benthic macroinvertebrate abundance and species richness with increasing macroalgal biomass. In addition, Valiela *et al*., (1992) related the long-term decline in the catch of the suspension-feeding bivalve *Argopecten irradians* in Waquoit Bay to the multiple effects of macroalgae reducing benthic oxygen levels, suppressing the efficiency of suspension-feeding and smothering the *Z. marina* meadows inhabited by this bivalve. A similar decline in the catch of the co-occurring suspension-feeding bivalve, *Mercenaria mercenaria*, was not observed and this was explained by different habitat preferences of this species (Valiela *et al*., 1992).

3.3. Microalgae

Benthic microalgae reside on or just below the sediment surface and are thus exposed to water column and sediment nutrient sources. Benthic processes often have a

regulatory role on processes occurring in the water column (Hopkinson and Wetzel, 1982; Sullivan *et al*., 1991; Fong *et al*., 1994). In addition, benthic microalgae can contribute significantly to the total system primary production (Oviatt *et al.*, 1986; Daehnick *et al*., 1992). Thus, benthic microalgae can have considerable influence over sediment and water quality characteristics.

Benthic microalgae increase sediment and water column oxygen levels during photosynthesis. In a series of lab incubations, Wiltshire (1992) recorded a net oxygen production by benthic microalgae of between 9.14 to 14.01 mmol O_2 m^{-2} d^{-1}, thus supersaturating the sediment pore-water.

By contributing to sediment oxygen concentrations through photosynthesis, benthic microalgae can regulate NH_4 flux from the sediments (Graneli and Sundbäck, 1985; Sundbäck and Graneli, 1988; Sundbäck *et al*., 1991; Wiltshire, 1992). Evidence for this relationship was provided by Sundbäck and Graneli (1988) and Wiltshire (1992) who detected negative correlation between ammonium flux and the amount of light reaching the sediment. Wiltshire (1992) recorded an NH_4 flux of -28.2 mmol N m^{-2} d^{-1} (-147 g N m^{-2} y^{-1}) in irradiated core incubations, compared with 5.97 mmol N m^{-2} d^{-1} (30.5 g N m^{-2} y^{-1}), in darkened incubations. Sundbäck *et al*., (1991) reported a similar decrease in ammonium flux in response to photosynthetic activities by benthic microalgae. Ammonium efflux was lower in irradiated incubations i.e. 0 to 50 µmol m^{-2} h^{-1} (0 to 6.13 g N m^{-2} y^{-1}) compared with dark incubations i.e. 6 to 120 µmol m^{-2} h^{-1} (0.73 to 14.7 g N m^{-2} y^{-1}). Sundbäck and Graneli (1988) concluded that the indirect influence on nitrogen flux, by oxygenating the sediments, was greater than the direct uptake of nitrogen by these algae. In field and laboratory studies, Graneli and Sundbäck (1985) estimated that benthic microalgae were responsible for 20% of the nitrogen uptake within the sediments with the remaining 80% being lost through denitrification.

In addition to regulating nutrient processes within the sediments, benthic microalgae can contribute significantly to system primary production. Masini (1987) reported a gross production by benthic microalgae of 570 g C m^{-2} y^{-1} compared with seagrass at 350 g C m^{-2} y^{-1}. Using the Redfield C:N ratio of 6.6 this equates to 86 g N m^{-2} y^{-1}. Daehnick *et al*., (1992) calculated that benthic microalgae were responsible for between 8-42% of system primary production. This equated to an annual production of approximately 339 g C m^{-2} (52 g N m^{-2} y^{-1}). Fielding *et al*., (1988) calculated that benthic microalgae were responsible for 22% of total system primary production and estimated rates of between 152 g C m^{-2} y^{-1} (22.5 g N m^{-2} y^{-1}) in exposed sites to 609 g C m^{-2} y^{-1} (92 g N m^{-2} y^{-1}) in sheltered sites. Moncreiff *et al*., (1992) found that annual production of benthic microalgae was 339 g C m^{-2} (52 g N m^{-2} y^{-1}) compared with 256 g C m^{-2} y^{-1} by seagrass and 905 g C m^{-2} y^{-1} by seagrass-associated epiphytes. In a mesocosm study, Oviatt *et al*., (1986) observed that system primary production was highly related to diatom abundance and system switching from net autotrophy to heterotrophy was related to silicon limitation of diatom growth in winter and grazing pressure on diatoms in summer.

Benthic microalgae often represent a higher biomass than that of phytoplankton in the overlying water column. For example, in a shallow estuarine system, Lukatelich and McComb (1986) recorded estimates of water column chlorophyll *a* of between 0.47 to 0.54 tonnes compared with 19.84 to 22.02 tonnes in the sediments. Cahoon *et al*.,

(1993) measured sediment chlorophyll *a* concentrations of 39.8 mg m^{-2} compared with integrated water column concentrations of 25.9 mg m^{-2}. Additionally, benthic microalgae have the potential to contribute significantly to phytoplankton composition and primary production. Shaffer and Sullivan (1988) found that benthic diatoms accounted for 74% of the taxa occurring in the water column. Lukatelich and McComb (1986) found that summer-time water column chlorophyll *a* concentrations were largely due to resuspended benthic microalgae caused by wind-stirring. De Jonge and Van Beusekom (1992) found that benthic microalgae accounted for about 22% of water column production in the Ems estuary and over 60% in the Dollard estuary.

Conversely, benthic microalgae may regulate water column productivity through competitive exclusion of phytoplankton. In a mesocosm study, Fong *et al*., (1993) found that benthic microalgal mats could outcompete phytoplankton and floating macroalgae under nutrient enriched conditions. However, Sundbäck and Jonsson (1988) found that, although benthic microalgae were initially stimulated by increasing nutrient concentrations, as enrichment increased further, phytoplankton production impeded benthic microalgal production by increasing water turbidity.

Benthic microalgae are important in the diets of infaunal deposit-feeders (Murphy and Kremer, 1992), and via resuspension, can contribute to diets of suspension-feeders (De Jonge and Van Beusekom, 1992). Using stable carbon isotope analysis, Murphy and Kremer (1992) identified that benthic microalgae contributed up to 100% of the diet of infaunal callianassids. Page *et al*., (1992) detected a negative correlation between sediment chlorophyll *a* concentrations and the abundance of the deposit-feeding mollusc *Macoma nasuta*. De Jonge and Van Beusekom (1992) estimated that resuspended benthic microalgae accounted for 50% of the food resources available to suspension-feeders in the Ems-Dollard estuarine system.

3.4. Benthic Macrofauna

In Port Phillip Bay, suspension-feeders and deposit-feeders dominate the invertebrate macrofauna (Poore, 1992). In the Bay, suspension-feeders have been calculated to represent approximately 50% of the total biomass and be responsible for 15% of all organic material ingested and, because of their high assimilation efficiency, 42% of all organic matter assimilated (Wilson *et al*., 1993). Deposit-feeders represent approximately 35% of the biomass, 85% of the organic matter ingested and 50% of the organic matter assimilated (Wilson *et al*., 1993).

3.4.1. Suspension-feeders

Suspension-feeders promote the flux of ammonium from sediments. For example, in a study of the interactive effects of nutrient enrichment and mussel density, Prins *et al*., (1995) found that under ambient nutrient conditions, NH_4 flux ranged from 10.2 to 19.5 µmol m^{-2} h^{-1} showing no consistent pattern with mussel density. However, under enriched conditions, NH_4 efflux was higher than in the ambient treatments, and increased from 15.5 to 72 µmol m^{-2} h^{-1} as mussel density increased from 18 to 142

mussels per m^{-2}. These values equate to 1.25 to 2.39 and 1.90 to 8.83 g N m^{-2} y^{-1} for ambient and enriched conditions respectively.

The relative contributions of bivalve excretion, mortality, and sediment diffusion to DIN flux were investigated in a mesocosm study by Doering *et al*., (1986). These researchers observed that the efflux of dissolved inorganic nitrogen (DIN) was higher in tanks in which the infaunal bivalve *Mercenaria mercenaria* was present than where it was absent and this was considered to be related to clam mortality, excretion or bioturbation. These researchers detected an inverse relationship between DIN flux and bivalve mortality and calculated that mortality and subsequent decomposition accounted for 6%, of the flux (1.6 g N m^{-2} y^{-1}), whereas excretion accounted for between 34 to 63% of the DIN flux (9.23 to17.13 g N m^{-2} y^{-1}). In this study, the role of bioturbation in stimulating DIN flux was comparable to direct excretion by *M. mercenaria*, and accounted for 31 to 60% of the DIN flux (8.42 to 16.32 g N m^{-2} y^{-1}).

Suspension-feeders may improve water clarity by removing suspended particles from the water column and in some instances have a considerable filtration capacity. In a mesocosm study, Prins *et al*., (1995) found that at high mussel densities (up to 142 m^{-2}) , the rate of phytoplankton consumption was greater than production, leading to an overall decrease in phytoplankton biomass and production. At low bivalve densities (16 m^{-2}), Doering *et al*., (1986) however, found that suspension-feeders did not limit phytoplankton biomass but rather increased system production and promoted sedimentation. In a field based study, Cloern (1982) calculated that suspension-feeding bivalves were capable of filtering a volume of water equivalent to the volume of South Bay, San Francisco Harbour between 1.2 to 1.8 times per day and were the main factor regulating phytoplankton growth in summer and autumn. Loo and Rosenberg (1989) estimated that bivalves filtered the volume of water in Laholm Bay, Sweden, to a depth of 5 metres every three days. Despite this considerable filtration capacity, the majority of phytoplankton were advected from the bay by water currents (Loo and Rosenberg, 1989). In Port Phillip Bay, it has been estimated that suspension-feeders filter between 18 and 95 l g $AFDW^{-1}$ animal d^{-1}, depending on taxa. Given the abundance and biomass of suspension-feeders in the Bay, this filtration rate is equivalent to the entire volume of the Bay being filtered every 16 to 24 days (Poore, 1992; Wilson *et al*., 1993)

Additionally, suspension-feeders promote deposition to the sediments. For example, Hatcher *et al*., (1994) found that sedimentation rates were higher under suspended mussel rafts than at reference sites and that increased DIN flux from the sediments was related to the increased rate of sedimentation. In a mesocosm study, Doering and Oviatt (1986) found that the bivalve *Mercenaria mercenaria* increased sedimentation of carbon by up to 58%, with 32 % of this due to assimilative uptake, 47% due to bivalve respiration and 21% due to permanent biodeposition.

3.4.2. Deposit-feeders

Deposit-feeding infauna may be tube-builders or free-living burrowers and feed either at the sediment-water interface or at sub-surface levels (Bird, 1994). These fauna can have important direct influences on physical and chemical processes in the sediments by promoting particle and solute transport and their influence varies according to their feeding, burrowing or tube-building activities (Bird, 1994).

The effects of bioturbation on physical and chemical processes in marine sediments has been the subject of numerous reviews (Rhoads and Young, 1970; Gray, 1974; Rhoads and Boyer, 1982; Aller, 1982, 1983, 1988; Kristensen, 1988). Wilson *et al*., (1993) reviewed the effects of invertebrates, including deposit-feeders, on nutrient cycling in Port Phillip Bay and presented data on the ingestion, assimilation and excretion rates of these fauna. Although these reviews are extensive in their scope and detailed in their treatment of bioturbation and the role of deposit-feeders in nutrient cycling, they do not always quantify rates of nutrient flux or nitrification and denitrification in bioturbated sediments. The following section provides some empirical data.

Infaunal deposit-feeders promote the flux of solutes from the sediments through excretion or through irrigation and ventilation of tubes and burrows. For example, Kristensen and Blackburn (1987) measured a DIN flux of 3.07 mmol N m^{-2} d^{-1} (15.7 g N m^{-2} y^{-1}) from sediments inhabited by the polychaete *Nereis virens* at a density of 1800 individuals m^{-2}, compared with 0.89 mmol N m^{-2} d^{-1} (4.5 g N m^{-2} y^{-1}) from aerated sediments from which all fauna had been removed. In a study of the effects of *Nereis diversicolor* on NH_4 flux, Davey and Watson (1995) recorded flux rates of 140 - 422 g N m^{-2} y^{-1} in high faunal densities (2000 - 4000 m^{-2}), 135 - 501 g N m^{-2} y^{-1} at medium faunal densities (100 - 1000 m^{-2}), 31 - 327 g N m^{-2} y^{-1} at low faunal densities (50 - 450 m^{-2}) and -2.94 to 202 g N m^{-2} y^{-1} in relatively depauperate (control) sediments. Banta *et al*., (1995) reported DIN flux rates of 2 to 5 mmol N m^{-2} d^{-1} (5.11 to 25.5 g N m^{-2} y^{-1}), from sediments inhabited by between 20 000 to 100 000 individuals per m^{-2}, (typically consisting of the bivalve *Nucula annulata*, and the polychaetes *Nephtys incisa*, *Mediomastus ambiseta*, *Cyclinchna oryza* plus spionid polychaetes, representing 76 to 95% of the faunal community). Aller and Yingst (1985) measured the NH_4 flux rates from sediments inhabited by the polychaete *Heteromastus filiformis*, and the deposit feeding bivalves *Macoma balthica* and *Tellina texicana* of 15.84 g N m^{-2} y^{-1}, 12.97 and 44.15 g N m^{-2} y^{-1} respectively. These values are high compared with those estimated for sediments inhabited by callianassid shrimp i.e. 0.49 g N m^{-2} y^{-1} for *C. rathbunae* and *C. jonesi* in tropical waters (Murphy and Kremer, 1992), and 0.60 g m^{-2} y^{-1} in temperate waters (Mukai and Koike, 1984).

Thus, deposit-feeders perform an important function in nutrient regeneration and this may be a significant contribution to nutrient cycling in marine environments. For example, Murphy and Kremer (1992) estimated that the NH_4 flushed from callianassid burrows supplied 5% of the nitrogen demand for benthic primary production and the net nitrogen flux from these bioturbated sediments supplied 21% of the benthic primary production nitrogen demand. In the Tamar Estuary, south-western England, Davey and Watson (1995) calculated that the NH_4 released by burrows of *N. diversicolor*, assuming the worms cover an area of 0.7 km^2 at a density of 3000 individuals m^{-2}, contributed 10-20 times more NH_4 to the water column than did mean annual discharges from riverine or sewage sources. Although these figures are based on a number of assumptions and do not take seasonal variations in polychaete density and nitrogen loading into consideration, they imply that the regeneration of inorganic nitrogen from the sediments is potentially very high.

Although deposit-feeders may directly increase NH_4 flux from the sediments, they indirectly promote nitrification, the oxidation of NH_4 to NO_3 through aeration of the sediments (Koike and Mukai, 1983; Koike and Sørensen, 1988). Nitrification promotes denitrification, the reduction of NO_3 and NO_2 to nitrogen gas, by increasing the supply

of nitrate in the sediments and these processes are often tightly coupled (Koike and Sørensen, 1988). Nitrification and denitrification lead to the consumption of ammonium and the production and advection of nitrogen gas from the sediments and thus represent an important sink for nitrogen in marine sediments (Koike and Sørensen, 1988). Hüttel (1990) found that nitrate concentrations increased and ammonium concentrations decreased with increasing depth in the burrows of the polychaete *Arenicola marina*, and suggested that this was evidence of nitrification and consequent denitrification occurring in the burrows. Kristensen and Blackburn (1987) measured nitrification and denitrification in sediments inhabited by *N. virens* at 12.43 mmol NH_4 m^{-2} d^{-1} (63.3 g N m^{-2} y^{-1}) and 7.11 mmol N m^{-2} d^{-1} (36.3 g N m^{-2} y^{-1}) respectively, compared with defaunated sediments at 5.44 mmol m^{-2} d^{-1} (27.78 g N m^{-2} y^{-1}) and 3.01 mmol N m^{-2} d^{-1} (15.4 g N m^{-2} y^{-1}) respectively, but could not detect evidence of denitrification in anoxic sediments. Law *et al*., (1991) found that denitrification was strongly related to bioturbation by the polychaete *Nereis virens* and accounted for 8.5% (mean of 4.78 g N m^{-2} y^{-1}), of the annual N loading and up to 100% of the N loading to the sediments during summer. Sloth *et al*., (1995) reported that denitrification may be inhibited in the presence of hydrogen sulphide in the sediments, and Osinga *et al*., (1995) observed that the urchin *Echinocardium cordatum* facilitated sulphide oxidation by aerating the sediments.

Although bioturbation by infaunal deposit-feeders promotes the net loss of nitrogen from marine environments, many studies have shown that the potential for nitrification and denitrification to account for additional nitrogen loads under enriched conditions is limited. Sayama and Kurihara (1983) and Sloth *et al*., (1995) reported conflicting effects of nutrient enrichment on denitrification in the sediments. Sayama and Kurihara (1983) found that in the absence of nutrient enrichment, the polychaete *Neanthes japonica* increased denitrification from 12.88 g Kg DW $sediment^{-1}$ y^{-1} to 36.74 g kg DW $sediment^{-1}$ y^{-1}, whereas in enriched treatments there was little difference in the rates of denitrification for faunated and defaunated sediments respectively (44.15 and 33.11 g kg DW $sediment^{-1}$ y^{-1}). Under low nutrient conditions *N. japonica* promoted denitrification, probably through bioirrigation bringing oxygen and nitrate into the burrow, which would otherwise be nutrient limited, whereas under enriched conditions, simple diffusion of water column nitrate appeared to be high enough to support high levels of denitrification.

In contrast, Sloth *et al*., (1995) found that a moderate nutrient loading (30 g N m^{-2} of nitrate) stimulated denitrification whereas high loadings (100 g N m^{-2} of nitrate) inhibited denitrification. These authors speculated that the presence of hydrogen sulphide inhibited denitrification. Similarly, Law *et al*., (1991) found little relationship between the rate of denitrification in the sediments and nitrate concentrations in the overlying water column and conclude that denitrification does not automatically regulate water column nitrate levels when nitrate levels are enriched.

3.4.3. Interactions between deposit-feeders and suspension-feeders and implications for Port Phillip Bay

In marine sediments, interactions between benthic invertebrates can have important influences on infaunal community structure (Brenchley, 1982; Posey, 1987; Posey *et*

al., 1991; Flach, 1992). For example, bioturbation by deposit-feeders reduces the shear strength of surface sediments which promotes sediment resuspension (Davis, 1993). Increased sediment resuspension can have detrimental effects on suspension-feeders (Rhoads and Young, 1970), particularly those which compensate for increased particle concentrations by reducing clearance rates (Bricelj and Malouf, 1984). Mobile fauna may also physically disturb sessile fauna (Rhoads and Boyer, 1982; Posey *et al*., 1991). Conversely, the tubes of sessile suspension-feeders may physically obstruct the movement of burrowing infauna (Brenchley, 1982; Posey, 1987).

Posey (1987) found that mobile fauna could competitively exclude sedentary species through disturbance or physical disruption of burrows and tubes whereas sedentary species could exclude mobile species through binding the sediments or physical obstruction. Additionally, large species could exclude smaller species but smaller taxa were not found to exclude larger taxa. In a subsequent study, Posey *et al*., (1991) found that callianassid shrimp excluded some benthic infauna e.g. the infaunal bivalve *Macoma balthica* and polychaetes *Streblospio benedicti* and *Pseudopolydora kempi*, but promoted the abundance of other species e.g. the polychaetes *Cirriformia* sp., and *Heteromastus filiformis* and the amphipods *Corophium ascherusicum* and *Leptochelia dubia*. Rhoads and Boyer (1982) reported that small taxa may co-exist with larger taxa if they are spatially separated, e.g. if smaller taxa are restricted to the superficial sediments and larger taxa to the deeper sediments.

Wilson *et al*., (1993) pointed out that the effects of benthic community structure, e.g. of species composition and size-distribution on nutrient cycling in marine sediments could not be easily identified. In tidal flats in the German Wadden Sea, Asmus (1994) compared the contribution of the deposit-feeding gastropod *Hydrobia ulvae* and the large, suspension-feeding bivalve *Mytilus edulis* to energy flow. These organisms exhibited size-related peaks in biomass, production and respiration on these tidal flats. Asmus (1994) calculated that, given a 1% cover of the tidal flat by mussels, deposit-feeders would dominate the system, and the food-chain would be based on autochthonous primary production by benthic microalgae. If mussel beds covered 10% of the tidal flats, suspension-feeders would dominate system energy flow and the food chain would be based on water column primary production and allochthonous nutrient resources.

In Port Phillip Bay, the effects of the introduced suspension-feeding polychaete *Sabella spallanzanii* on benthic community structure and nutrient cycling in the Bay is an area of potential concern. Evidence from Cockburn Sound, Western Australia, which shares similar sediment and water depth characteristics with Port Phillip Bay, suggests that *S. spallanzanii* is capable of forming large, homogenous beds; up to 20 ha in area, with a density of up to 256 individuals m^{-2}, occurring at depths of 3 to 15m (Clapin and Evans, 1995). Although it is possible that newly settled larvae of *S. spallanzanii* may be competitively excluded by large, mobile fauna, these worms may achieve a size- or density-related protection from disturbance, either as the size of the individuals or size of the beds grow. Additionally, S. *spallanzanii* could begin to have detrimental impacts on bioturbators through physical obstruction.

This has important implications for the ecology of Port Phillip Bay where the sediments are considered to be a net sink for nutrients due to the high rate of sediment reworking by infaunal deposit-feeders (Wilson *et* al., 1993). A change in the benthic community from deposit-feeding bioturbators to suspension-feeders has the potential to decrease the role of sediment reworking and denitrification in nutrient cycling, promote ammonium flux from the sediments and shift the bay towards a phytoplankton based system.

4. CONCLUSIONS

Clear patterns of community change in relation to eutrophication can be identified and have been qualitatively described in coastal bays and estuaries throughout the world. For primary producers, there is a general shift from large macrophytes, which are capable of storing nutrient and are more competitive at low nutrient levels, towards ephemeral algae and phytoplankton which are distributed higher in the water column and are more competitive at higher nutrient loadings. An increased production of free-floating, ephemeral macrophytes and phytoplankton can increase water turbidity with subsequent negative impacts on benthic primary producers. Additionally, increased sedimentation of organic material may occur, which can initially promote deposit-feeders, increase benthic respiration and lead to hypoxia and anoxia in the sediments. Thus, for secondary producers, an overall reduction in species diversity and abundance is a typical response to eutrophication. There is a general loss of larger size-classes of fauna, and a shift towards small, opportunists, generally dominated by deposit-feeding polychaetes. Although these patterns can be observed in marine systems experiencing eutrophication, rarely have they been quantitatively linked to nutrient loadings.

So, although seagrass degradation and loss has been attributed to the effects of eutrophication, empirical relationships between nutrient loadings and seagrass decline have not been quantified. In the figures presented in this review, there appeared to be little relationship between environmental nitrogen concentrations and either seagrass shoot density, biomass or production. This is likely to be related to species- and site-specific differences in nitrogen demand. In some examples, seagrasses are able to rapidly deplete nitrogen in the sediments and nitrogen limitation of seagrass growth has been observed, whereas in other examples phosphorus limitation has been observed. Additionally, the capacity for nutrient storage and translocation further diminish direct correlation between water and sediment nitrogen concentrations and seagrass growth parameters.

In contrast, studies on light levels in the water column and seagrass abundance are highly correlated; seagrasses decline rapidly under low light regimes, and recover only slowly even months after the removal of artificial shading. In addition, the capacity of seagrass epiphytes and periphyton to attenuate light reaching the seagrass leaves and for epiphytes and periphyton to respond rapidly when nutrients and light are available has also been demonstrated. Thus, measuring relationships between nutrients, epiphytes and light attenuation may be more important than direct observations of nutrient-seagrass relationships when trying to determine the likely effects of eutrophication on seagrasses.

For macroalgae, although large scale blooms of floating macroalgae, typically *Ulva*, *Cladophora* and *Enteromorpha*, are a commonly reported symptom of eutrophication, few studies have empirically linked increases in algal biomass to increases in nutrient loadings. Relationships were inconsistent between nutrient concentrations and algal biomass and production reported in field and laboratory studies. Given the capacity of macroalgae for luxury uptake and storage of nutrients, and the release of nutrients during decomposition, it is not surprising that stronger relationships between nutrient concentrations and macroalgal growth were not observed. Additionally, nutrient uptake and release processes of macroalgae have the capacity to influence water and sediment

nutrient concentrations over large spatial scales. Thus, simultaneous measurements of environmental nutrient concentrations and macroalgal biomass may not be effective as early indicators of eutrophication. Other measures which integrate environmental conditions over longer time-frames are likely to provide more efficient tools for the early indication of eutrophication. The use of macroalgal tissue nutrient concentrations or changes in algal depth distribution are examples of this approach.

Changes in biomass or production of periphyton and benthic microalgae did not correlate with nitrogen concentrations. Periphyton biomass is likely to be highly influenced by the availability of living space provided by the host seagrass or by grazers. Field studies of benthic microalgae have shown that factors such as irradiance, water temperature, sediment-type, tidal influences and wave exposure have a greater direct influence on benthic microalgal assemblages than nutrient concentrations. Thus, relationships between environmental nutrient concentrations and microalgal biomass and production are likely to be difficult to detect due to the confounding effects of other factors.

Studies on shifts in microalgal community structure in relation to nutrient enrichment do not report consistent trends, although most studies report a shift from a diatom dominated to a cyanobacteria dominated assemblage. Grazing on diatoms by macrofauna, and nutrient enriched growth of cyanobacteria have been implicated as mechanisms influencing this transition. The relatively low transfer of energy to higher trophic groups under nutrient enriched conditions in mesocosm studies has been linked to the dominance of cyanobacteria which are generally poor food substrates for grazers.

The abundance, biomass and production of macrofauna did not exhibit clear relationships with environmental nitrogen concentrations except in studies carried out over long-time periods e.g. 15 years. In addition, transitions between trophic groups could not be detected in relation to nitrogen concentrations. However, clear and consistent patterns of community change have been observed in sediments adjacent to sewage outfalls from a wide range of geographical locations although these patterns have rarely been empirically related to increases in nutrient loadings. These links are difficult to derive from the literature, either due to limitations of the study e.g. environmental parameters not measured or limited spatial and temporal scales. Alternatively, the links between nutrient loads and macrofaunal community parameters may be difficult to isolate due to the scales of natural variability associated with measurements of these parameters, or due to the diffuse nature of the associations. In contrast, the detrimental effects of water column anoxia on benthic macrofauna can be easily measured and positive relationships between water column oxygen concentrations and macrofaunal density were observed. An examination of links between nutrient loadings and episodes of water column hypoxia or anoxia and between water column oxygen concentrations and macrofaunal abundance, species composition, biomass or production may yield more useful information on the influence of nutrients on macrobenthic communities.

Increases in fish abundance, growth rate, biomass and productivity have been reported in areas experiencing eutrophication. However, increases in fisheries yields have generally been linked with greater fishing effort rather than to the direct influence of eutrophication. In addition, empirical links between nutrient loads and fish abundance,

biomass and production are difficult to quantify due to the high degree of variability associated with measurements of these parameters. In contrast, changes in community size-structure and species composition have been related to the effects of eutrophication, either as a result of changes in the quality of benthic habitats or as a result of episodic anoxia. The effects of anoxia on fish are direct and can be relatively easily measured and declines in fish biomass have been empirically linked to low water column oxygen concentrations.

Based on the information available on Port Phillip Bay, it would appear that present nutrient levels in the Bay, are unlikely to cause the severe, bay-wide effects associated with eutrophication which have been observed in northern European and American estuaries, coastal embayments and seas. Effects of the Werribee treatment plant can only be detected within a few hundred metres of the outfall and elsewhere in the bay, nitrogen limitation of primary production has been observed. Unlike examples from the Baltic Sea, Mediterranean Sea, and Japanese and North American waters, where water column anoxia has had severe impacts on the benthos, water column oxygen concentrations in Port Phillip Bay appear high and capable of supporting a rich diversity of benthic macrofauna. Although macrofaunal communities near the Werribee treatment plant are dominated by deposit-feeding polychaete species which are characteristic of disturbed sites elsewhere, in the Bay, macrofaunal communities are dominated by large, relatively long-lived fauna such as infaunal callianassid crustaceans, urchins, and bivalve molluscs. These infauna facilitate important benthic processes such as denitrification, which can be an important sink for the advection of nitrogen from coastal marine systems. Although the current distribution and rate of invasion of the polychaete worm *Sabella spallanzanii* in Port Phillip Bay is unknown, there exists the potential for this species to have negative impacts on infaunal bioturbators through competitive exclusion within the sediments. This is likely to impact on key processes such as sedimentation and denitrification and potentially shift the Bay towards a phytoplankton based system.

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6. REFERENCES

Aller, R. C., 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: *Animal-Sediment Relations: the Biogenic Alteration of Sediments.* edited by P. L. McCall & M. J. S. Tevesz., Plenum, New York., pp. 53-102.

Aller, R. C., 1983. The importance of the diffusive permeability of animal burrow lining in determining marine sediment chemistry. *J. Mar. Res.* 41: 299-322.

Aller R. C., 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. In: *Nitrogen Cycling in Coastal Marine Environments.* edited by T. H. Blackburn & J. Sørensen, John Wiley & Sons, Chichester, New York, Brisbane, Toronto, Singapore, pp 301-340.

Aller, R. C. & Yingst, J. Y., 1985. Effect of the marine deposit-feeder *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia), and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates and microbial distributions. *J. Mar. Res.* 43: 615-645.

Almasi, M. N., Hoskin, *C.* M., Reed, J. K. & Milo, J., 1987. Effects of natural and artificial *Thalassia* on rates of sedimentation. *J. Sed. Petr.* 57: 901-906.

Asmus, H. 1994. Benthic grazers and suspension feeders: which one assumes the energetic dominance in Konigshafen? *Helgol. Meeresunt.* 48: 217-231.

Asmus, H., Asmus, R. M., & Zubilliga, G. F., 1995., Do mussel beds intensify the phosphorus exchange between sediment and tidal waters. *Ophelia.* 41: 37-55.

Axelrad, D. M., Poore, G. C. B., Arnold, J., Bauld, V. B., Edwards, R. R. C. & Hickman, N. J., 1981. The effects of treated sewage discharge on the biota of Port Phillip Bay, Victoria Australia. In.: *Proceedings of the First International Symposium on Nutrient Enrichment of Estuaries.* edited by B. J. Neilson & L. E. Cronic, Virginia, USA. pp 279-306.

Baden, S. P., Loo, L-O., Pihl, L., & Rosenberg, R. 1990., Effect of eutrophication on benthic communities including fish: Swedish West Coast. *Ambio.* 19: 113-122.

Banta, G., Giblin, A. E., Hobbie, J. E., & Tucker, J., 1995. Benthic respiration and nitrogen release in Buzzards Bay, Massachusetts. *J. Mar. Res.* 53: 107-135.

Beardall, J. & Light, B., 1994. Biomass, productivity and nutrient requirements of microphytobenthos. Technical Report No 16. CSIRO Port Phillip Bay Environmental Study. Melbourne, Australia. 35p.

Bell, S. S., Hicks., G. R. F. & Walters, K., 1988. Active swimming in meiobenthic copepods of seagrass beds: Geographic comparisons of abundances and reproductive characteristics. *Mar. Biol.* 98: 351-358.

Beukema, J. J. & Cadée, G. C., 1986. Zoobenthos, responses to eutrophication of the Dutch Wadden Sea. *Ophelia.* 26: 55-64.

Bilyard, G. R., 1987. The value of benthic infauna in marine pollution monitoring studies. *Mar. Poll. Bull.* 18: 581-585.

Bird, F. L., 1994. The effects of bioturbation in Port Phillip Bay. Technical Report No 14. CSIRO Port Phillip Bay Environmental Study. Melbourne, Australia. 22p.

Bogdanos, *C.* & Satsmadjis, J., 1992. Factors ruling the benthic communities of the Messolonghi Lagoons. *Rev. Int. Oceanogr. Tomes.* 105/106: 50-57.

Boon, P. I., 1986. Uptake and release of nitrogen compounds in coral reef and seagrass, Thalassia *hemprichii* (Enrenb.) Aschers., bed sediments a Lizard Island, Queensland. *Aust. J. Mar. Freshw. Res.* 37: 11-19.

Borum, J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Mar. Biol.* 87:211-218.

Boynton, W. R., Kemp, W. M. & Keefe, C. W., 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: *Estuarine Comparisons.* edited by V. S. Kennedy, Academic Press, New York. pp 69-90.

Brenchley, G. A., 1982. Mechanisms of spatial competition in marine soft-bottom communities. *J. Exp. Mar. Biol. Ecol.* 60: 17-33.

Breitburg, D. L., 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behaviour, and physical disturbance. *Ecol. Monogr.* 62: 525-546.

Bricelj, V. M. & Malouf. R. E., 1984. Influence of algal and suspended sediment concentration on the feeding physiology of the hard clam *Mercenaria mercenaria*. *Mar. Biol.* 84: 155-165.

Brown, I. W., 1977. Ecology of three sympatric flatheads (Platycephalidae) in Port Phillip Bay, Victoria. Ph.D. Thesis, Monash University, Victoria.

Brown, I. W. & Negilski, D. S., 1976. An exploratory investigation to assess the nature and importance of fish communities in the Werribee sewage treatment form outfall region. Marine Pollution Studies Group Report P. 5-05., Melbourne, Victoria.

Brown, V. B., 1988. Nutrient limitation in Port Phillip Bay: current knowledge and proposals for the future. Environmental Services Section, Investigation and Research Branch, Systems Planning Division, Melbourne and Metropolitan Board of Works.

Brown, V. B., Rowan, K. S. & Ducker, S. C., 1980. The effects of sewage effluent on the macrophytes off Werribee, Port Phillip Bay. Environmental Studies Program Report No. 273, Ministry for Conservation, Victoria.

Brown, V. & Davies, S., 1991. The environmental quality of north-western Port Phillip Bay. Melbourne Water, Environmental Services, Series No. 91/005. 100p, 114 Figures, 59 Tables.

Bulthuis, D. A., 1983. Effects of temperature on the photosynthesis - irradiance curve of the Australian seagrass, *Heterozostera tasmanica*. *Mar. Biol. Lett.* 4: 47-57.

Bulthuis, D. *A.* & Woelkerling, Wm. J., 1981. Effects of in situ nitrogen and phosphorous enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *J. Exp. Mar. Biol. Ecol.* 53: 193-207.

Bulthuis, D. A. & Woelkerling. Wm.J. 1983a. Seasonal variation in standing crop, density and leaf growth rate of the seagrass, *Heterozostera tasmanica*, in Western Port and Port Phillip Bay, Victoria, Australia. *Aquat. Bot.* 16: 111-136.

Bulthuis, D. A. & Woelkerling, Wm. J., 1983b. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquat. Bot.* 16: 137-148.

Bulthuis, D. A., Brand, G. W. & Mobley, M. C., 1984. Suspended sediments and nutrient in water ebbing from seagrass-covered and denuded tidal mudflats in a Southern Australian embayment. *Aquat. Bot.* 20: 257-266.

Bulthuis, D. A., Axelrad, D. M. & Mickelson, M. J., 1992. Growth of the seagrass *Heterozostera tasmanica* limited by nitrogen in Port Phillip Bay, Australia. *Mar. Ecol. Prog. Ser.* 89: 269-275.

Burkholder, J. M., Mason, K. M. & Glasgow, H. B., 1992. Water- column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Mar. Ecol. Prog. Ser.* 81:163-178.

Burkholder, J. M., Glasgow, H. B. & Cooke, J. E., 1994. Comparative effects of water-column nitrate enrichment on eelgrass *Zostera marina*, shoalgrass *Halodule wrightii* and widgeongrass *Ruppia maritima*. *Mar. Ecol. Prog. Ser.* 105: 121-138.

Burt, J. S., Kendrick, G. A., Masini, R. J. & Simpson, C. J., 1995. Light and *Posidonia sinuosa* meadows in the temperate coastal waters of Western Australia II. Effect of epiphyte biomass and species composition on attenuating light to the leaf surface. Environmental Protection Authority Technical Series No 64., Department of Environmental Protection, Perth, Western Australia. 31p.

Cahoon, L. B. & Cooke, J. E., 1992. Benthic microalgal production in Onslow Bay. North Carolina, USA. *Mar. Ecol. Prog. Ser.* 84: 185-196.

Cahoon, L. B., Beretich, G. R., Thomas, C. J. & McDonald, A. M., 1993. Benthic microalgal production at Stellwagen Bank. Massachusetts Bay, USA. *Mar. Ecol. Prog. Ser.* 102: 179-185.

Cambridge, M. L. & McComb, A. J., 1984. The loss of seagrasses in Cockburn Sound, Western Australia. 1. The time course and magnitude of seagrass decline in relation to industrial development. *Aquat. Bot.* 20: 229-243.

Cambridge, M. L., Chiffings, A.W., Brittan, C., Moore, L. & McComb, A. J., 1986. The loss of seagrass in Cockburn Sound, Western Australia. II. Possible causes of seagrass decline. *Aquat. Bot.* 24: 269-285.

Clapin, G., & Evans, D. R., 1995. The status of the introduced marine fanworm Sabella spallanzanii in Western Australia: A preliminary investigation. CSIRO Centre for Research on Introduced Marine Pests, Technical Report No 2., CSIRO Division of Fisheries, Hobart, Tasmania.

Cloern, J. E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay. *Mar. Ecol. Prog. Ser.* 9: 191-202.

Coleman, V. L. & Burkholder, J. M., 1994. Community structure and productivity of epiphytic microalgae on eelgrass (*Zostera marina* L.) under water-column nitrate enrichment. *J. Exp. Mar. Biol. Ecol.* 179: 29-48.

Coleman, V. L. & Burkholder, J. M., 1995. Response of microalgal epiphyte communities to nitrate enrichment in an eelgrass (*Zostera marina* L.) meadow. *J. Phycol.* 31: 36-43.

Colijn, F. & De Jonge, V.N., 1984. Primary production of microphytobenthos in the Ems-Dollard Estuary. *Mar. Ecol. Prog. Ser.* 14: 185-196.

Colodey, A. G., Wells, P. G., 1992. Effects of pulp and paper mill effluents on estuarine and marine ecosystems in Canada: a review. *J. Aquat. Eco. Health.* 1: 201-226.

Crossland, C. J., 1988. Nitrogen fixation (acetylene reduction) in a temperate coastal lagoon off Perth, Western Australia. CSIRO. Marine Laboratories Report. Number 182., CSIRO Division of Fisheries, Perth, Western Australia. 12p.

Daehnick, A. E., Sullivan, M. J. & Moncreiff, C. A., 1992. Primary production of the sand microflora in seagrass beds of Mississippi Sound. *Bot. Mar.* 35: 131-139.

Dauer, D. M., Rodi, A. J. J. & Ranasinghe, J. A., 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries.* 15: 384-391.

Davey, J. T. & Watson, P. G., 1995. The activity of *Nereis diversicolor* (Polychaeta) and its impact on nutrient fluxes in estuarine waters. *Ophelia.* 41: 57-70.

Davies, S. & Brown, V. B., 1986. Seaweed deposition on north-western Port Phillip Bay beaches - results of monitoring programs 1983-1984. Working Paper No. 86/16, Research and Investigation Department, Melbourne and Metropolitan Board of Works.

Davis, M. W. & McIntire, C. D., 1983. Effects of physical gradient on the production dynamics of sediment associated algae. *Mar. Ecol. Prog. Ser.* 13: 103-114.

Davis, W. R., 1993. The role of bioturbation in sediment resuspension and its interaction with physical shearing. *J. Exp. Mar. Biol. Ecol.* 171: 187-200.

De Jonge, V. N. & Van Beusekom, J. E. E., 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems Estuary and its possible role for grazers. *Neth. J. Sea. Res.* 30: 91-105.

De Jonge, V.N., Van Raaphorst, W., 1995. Eutrophication of the Dutch Wadden Sea (Western Europe), an estuarine area controlled by the River Rhine. In: *Eutrophic Shallow Estuaries and Lagoons.* edited by A. J., McComb, CRC Press, Boca Rotan, London, Tokyo. pp. 129-149.

De Zwaan, A., Cortesi, P., van den Thillart, G., Brooks, S., Storey, K. B., van Lieshout, G., Cattani, O. & Vitali, G., 1992. Energy metabolism of bivalves at reduced oxygen tensions. *Mar. Coast Eutroph. 1029-1039.*

Delgado, M., 1989. Abundance and distribution of microphytobenthos in the Bays of Ebro Delta (Spain). *Estuar. Coast. Shelf. Sci.* 29: 183-194.

Den Hartog, C. & Polderman, P. J. G., 1975. Changes in the seagrass populations of the Dutch Waddenzee. *Aquat. Bot.* 1: 141-147.

Dennison, W. C., 1992. SAV and water quality relationships. In: *Submerged Aquatic Vegetation Habitat Requirements and Restoration Targets: A Technical Synthesis.* United States Environmental Protection Agency, Annapolis, Maryland. 186p.

Desprez, M., Rybarczyk, H., Wilson, J. G., Ducrotoy, J. P., Sueur, F., Olivesi, R. & Eklaim, B., 1992. Biological impact of eutrophication in the Bay of Somme, and the induction and impact of anoxia. *Neth. J. Sea. Res.* 30: 149-159.

Doering, P. H. & Oviatt, C. A., 1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. *Mar. Ecol. Prog. Ser.* 31: 265-275.

Doering, P. H., Oviatt, C. A. & Kelly, J. R., 1986. The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. *J. Mar. Res.* 44: 839-861.

Doering, P. H., Oviatt, C.A., Beatty, L. L., Banzon, V. F., Rice, R., Kelly, S. P., Sullivan, B. K. & Frithsen, J. B., 1989, Structure and function in a model coastal ecosystem: silicon, the benthos and eutrophication. *Mar. Ecol. Prog. Ser.* 52: 287-299.

Duarte, C. M., 1991. Seagrass depth limits. *Aquat. Bot.* 40: 363-377.

Duarte, C. M., 1992. Nutrient concentration of aquatic plants: Patterns across species. *Limnol. Oceanogr.* 37: 882-889.

Duarte, C. M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia.* 41: 87-112.

Ducker, S. C., Foord, N. J. & Knox, R.B., 1977. Biology of Australian seagrasses : The genus *Amphibolis* C. Agardh (Cymodoceaceae). *Aust. J. Bot.* 25: 67-95.

Edgar, G. J., 1983. The ecology of South-East Tasmanian phytal animal communities I. spatial organisation on a local scale. *J. Exp. Mar. Biol. Ecol.* 70 : 129-157.

Edgar, G. J., Hammond, L. S. & Watson, G. F., 1993. Consequences for commercial fisheries of loss of seagrass beds in southern Australia. Final Report to FIRDC Committee on the Project 88/91.

Fielding, P. J., Damstra, K. St. & Branch, G. M., 1988. Benthic diatom biomass production and sediment chlorophyll in Langebaan lagoon, South Africa. *Estuar. Coast. Shelf. Sci.* 27: 413-426.

Fitzpatrick, J. & Kirkman, H., In press. The effects of prolonged shading stress on the growth and survival of the seagrass *Posidonia australis* in Jervis Bay, New South Wales. *Mar. Ecol. Prog. Ser.*

Flach, E. C., 1992. Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. *Neth. J. Sea. Res.* 30: 81-89.

Flothman, S & Werner, I., 1992. Experimental eutrophication on an intertidal sandflat: effects on microphytobenthos, meio- and macrofauna. In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I. Ferrari, V.U. Ceccherelli & R. Rossi., Olsen and Olsen, Fredensborg, Denmark. pp. 93-100.

Fong, P., Donohoe, R. M. & Zedler, J. B., 1993. Competition with macroalgae and benthic cyanobacterial mats limits phytoplankton abundance in experimental microcosms. *Mar. Ecol. Prog. Ser.* 100: 97-102.

Fong, P., Donohoe, R. M. & Zedler, J. B., 1994. Nutrient concentration in tissue of the macroalga *Enteromorpha* as a function of nutrient history: an experimental evaluation using field microcosms. *Mar. Ecol. Prog. Ser.* 106: 273-281.

Fonseca, M. S., Fisher, J. S., Zieman, J. C. & Thayer, G. W., 1982. Influence of seagrass, *Zostera marina* L., on current flow. *Est. Coastl. Shelf. Sci.* 15: 351-364.

Fonseca, M. S., Zieman, J. C., Thayer, G. W. & Fisher. J. S., 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Est. Coastl. Shelf. Sci.* 17: 367-380.

Forbes, T. L. & Lopez, G. R., 1990. The effect of food concentration, body size and environmental oxygen tension on the growth of the deposit-feeding polychaete, *Capitella* species 1. *Limnol. Oceanogr.* 35: 1535-1544.

Forbes, T. L., Forbes, V. E. & Depledge, M. H., 1994. Individual physiological responses to environmental hypoxia and organic enrichment: Implications for early soft-bottom community succession. *J. Mar. Res.* 52: 1081-1100.

Friligos, N., 1989. Nutrient and oxygen conditions in the Elefris Bay, an intermittently anoxic Mediterranean basin. *Tox. Environ. Chem.* 19: 179-186.

Fuller, C. M., 1994. Effects of porewater hydrogen sulphide on the feeding activity of the subsurface deposit-feeding polychaete, *Clymenella torquata*, Leidy. *J. Mar. Res.* 52: 1101-1127.

Gabric, A. J. & Bell, P. R. F., 1993. Review of the effects of non-point nutrient loading on coastal ecosystems. *Aust. J. Mar. Freshw. Res.* 44: 261-283.

Gaston, G. R. & Edds, K. A., 1994. Long-term study of benthic communities on the continental shelf off Cameron, Lousiana: a review of brine effects and hypoxia. *Gulf. Res. Reports.* 9: 57-64.

Giesen, W. B. J. T, van Katwijk, M. M. & den Hartog, C., 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat Bot.* 37: 71-85.

Goldberg, E. D., 1993. Pollutants and contaminants. *Wat. Sci. Tech.* 28: 13-18.

Gordon, D. M., Grey, K. A., Chase, S. C. & Simpson, C. J., 1994. Changes to the structure and productivity of a Posidonia sinuosa meadow during and after imposed shading. *Aquat. Bot.* 47: 265-275.

Graneli, E. & Sundbäck, K., 1985. The response of plankton and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters , southwest Sweden. *J. Exp. Mar. Ecol.* 85: 253-268.

Grant, J. & Thorpe, B., 1991. Effects of suspended sediment on growth, respiration and excretion of the soft-shelled clam (*Mya arenaria*). *Can. J. Fish. Aquat. Sci.* 48: 1285-1292.

Gray, C. A., Otway, N. M., Laurenson, F. A., Miskiewicz, A. G. & Pethebridge, R. L., 1992. Distribution and abundance of marine fish larvae in relation to effluent plumes from sewage outfalls and depth of water. *Mar. Biol.* 113: 549-559.

Gray, J. S., 1974. Animal sediment relationships. *Oceanogr. Mar. Biol. Ann. Rev.* 12: 223-261.

Gray, J. S., 1992. Eutrophication in the sea. In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I. Ferrari, V. U. Ceccherelli & R. Rossi. Olsen and Olsen, Fredensborg, Denmark. pp. 3-16.

Gray, J. S., Aschan, M., Carr, M. R., Clarke, K. R., Green, R. H., Pearson, T. H., Rosenberg, R. & Warwick, R. M., 1988. Analysis of community attributes of benthic macrofauna of Frierfjord/Langesundefjord and in a mesocosm experiment. *Mar. Ecol. Prog. Ser. 46: 151-165.*

Gwyther, D., 1990. Review of fisheries productivity in Port Phillip Bay. Part 1: in relation to nutrient inputs. Part 2: some empirical comparisons with other marine embayments. Environmental Services Series No 91/007. Melbourne Board of Works, Victoria, Australia.

Hanisak, M. D., 1983. The nitrogen relationships of marine macroalgae. In*: Nitrogen in the Marine Environment.* edited by E. J. Carpenter & D. G. Capone, Academic Press, New York. pp 699-730.

Hanisak, M. D., 1993. Nitrogen release from decomposing seaweed species and temperature effects. *J. Appl. Phycol*. 5:175-181.

Hansson, S. & Rudstam, L. G., 1990. Eutrophication and Baltic fish communities. *Ambio.* 19: 123-125.

Harlin, M. M., 1975. Epiphyte-host relations in seagrass communities. *Aquat. Bot.* 1: 125-131.

Harlin, M. M. & Thorne-Miller, B., 1981. Nutrient enrichment of seagrass beds in a Rode Island coastal lagoon. *Mar. Biol*. 65: 221-229.

Harlin, M. M., Thorne-Miller, B. & Boothroyd, J. C., 1982. Seagrass-sediment dynamics of a flood-tide delta in Rhode Island (USA). *Aquat. Bot.* 14: 127-138.

Harlin, M. M., 1995, Changes in major plant groups following nutrient enrichment. In: *Eutrophic Shallow Estuaries and Lagoons.* edited by A. J. McComb, CRC Press, Boca Rotan, London, Tokyo. pp. 173-187.

Hatcher, A., Grant, J. & Schofield, B., 1994. Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Mar. Ecol. Prog. Ser.* 115: 219-235.

Hemminga, M. A., Harrison, P.G. & Van Lent, F., 1991. The balance of nutrient losses and gains in seagrass meadows. *Mar. Ecol. Prog. Ser.* 71: 85-96.

Hillman, K. Walker, D. I., Larkum, A. W. D. & McComb, A. J., 1989. Productivity and nutrient limitation. In*: Biology of Seagrasses.* Edited by A. W. D. Larkum, A. J. McComb & S. A. Shepherd, Elsevier. Amsterdam, Oxford, New York and Tokyo, pp. 635-685.

Hillman, K., Lukatelich, R. J., Bastyn, G. & McComb, A. J., 1991. Water quality and seagrass biomass, productivity and epiphyte load in Princess Royal Harbour, Oyster Harbour and King George Sound. Environmental Protection Authority, Technical Series 39. Perth, Western Australia. 44p.

Hinga, K. R., Jeon, H. & Lewis, N. F., 1995, Marine Eutrophication Review Part 1: Quantifying the effects of nitrogen enrichment on phytoplankton in coastal ecosystems. NOAA Coastal Ocean Program Decision Analysis Series No. 4. NOAA Coastal Ocean Office, Silver Spring, MD. 36pp.

Hopkinson, C. S. & Wetzel, R. L., 1982. In situ measurements of nutrient and oxygen fluxes in a coastal marine benthic community. *Mar. Ecol. Prog. Ser.* 10: 29-35.

Horne, A., McClelland, J. & Valiela, I., 1994. The growth and consumption of macroalgae in estuaries: The role of invertebrate grazers along a nutrient gradient in Waquoit Bay, Massachusetts. *Biol. Bull.* 187: 279-280.

Howard, R. K., Edgar, G. J. & Hutchings, P. A., 1989. Faunal assemblages of seagrass beds. In: *Biology of Seagrasses.* Edited by A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier. Amsterdam, Oxford, New York and Tokyo, pp. 536-564.

Howarth, R. W., 1988. Nutrient limitation of net primary production in marine ecosystems. *Ann. Rev. Ecol.* 19: 89-110.

Hüttel, M., 1990. Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sand flat sediment. *Mar. Ecol. Prog. Ser.* 62: 241-248.

Iizumi, H., Hattori, A. & McRoy, C. P., 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *J. Exp. Mar. Biol. Ecol.* 47: 191-201.

Iizumi, H., Hattori, A. & McRoy C. P., 1982. Ammonium regeneration and assimilation in eelgrass (*Zostera marina*) beds. *Mar. Biol.* 66: 59-65.

Isaksson, I & Pihl, L., 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. *Neth. J. Sea. Res.* 30: 131-140.

Josefson, A. B. & Jensen, J. N., 1992. Effects of hypoxia on soft-sediment macrobenthos in southern Kattegat, Denmark. In: *Marine Eutrophication and Population Dynamics*. edited by G. Colombo, I. Ferrari, V. U. Ceccherelli & R. Rossi. Olsen and Olsen, Fredensborg, Denmark. pp. 21-28.

Kaspar, H. F., 1983. Denitrification, nitrate reduction to ammonium, and inorganic nitrogen pools in intertidal sediments. *Mar. Biol.* 74: 133-139.

Kautsky, N., Kautsky, H., Kautsky, U., & Waern. M., 1986. Decreased depth penetration of Fucus vesiculosus (L.) since the 1940's indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28: 1-8.

Keller, A. A., Doering, P. H., Kelly, S. P. & Sullivan, B. K., 1990. Growth of juvenile Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae) in MERL mesocosms: Effects of eutrophication. *Limnol. Oceanogr.* 35: 109-122.

Kenworthy, W. J. & Thayer, G. W., 1984. Production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems. *Bull. Mar. Sci.* 33: 364-379.

Kenworthy, W. J. & Fonseca, M. S., 1992. The use of fertiliser to enhance the growth of transplanted seagrasses *Zostera marina* L. and *Halodule wrightii* Aschers. *J. Exp. Mar. Biol. Ecol*. 163: 141-161.

Kerr, S. R. & Ryder, R. A., 1992. Effects of cultural eutrophication on coastal marine fisheries: a comparative approach. In: *Marine Coastal Eutrophication.* edited by Vollenweider, R. A., Marchetti, R. & Viviani, R., Elsevier, Amsterdam, London, New York, Tokyo. pp. 599-614.

Kirkman, H., Paling E. & Meynert, H., 1991. The effects of nutrient loading on local marine communities: a review. In: *Beenyup Ocean Outlet: Adaptive Environmental Assessment and Management Workshop Held At Edith Cowan University, Claremont, Perth, December 1991.* Water Authority of Western Australia, Perth, Western Australia.

Klumpp, D. W. & Nichols, P. D., 1983. A study of food chains in seagrass communities: II. food of the rock flathead, *Platycephalus laeviga*tus Cuvier, a major predator in a Posidonia australis seagrass bed. *Aust. J. Mar. Freshw. Res.* 34: 745-754.

Koike, I. & Mukai, H., 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. *Mar. Ecol. Prog. Ser.* 12:185-190.

Koike, I & Sørensen, J., 1988. Nitrate reduction and denitrification in marine sediments. In: *Nitrogen Cycling in Coastal Marine Environments.* edited by T. H. Blackburn & J. Sørensen., John Wiley & Sons, Chichester, New York, Brisbane, Toronto, Singapore. pp 251-274.

Koivisto, V. M., & Blomqvist, E. M., 1988. Does fish farming affect natural Baltic fish communities. *Kiel. Meeres. Sond.* 6: 301-311.

Kristensen, E., 1988. Benthic fauna and biogeochemical processes in marine sediments: microbial activities and fluxes. In: *Nitrogen Cycling in Coastal Marine Environments.* edited by T. H. Blackburn & J. Sørensen., John Wiley & Sons, Chichester, New York, Brisbane, Toronto, Singapore. pp 275-300.

Kristensen, E. & Blackburn, T. H., 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *J. Mar. Res.* 45: 231-257.

Lapointe, B. E. & O'Connell, J., 1989. Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: Eutrophication of a confined, phosphorus-limited marine ecosystem. *Est. Coastal. Shelf. Sci.* 28: 347-360.

Lapointe, B. E. & Clark, M. W., 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries.* 15: 465-476.

Lapointe, B. E., Littler, M. M. & Littler, D. S., 1992. Nutrient availability to marine macroalgae in siliciclastic versus carbonate rich coastal waters. *Estuaries.* 15: 75-82.

Larkum, A. W. D., 1976. Ecology of Botany Bay. I. Growth of *Posidonia australis* (Brown). Hook. f. in Botany Bay and other bays of the Sydney basin. *Aust. J. Mar. Freshw. Res.* 27: 117-127.

Larkum, A. W. D. & West, R. J., 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. *Aquat. Bot.* 37: 55-70.

Law, C. S., Rees, A. P. & Owens, N. J. P., 1991. Temporal variability of denitrification in estuarine sediments. *Est. Coastal. Shelf. Sci.* 33: 37-56.

Lee, G. F., Jones, P. E. & Jones, R. A., 1991. Effects of eutrophication on fisheries. *Rev. Aquat. Sci.* 5: 287-305.

Lenanton, R. C. J., 1982. Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Aust. J. Mar. Freshw. Res*. 33: 881-900.

Light, B. R. &. Woelkerling, Wm. J., 1992. Literature and information review of the benthic flora of Port Phillip Bay, Victoria, Australia. Technical Report No. 6, CSIRO Port Phillip Bay Environmental Study, Melbourne, Australia. 112p.

Lim, H. & Hong, J., 1994. Ecology of the macrobenthic community in Chinhae Bay, Korea. *Bull. Korea. Fish. Soc.* 27: 200-214.

Lobban, C. S., Harrison, P. J. & Duncan, M. J., 1985. *The physiological ecology of seaweeds.* Cambridge University Press., Cambridge, London, New York, New Rochelle, Melbourne, Sydney. 242p.

Loo, L-O. & Rosenberg, R., 1989. Bivalve suspension feeding dynamics and benthic-pelagic coupling in an eutrophied marine bay. *J. Exp. Mar. Biol. Ecol.* 130: 253-276.

Lukatelich, R. J. & McComb, A. J., 1986. Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Mar. Ecol. Prog. Ser.* 27:287-297.

Lumb, C. M., 1989. Algal depth distribution as an indicator of long-term turbidity change. In: *Developments in Estuarine and Coastal Techniques.* Olsen and Olsen, Fredensborg, Denmark. pp. 69-74.

Lüning, K., 1990. *Seaweed. Their environment, biogeography and ecophysiology.* John Wiley and Sons, New York, Chichester, Brisbane, Toronto, Singapore, 527p.

Lyngby, J. E., 1990. Monitoring of nutrient availability and limitation using the marine macroalga *Ceramium rubrum* (Huds.) C. Ag. *Aquat. Bot.* 38: 153-161.

Mann, K. H., Chapman, A. R. O. & Gagné, J., 1982. Seasonal patterns of carbon assimilation and utilisation by kelps. In: *Synthetic and degradative processes in marine macrophytes.* Walter de Gryther & Co., Berlin, New York. pp. 23-28.

Masini, R. J., 1987. Preliminary Studies on the Productivity of Benthic Microalgae in the Swan River Estuary. In: *Swan River estuary, Ecology and Management.* edited by J. John, Curtin University Environmental Studies Group Report No 1., Curtin University, Western Australia. pp. 91-101.

Masini, R. J., 1990. The ecological significance of benthic microalgae in Western Australian aquatic ecosystems. Ph.D. Thesis. University of Western Australia, Perth, Western Australia. 195p.

McComb, A. J. & Humphries, R., 1992. Loss of nutrients from catchments and their ecological impacts in the Peel-Harvey estuarine system, Western Australia. *Estuaries.* 15: 529-537.

McGlathery, K. J., 1992. Physiological controls on the distribution of the macroalga *Spyridea hypnoides*: patterns along a eutrophication gradient in Bermuda. *Mar. Ecol. Prog. Ser.* 87: 173-182.

MMBW & FWD., 1973. Environmental Study of Port Phillip Bay - Report on Phase One 1968-1971. Melbourne and Metropolitan Board of Works & Fisheries and Wildlife Department, Melbourne, Victoria.

Moncreiff, C. A., Sullivan, M. J. & Daehnick A. E., 1992. Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora and phytoplankton. *Mar. Ecol. Prog. Ser.* 87: 161-171.

Moriarty, D. J. W. & Boon, P. I., 1989. Interactions of seagrasses with sediment and water. In: *Biology of Seagrasses.* Edited by A.W.D. Larkum, A.J. McComb & S.A. Shepherd, Elsevier. Amsterdam, Oxford, New York and Tokyo, pp. 500-535.

Mukai, H. & Koike, I., 1984. Behaviour and respiration of the burrowing shrimps *Upogebia major* (de Haan) and *Callianassa japonica* Stimpson. *J. Crust. Biol.* 4: 191-200.

Murphy, R. C. & Kremer, J. N., 1992. Benthic community metabolism and the role of deposit-feeding callianassid shrimp. *J. Mar. Res.* 50: 321-340.

Neckles, H. A., Wetzel, R. L., Orth, R. J., 1993. Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia.* 93: 285-295.

Neckles, H. A., Koepfler, E. T., Haas, L. W., Wetzel, R. L. & Orth, R. J., 1994. Dynamics of epiphytic photoautotrophs and heterotrophs in *Zostera marina* (eelgrass) microcosms: Responses to nutrient enrichment and grazing. *Estuaries.* 17: 597-605.

Neverauskas, V. P., 1987. Accumulation of periphyton biomass on artificial substrates deployed near a sewage outfall in South Australia. *Est. Coastal. Shelf. Sci.* 25: 509-517.

Neverauskas, V. P., 1988. Response of a *Posidonia* community to prolonged reduction in light. *Aquat. Bot.* 31: 361-366.

Nicholson, G. J., 1992. The present state of knowledge on fish stocks and commercial and recreational fisheries in Port Phillip Bay, Victoria, and their interactions with

nutrients and toxicants. Technical Report No 7. CSIRO Port Phillip Bay Environmental Study. Melbourne, Australia. 50p.

Nienhuis, P. H., 1983. Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary of the Netherlands, dominated by human activities. *Mar. Tech. Soc. J.* 17: 69-77.

Nienhuis, P. H., 1992. Eutrophication, water management and the functioning of Dutch estuaries and coastal lagoons. *Estuaries.* 15: 538-548.

Nilsson, H. C. & Rosenberg, R., 1994. Hypoxic response of two marine benthic communities. *Mar. Ecol. Prog. Ser.* 115: 209-217.

Nixon, S. W., Oviatt, C. A., Frithsen, J. & Sullivan, B., 1986. Nutrients and the productivity of estuaries and coastal marine ecosystem. *J. Limnol. Soc. Sth. Afr.* 12: 43-71 .

Osinga, R., Lewis, W. E., Wopereis, J. L. M., Vriezen, C. & Van Duyl, F. C., 1995. Effects of the sea urchin *Echinocardium cordatum* on oxygen uptake and sulphate reduction in experimental benthic systems under increasing organic loading. *Ophelia.* 41: 221-236.

Oviatt, C. A., Keller, A. A., Sampou, P. A. & Beatty, L. L., 1986. Patterns of production during eutrophication a mesocosm experiment. *Mar. Ecol. Prog. Ser.* 28: 69 -80.

Oviatt, C. A., Doering, P. H., Nowicki, B. L. & Zoppini, A., 1993. Net system production in coastal waters as a function of eutrophication, seasonality and benthic macrofaunal abundance. *Estuaries.* 16: 247-254.

Page, H. M., Dugan, J. E., Huddard, D. M. & Sündback, K., 1992. Comparative effects of infaunal bivalves on an epibenthic microalgal community. *J. Exp. Mar. Biol. Ecol.* 157:247-262.

Pearson, T. H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16: 229-311.

Pearson, T. H. & Stanley, S. O., 1979. Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. *Mar. Biol.* 53: 371-379.

Peckol, P., DeMeo-Anderson, B., Rivers, J., Valiela, I. M. M. & Yates J. 1994. Growth, nutrient uptake capabilities and tissue constituents of the macroalgae *Cladophora vagabunda* and *Gracilaria tikvahiae* related to site-specific nitrogen loading rates. *Mar. Biol.* 121: 175-185.

Pedersen, M. F., 1995. Nitrogen limitation of photosynthesis and growth: comparison across aquatic plant communities in a Danish Estuary (Roskilde Fjord). *Ophelia.* 41: 261-272.

Pedersen, M. F. & Borum, J., 1993. An annual nitrogen budget for a seagrass *Zostera marina* population. *Mar. Ecol. Prog. Ser.* 101: 169-177.

Phillipart, C. J. M. & Dijkema, K. S., 1995. Wax and wane of *Zostera noltii* Hornem. in the Dutch Wadden Sea. *Aquat. Bot.* 49: 255-268.

Pihl, L., 1992. Effects of oxygen depletion on demersal fish in coastal areas of the south-east Kattegat. In: *Reproduction, Genetics and Distributions of Marine Organisms.* Edited by J.S. Ryland and P. A. Thayer., Olsen and Olsen, Denmark. pp. 431-440.

Piriou, J-Y. & Ménesguen, A., 1992. Environmental factors controlling the Ulva sp., bloom in Brittany, France. In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I. Ferrari, V.U. Ceccherelli, & R. Rossi. Olsen and Olsen, Fredensborg, Denmark. pp. 111-116.

Plante, R., Planta-Cuny, M-R. & Reys, J-P., 1986. Photosynthesis pigment of sandy sediments on the north Mediterranean coast: their spatial distribution and its effect on sampling strategies. *Mar. Ecol. Prog. Ser.* 34:133-141.

Pollard, D. A., 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. *Aquat. Bot.* 18: 3-42.

Poore, G. C. B., 1992. Soft-bottom macrobenthos of Port Phillip Bay: a literature review. Technical Report No 2. CSIRO Port Phillip Bay Environmental Study. Melbourne, Australia. 24p.

Poore, G. C. B. & Kudenov, J. D., 1976, The benthic environment and fauna around a Werribee sewage-treatment farm drain. Project Report No. P 501/Environmental Studies Series No. 118, Marine Pollution Studies Group, Fisheries and Wildlife Division, Ministry for Conservation, Victoria.

Poore, G.C.B. & Kudenov, J. D. 1978a. Benthos around an outfall of the Werribee sewage-treatment farm, Port Phillip Bay, Victoria. *Aust. J. Mar. Freshw. Res.* 29: 157-167.

Poore, G. C. B. & Kudenov, J. D., 1978b. Benthos of the Port of Melbourne: the Yarra River and Hobsons Bay, Victoria. *Aust. J. Mar. Freshwater Res.* 29: 141-155.

Poore, G. C. P. & Rainer, S., 1974. Distribution and abundance of soft-bottom molluscs in Port Phillip Bay, Victoria, Australia. *Aust. J. Mar. Freshw. Res.* 25: 371-411.

Poore, G. C. B. & Rainer, S., 1979. A three-year study of benthos of muddy environments in Port Phillip Bay, Victoria. *Est. Coast. Mar. Sci.* 9: 477-497.

Posey, M. H., 1987. Influence of relative mobility's on the composition of benthic communities. *Mar Ecol. Prog. Ser.* 39: 99-104.

Posey, M. H., Rumbauld, B. R. & Armstrong, D. A., 1991. Effects of a burrowing mud shrimp *Upogebia pugetensis* (Dana), on abundances of macro-infauna. *J. Exp. Mar. Biol. Ecol.* 148: 283-294.

Posey, M., Powell, C., Cahoon, L. & Lindquist, D., 1995. Top down vs. bottom up control of benthic community composition on an intertidal flat. *J. Exp. Mar. Biol. Ecol.* 185: 19-31.

Powell, G. V. N., Kenworthy, J. & Fourqurean, J. W., 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. Mar. Sci.* 44: 324 -340.

Prins, T. C., Escaravage, V., Smaal, A. C. & Peeters, J. C. H., 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. *Ophelia.* 41: 289-315.

Rasmussen, M. B., Henricksen, K. & Jensen, A., 1983. Possible causes of temporal fluctuation in primary production of the microphytobenthos in the Danish Wadden Sea. *Mar. Biol.* 73: 109-114.

Reay, W. G., Gallagher, D. L., Simmons, G. M., 1995. Sediment-water column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. *Mar. Ecol. Prog. Ser.* 118: 215-227.

Reynoldson, T. F., 1987. Interactions between sediment contaminant and benthic organisms. *Hydrobiologia.* 149: 53-66.

Rhoads, D. C. & Boyer, L. F., 1982. The effects of marine benthos on physical properties of sediments. In: *Animal-Sediment Relations: the Biogenic Alteration of Sediments.* edited by P. L. McCall & M. J. S. Tevesz., Plenum, New York., pp. 3-52.

Rhoads, D. C. & Young, D. K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* 28: 150-178.

Reise, K., 1994. Changing life under the tides of the Wadden Sea during the 20th Century. *Ophelia Suppl.* 6: 117-125.

Rivers, J. S. & Peckol, P., 1995. Interactive effects of nitrogen and dissolved inorganic carbon on photosynthesis, growth, and ammonium uptake of the macroalgae *Cladophora vagabunda* and *Gracilaria tikvahiae*. *Mar. Biol.* 121 4 747-753.

Rosenberg, R., Arntz, W. E., De Flores, E. C., Flores, *L.* A., Carbajal, G., Finger, I. & Tarazona, J., 1983. Benthos, biomass and oxygen deficiency in the upwellimg system off Peru. *J. Mar. Res.* 41: 263-279.

Russo, G. F., Fresi, E., Vinci, D. & Chessa, L. A., 1984. Mollusk syntaxon of foliar stratum along a depth gradient in a *Posidonia oceanica* (L.) Delile meadow: Seasonal variability. *Int. Workshop. Posidonia Oceanica Beds.* 1: 311-318.

Sabbe, K., 1993. Short-term fluctuations in benthic diatom numbers on an intertidal sandflat in the Westerschelde estuary (Zeeland, The Netherlands). *Hydrobiologia.* 269/270: 275-284.

Sand-Jensen, K., 1977. Effects of epiphytes on eelgrass photosynthesis. *Ophelia.* 14: 185-201.

Sarda, R., Foreman, K. & Valiela, I., 1992. Controls of benthic invertebrate populations and production of salt marsh tidal creeks: experimental enrichment and short- and long-term effects. In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I. Ferrari, V. U. Ceccherelli, & Rossi, R., Olsen and Olsen, Fredensborg, Denmark. pp. 85-92.

Sayama, M. & Kurihara, Y., 1983. Relationship between burrowing activity of the polychaetous annelid, *Neanthes japonica* (Izuka) and nitrification - denitrification processes in the sediment. *J. Exp. Mar. Biol. Ecol.* 72: 233-241.

Schaffner, L. C., Jonsson, P., Diaz, R. J., Rosenberg, R. & Gapcynski, P., 1992. Benthic communities and bioturbation history of estuarine and coastal systems: effects of hypoxia and anoxia. In: *Marine Coastal Eutrophication.* edited by Vollenweider, R. A., Marchetti, R. & Viviani, R., Elsevier, Amsterdam, London, New York, Tokyo. pp. 1001-1016.

Schramm, W., Abele, D. & Breuer, G., 1988. Nitrogen and phosphorus nutrition and productivity of two community forming seaweeds (*Fucus vesciculosus*, *Phycodrys rubens*) from the Western Baltic (Kiel Bight) in the light of eutrophication processes. *Kiel. Meeres. Sond.* 6: 221-240.

Sfriso, A., Pavoni, B., Marcomini, A. & Orio, A. A., 1992. Macroalgae, nutrient cycles and pollutants in the lagoon of Venice. *Estuaries.* 15: 517-528.

Shaffer, G. P., 1988. K-system analysis for determining the factors influencing benthic microfloral productivity in a Louisiana estuary, USA. *Mar. Ecol. Prog. Ser.* 43: 43-54.

Shaffer, G. P. & Sullivan, M. J., 1988. Water column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *J. Phycol.* 24:132-140.

Short, F. T., 1983a. The response of interstitial ammonium in eelgrass (*Zostera marina* L) beds to environmental perturbation. *J. Exp. Mar. Biol. Ecol.* 68:195-208.

Short, F. T. 1983b. The seagrass *Zostera marina* L: Plant morphology and Bed structure in relation to sediment ammonia in Izembek Lagoon, Alaska. *Aquat. Bot.* 16:149-161.

Short, F. T., 1987. Effect of sediment nutrient on seagrasses: literature review and mesocosm experiment. *Aquat. Bot.* 27:41-57.

Silberstein, K., Chiffings, A. W. & McComb, A. J., 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on productivity on *Posidonia australis* Hook. f. *Aquat. Bot.* 24: 355-371.

Sloth, N. P., Blackburn, H., Hansen, L. S., Risgaard-Petersen, N. & Lomstein, B. A., 1995. Nitrogen cycling in sediments with different organic loading. *Mar. Ecol. Prog. Ser.* 116: 163-170.

Stachowitsch, M., 1992. Benthic communities: eutrophication's "memory mode". In: *Marine Coastal Eutrophication.* edited by Vollenweider, R. A., Marchetti, R. & Viviani, R., Elsevier, Amsterdam, London, New York, Tokyo. pp. 1017-1028.

Sullivan, B. K., Doering, P. H., Oviatt, C. A., Keller, A. A., Frithsen, J. B., 1991. Interactions with the benthos alter pelagic food web structure in coastal waters. *Can. J. Fish. Aquat. Sci.* 48: 2276-2284.

Sündback, K. & Graneli, W., 1988. Influence of microphytobenthos on the nutrient flux between sediment and water: a laboratory study. *Mar. Ecol. Prog. Ser.* 43: 63-69.

Sündback, K. & Jonsson, B., 1988. Microphytobenthic productivity and biomass in sublittoral sediments of a stratified bay, southeastern Kattegat. *J. Exp. Mar. Biol. Ecol.* 122:63-81.

Sündback, K., Enoksson, V., Graneli, W. & Pettersson, K., 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. *Mar. Ecol. Prog. Ser.* 74: 263-279.

Sündback, K. & Snoijs, P., 1991. Effects of nutrient enrichment on microalgal community composition in a coastal shallow sediment system: An experimental study. *Bot. Mar.* 34: 341-358.

Tamai, K., 1993. Tolerance of *Theora fragilis* (Bivalvia: Semelidae) to low concentrations of dissolved oxygen. *Nippon Suisan Gakkaishi.* 59: 615-620.

Tamai, K., 1994. Tolerance of *Theora fragilis* (Bivalvia: Semelidae) to Sulfide. *Benthos Research.* 46: 41-48.

Tomasko, D. A. & Lapointe, B. E., 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Mar. Ecol. Prog. Ser.* 75: 9-17.

Ueda, N., Tsutsumi, H., Yamada, M., Takeuchi, R. & Kido, K., 1994. Recovery of the marine bottom environment of a Japanese bay. *Mar. Poll. Bull.* 28: 676-682.

Valiela, I., Foreman, K., LaMontagne M., Hersh, D., Costa, J., Peckol, P., DeMeo-Anderson, B., D'Avazano, C., Babione, M., Sham, C-H., Brawley, J. & Lajtha, K., 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries.* 15: 443-457.

Van Lent, F., Verschuure, J. M. & Van Veghel, M. L. J., 1995. Comparative study of populations of *Zostera marina* L. (eelgrass): in situ nitrogen enrichment and light manipulation. *J. Exp. Mar. Biol. Ecol.* 185: 55-76.

Viaroli, P., Pugnetti, A. & Ferrari, I., 1992. *Ulva rigida* growth and decomposition processes and related effects on nitrogen and phosphorus cycles in a coastal lagoon (Sacca di Goro, Po River Delta). In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I. Ferrari, V. U. Ceccherelli, & R. Rossi., Olsen and Olsen, Fredensborg, Denmark. pp. 77-84.

Walker, D. I. & McComb, A. J., 1992. Seagrass degradation in Australian coastal waters. *Mar. Poll. Bull.* 25: 191-195.

Walker, D. I., Paling, E. I., Sim, C., Pennifold, M., Manning, C. & Kirkman, H., 1994. Relationship between nitrogen and primary production. Perth Coastal Waters Study. Project E3.1. Water Authority of Western Australia. Perth. Western Australia. 224p.

Warwick, R. M., 1993. Environmental impact studies on marine communities: Pragmatical considerations. *Aust. J. Ecol.* 18: 63-80.

Weston, D.P., 1990. Quantitative examination of macrobenthic community changes along an organic enrichment gradient. *Mar. Ecol. Prog. Ser.* 61: 233-244.

Wetzel, R. L. & Neckles, H. A., 1986. A model of *Zostera marina* L. photosynthesis and growth: simulated effects of selected physical-chemical variables and biological interactions. *Aquat. Bot.* 26: 307-323.

Widbom, B. & Frithsen, J. B., 1995. Structuring factors in a marine soft bottom community during eutrophication - an experiment with radio-labelled phytodetritus. *Oecologia.* 101: 156-168.

Wilson, R. S., Cohen, B., Poore, G. C. B., 1993. The role of suspension-feeding and deposit-feeding benthic macroinvertebrates in nutrient cycling in Port Phillip Bay. Technical Report No 10, CSIRO Port Phillip Bay Environmental Study. 41p.

Wiltshire, K. H., 1992. The influence of microphytobenthos on oxygen and nutrient fluxes between eulittoral sediments and associated water phases in the Elbe Estuary. In: *Marine Eutrophication and Population Dynamics.* edited by G. Colombo, I., Ferrari, V. U. Ceccherelli, & R. Rossi., Olsen and Olsen, Fredensborg, Denmark. pp. 63-70.

Zimmerman, R. C., Smith, R. D. & Alberte, R. S., 1987. Is growth of eelgrass nitrogen limited? A numerical simulation of the effects of light and nitrogen on the growth dynamics of *Zostera marina*. *Mar. Ecol. Prog. Ser.* 41: 167-176.

7. TABLES

Table 1: Synopsis of information on changes in seagrass communities in relation to changes in water or sediment quality.

Reference	Focus of Study	Location	Space/Time scales	Parameters Measured / Reported	Conclusions
Den Hartog and Polderman (1975).	Changes in seagrass populations in the Dutch Wadden Sea.	Dutch Wadden Sea, Netherlands. 53°N.	From 1869 to present.	Documented seagrass change and decline in Wadden Sea but did not quantify amount of change or water/sediment quality parameters.	(i) Considerable change occurred in *Z. marina* before 'wasting disease' of the 1930's. (ii) After 1965, a decline of *Z. marina* and *Z. noltii* occurred to present which was considered to be a consequence of pollution.
Harlin (1975).	Review paper of epiphyte - seagrass interactions.	No specific location.	No specific spatial or temporal scales.	(i) No empirical data presented.	(i) Epiphytes have the advantage of better light fields than their seagrass host. (ii) Epiphytes may receive nitrogen and phosphorus from their seagrass host but not carbon.
Larkum (1976).	Growth of *Posidonia australis* in Botany Bay and other bays.	Botany Bay, New South Wales. 35°S.	6 quadrats sampled from 5 sites.	(i) Water depth and degree of wave exposure. (ii) Seagrass leaf length, width, areal cover and shoot density. (iii) No empirical data on water or sediment quality parameters reported.	(i) Seagrasses were restricted to 3m water depth. (ii) Recolonisation from seeds was low. (iii) Evidence of losses due to dredging and pollution. (iv) Suggested seagrass loss may become autocatalytic due to increased water turbidity and scouring.
Sand-Jensen (1977).	Effects of epiphytes on seagrass photosynthesis.	Vellerup Vig, Denmark. 55°N.	2 treatments - clean leaves, fouled leaves.	(i) Irradiance and carbonate levels. (ii) Observed PI curves for cleaned and fouled leaves across a range of irradiance and carbonate combinations. (iii) Epiphyte biomass not quantified.	(i) At optimal light levels and ambient carbonate levels, epiphytes reduced seagrass photosynthesis by 31%.
Bulthuis and Woelkerling (1981).	Effect of nitrogen and phosphorus enrichment on *Heterozostera tasmanica.*	Western Port Bay, Victoria. 38°S.	1 site 7 month study period. Enrichment rates: Nitrogen = 100 g m^{-2}. Phosphorus = 20 g m^{-2}.	(i) Water column and interstitial NH_4 and PO_4. (ii) Seagrass biomass, tissue nitrogen and phosphorus, growth rates.	(i) Nitrogen enrichment caused an increase in nitrogen concentration in the rhizomes and leaves, and a 20% increase in growth. (ii) Phosphorus enrichment caused an increase in phosphorus concentration in the rhizomes, but no change in the leaves and no change in growth rate. (iii)Neither nitrogen or phosphorus caused an increase in shoot density or biomass. (iv) A 5 to 100 x increase in nitrogen had little or no effect on growth in the first year of enrichment.
Harlin and Thorne-Miller (1981).	Effects of nutrient enrichment on seagrass beds.	Rhode Island Coastal Lagoon. 41°N.	3 experimental sites. 3 nutrient treatments: NH_4, NO_3, PO_4.	(i) Water column NH_4, NO_3, and PO_4. (ii) Seagrass shoot density and biomass (iii) Macroalgal biomass.	(i) Ammonium enrichment stimulated growth of *Ulva* and *Enteromorpha.* (ii) The growth of Z. *marina* was also stimulated, particularly at higher water current flow rates. (ii) The growth of *Ruppia maritima* was inversely related to the growth of the green algae. (iii) Phosphate additions stimulated growth of *Zostera* and *Ruppia* but not of the green algae.
Bulthuis (1983).	Effects of light reduction on *Heterozostera tasmanica.*	Western Port Bay, Victoria. 38°S.	(i) 3 experiments carried out over 15 month period. (ii) 5 light levels: 2, 9, 25, 35 and 100% of ambient.	(i) Review of depth limits, attenuation coefficient and % PAR at lower depth limit of *H. tasmanica*. (ii) Seagrass leaf cluster density, leaf density (biomass per unit area of leaf), leaf growth rate.	(i) At 2% irradiance, all leaf clusters died within 2 months in summer and within 4 months in winter (60% decline at 2 months in winter). (ii) At 9% irradiance there was a 25-35% decline in seagrass after 2 months. (iii) At 25 and 35% irradiance there was no declined and no differences between these treatments. There was also an interaction with fouling by drift weed but the seagrass didn't seem to be directly affected by shading by this weed. (iv) The lower depth limit was 3.8 to 9.8 m (2.3-7.0% of surface irradiance) and this limit was

					very clearly demarcated. (v) Seagrasses require about 5% of surface irradiance for survival. At 20°C, 127 µE m^{-2} s^{-1} is limiting for *H. tasmanica*
Bulthuis and Woelkerling (1983a).	Seasonal growth patterns of *Heterozostera tasmanica*.	Western Port and Port Phillip Bay, Victoria. 38°S.	(i) 15 month study period. (ii) 4 sites, mean depth range 0.6 - 3.6m	(i) Irradiance, water column NH_4, NO_3, NO_2, PO_4, Total P, SiO_4, salinity and temperature. (ii)Above-ground biomass, shoot density, leaf growth rate and production.	(i) Maximum and minimum seagrass biomass occurred in summer and winter respectively, at three sites. (ii) At the site receiving the lowest irradiance, biomass, shoot density and annual production were lowest.
Bulthuis and Woelkerling (1983b).	Shading effects of epiphytes on *Heterozostera tasmanica*.	Western Port Bay and Port Phillip Bay, Victoria. 38°S.	10 month study period. 4 sites, mean depth range 0.6 - 3.6m	(i) Epiphyte biomass on seagrass leaves. (ii) Relationship between epiphyte biomass and light attenuation.	(i) Epiphyte biomass increased with the age of the leaves. (ii) Light attenuation increased linearly with epiphyte biomass. (iii) Epiphytes can accumulate fast enough to cause shading of seagrass leaves.
Nienhuis (1983).	Temporal and spatial pattern of *Zostera marina* distribution.	Lake Grevelingen, SW Netherlands. 52°N.	Study period from 1969 to 1981.	(i) Water column NO_3, NH_4, PO_4, % chlorinity and secchi depth. (ii) *Zostera marina* distribution from 1968 to 1981 (presented as areal cover on maps). (iii) *Chaetomorpha* distribution from 1973 to 1981 (presented as areal cover on maps). (iv) Empirical data on seagrass density, biomass or production not presented.	(i) A rapid decline in seagrass occurred from 1978 to 1980 (about 50%) following closure to the sea. (ii) The rapid decline in seagrass was considered to be related to an increase in the deposition of organic matter following an increase in nutrient loading, leading to rapid deoxygenation and toxicity of the sediments.
Short (1983a).	Relationship between seagrass disturbance and sediment ammonium concentrations.	Izembek Lagoon, Alaska. 55°N.	4 year period. 4 perturbation treatments i.e. ice scour; introduced substrates; seagrass leaf removal; seagrass removal + sealing the sediment surface.	(i) Sediment NH_4 profiles. (ii) Shoot density and biomass.	(i) Removal of seagrass and sealing the sediment surface resulted in a rapid increase in sediment NH_4. Thus, the inverse relationship between shoot density and NH_4 was related to rapid depletion through uptake by seagrasses. (ii) Nitrogen limitation was observed in some meadows.
Short (1983b).	Relationship between seagrass morphology and sediment NH_4.	Izembek Lagoon, Alaska. 55°N.	16 stations sampled over a two year period.	(i) Seagrass leaf area, length and width, rhizome length, shoot and flower density plotted as a function of sediment ammonium.	(i) Seagrass leaf area, length and width and rhizome length displayed strong positive logarithmic relationship with interstitial NH_4, whereas shoot and flower density displayed strong inverse relationships with interstitial NH_4.
Cambridge and McComb (1984).	Time course of seagrass loss in Cockburn Sound.	Cockburn Sound, Western Australia. 32°S.	Bay wide survey of seagrass loss from Cockburn Sound since 1950's.	(i) Seagrass biomass and production from a variety of sites in Cockburn and Warnbro Sounds.	(i) Areal extent of seagrass diminished from 4200 to 900 ha from 1954 to 1978. (ii) Detrital production declined from 23 000 to 4000 tonnes dry weight per year. (iii) Seagrass loss was related to development of heavy industry along the coast.
Cambridge *et al.*, (1986).	Causes of seagrass decline in Cockburn Sound.	Cockburn Sound, Western Australia. 32°S.	(i) Physical parameters measured over 16 month period. (ii) Transplant	(i) Irradiance, temperature, chlorophyll, salinity. (ii) Leaf area of transplanted seedlings over time.	(i) Transplanted seedlings: in Cockburn Sound were covered by epiphytes e.g. *Ectocarpus*, *Ulva*, *Enteromorpha* and *Polysiphonia*, after 2 to 3 weeks. (ii) Start of seagrass losses coincided with start of nutrient enrichment by heavy industry. (iii) Heavy epiphyte growth in response to nutrient enrichment was considered to be the

			experiment carried out at two sites over 48 days.	(iii) Light attenuation data with depth for four sites and within and outside of exclusion cages.	cause of wide-spread losses of seagrass. (iv) Light attenuation coefficients were: Open Ocean = 0.07 ± 0.01; Warnbro Sound = 0.1 ± 0.01; Cockburn Sound = 0.13 ± 0.1.
Silberstein *et al.*, (1986).	Effects of epiphytes on *Posidonia australis*.	Cockburn Sound, Western Australia. 32°S.	2 sites: one near sewage outfall (Woodman Pt) one further from affected sites (Carnac Is).	(i) Water column Chlorophyll *a*, PO_4, NO_3+NO_2, NH_4, N:P ratios. (ii) Seagrass biomass, production (per day and per year). (iii) Epiphyte chlorophyll *a* and light attenuation by epiphytes.	Results of this study support contention that epiphytes are responsible for seagrass loss in shallow waters of Cockburn Sound.
Wetzel and Neckles (1986).	Simulated effects of irradiance and temperature on *Zostera marina* photosynthesis.	Chesapeake Bay, USA 38°N.	Modelling approach. Simulations carried out over annual cycles.	(i) Simulated effects of irradiance, light attenuation, photoperiod, temperature and water depth and grazing on seagrass photosynthesis.	(i) Small changes in photosynthetically active radiation (PAR) or temperature result in decreased plant productivity and eventual loss of the seagrass community. (ii) Empirical and hypothetical relationships indicate that *Z. marina* growth and long-term survival in Chesapeake Bay, are potentially governed by factors that control or limit the attached epiphyte community e.g. epiphyte grazing and ambient light levels.
Neverauskas (1987).	Sewage sludge effects on seagrasses.	Gulf St Vincent, South Australia. 34°S.	7 locations, 2 sites at each location. 3 year study period.	(i) Seagrass biomass, leaf density, epiphyte biomass. (ii) No empirical environmental data presented.	(i) Discharge of sewage sludge caused decline of seagrass over a 1900 ha area. (ii) This study showed that there was no ongoing decline. (iii) Epiphytes on leaves are implicated as the cause of seagrass decline.
Short (1987).	Effects of sediment nutrients on *Zostera marina* in terrigenous and carbonate sediments.	Mesocosm study: Great Bay Estuary, New Hampshire, USA. 43°N.	4 month study.	(i) Irradiance, salinity, temperature, interstitial NH_4. (ii) Shoot density, biomass, height, width, leaf loss rate, leaf carbon, nitrogen and phosphorus concentrations.	(i) Nitrogen is generally considered to be limiting for primary production in terrigenous sediments whereas phosphorus is considered limiting in carbonate sediments. (ii) Significantly lower seagrass growth occurred in nitrogen poor sediments which supported the hypothesis of nitrogen limitation in these sediments.
Zimmerman *et al.*, (1987).	Modelling simulations of nitrogen limitation in *Zostera marina*.	No specific location.	No specific spatial or temporal scales.	(i) Nitrogen uptake vs irradiance, uptake vs external nitrogen concentrations. (ii) Constants used in model were derived from a review of the literature. (iii) No empirical data presented.	(i) The model is robust for steady state predictions. (ii) Seagrass roots appeared more important than leaves for N-uptake and accounted for > 50% uptake at high light regimes. (iii) Leaves appeared more important for N-uptake in low light regimes. (iv) NH_4 was more important source than NO_3/NO_2. (v) N concentration required to saturate growth is 50% less than concentrations reported *in situ*. Therefore N limitation of *Z. marina* growth, based on these observations, is considered to be rare.
Neverauskas (1988).	Effects of light reduction on *Posidonia* spp.	Spencer Gulf, South Australia. 34°S.	1 yr study, 3 month sampling intervals. 50% light reduction regime.	(i) Leaf density, shoot density, shoot biomass. (ii) Epiphyte biomass. (iii) No empirical data on nutrients or water turbidity resulting from sludge dumping.	Effects of shading: (i) Seagrass biomass declined by 20% after 6mo, 90% after 9 months, 95% after 12 months. (ii) Seagrass leaf density declined by 12% after 3 months, 29 % after 6mo, 77% after 9 months, 88% after 12 months. (iii) Seagrass shoot density declined by 0% decline after 6 months, 66% after 9 months, 83% after 12 months. (iv) Epiphyte biomass declined by 20% after 3 months, 30% after 6 months, 85% after 9 months, > 96% after 12 months. (v) Rate of seagrass and epiphyte decline followed similar path over the same time-frame. (vi) Seagrass shoot density remained the same in first 6 mo despite loss of seagrass leaves indicating that leaf loss was evenly distributed among the shoots.

Moriarty and Boon (1989).	Review of nutrient cycles in seagrass meadows.	Particular emphasis on Australian meadows.	No specific spatial or temporal scales.	(i) No empirical data presented.	(i) NH_4 pools in seagrass meadows may be larger or smaller than in adjacent unvegetated sediments depending on the rate of NH_4 generation from de-amination of amino-acids, relative to the demand by the seagrass and diffusion from the sediments. (ii) NH_4 flux is likely to be important in the nutrition of seagrasses and associated epiphytes. (iii) NO_3/NO_2 pools are low in seagrass sediments, either related to rapid denitrification to N_2 gas, or ammonification to NH_4. (iv) Seagrasses promote nitrification and therefore denitrification by aerating the sediments through discharge of oxygen and organic compounds from the roots.
Powell *et al*., (1989).	Nutrient limitation of seagrasses.	Florida Bay, USA 25°N.	4 yr study.	(i) Time course for nitrogen and phosphorus uptake and sediment nutrient profiles. (ii) Seagrass biomass, leaf length and areal production, tissue nitrogen and phosphorus concentrations and acetylene reduction at enriched and control sites.	(i) At enriched sites NH_4 conc was low at sediment surface and increased rapidly with depth to a depth of 20cm, whereas for phosphorus there was a high concentration at the sediment surface which declined with increasing sediment depth. Therefore there was a rapid uptake and demand for mineralised nitrogen at these sites. (ii) Nitrogen enrichment caused an increase in leaf production and biomass of *Thalassia testudinum* and *Halodule wrightii*. (iii) Above-ground biomass was 2x higher at enriched site than at control site. (iv) Production of *T. testudinum* was 60% higher and of *H. wrightii* was 3 orders of magnitude higher than at the control site. (v) Phosphorus was considered to be generally limiting on a bay-wide scale i.e. is limiting at the control sites, but nitrogen was limiting where sediments were enriched with bird faeces. (vi) There was also evidence that nitrogen and phosphorus synergystically increased seagrass production and growth.
Giesen *et al*., (1990).	Turbidity effects on *Zostera marina*.	Dutch Wadden Sea, Netherlands. 53°N.	Review of changes in *Z. marina* communities since the 1930's.	(i) Secchi depth and light attenuation coefficients. (ii) Seagrass depth distributions in the Dutch Wadden Sea. (iii) No empirical data on seagrass density, biomass, production or of nutrient concentrations presented.	(i) Losses of seagrasses considered to be related to changes in water turbidity. (ii) Increasing turbidity can be linked to eutrophication and dredging activities.
Larkum and West (1990).	Long-term loss of seagrass from Botany Bay.	Botany Bay, New South Wales. 35°S.	From 1930 to 1990.	(i) Total areal extent of seagrasses (ha) between 1930-1990 and of *P. australis* and Z. *capricomi* area between 1950-1990. (ii) Loss of seagrass biomass after a storm event in 1977 and 1978. (iii) No empirical water or sediment quality data.	(i) From 1942 to 1984: 58% (257 ha) seagrass lost from southern shore. (ii) Losses were considered to be related to industry, urban development and dredging. (iii) Dredging increased wave height, erosion of beds, and an increase in erosion during storm events e.g. *Posidonia* leaf biomass declined by 70% due to storms. (iv) From 1980-1986: Grazing by *Heliocidaris erythryogramma* was responsible for localised losses. (v) From 1930-1987*: Z. capricomi* has exhibited cyclic fluctuations and has colonised areas previously vegetated by *P. australis*.
Duarte (1991).	Depth limits of seagrasses: a modelling approach and review of the literature.	No specific location.	No specific spatial or temporal scales.	(i) Seagrass colonisation depths for 30 spp of seagrass. (ii) Colonisation depth with light attenuation coefficient and calculated regression equations. (iii) Biomass attenuation with light attenuation coefficients.	(i) Regression equation developed for seagrass depth limits: log Zc = 0.26 - 1.07 log K (m^{-1}) where Zc is depth in metres and K is light attenuation coefficient. (ii) Decline in seagrass biomass from the depth of maximum biomass to depth limit is closely related to light attenuation coefficient. (iii) Deep species such as *Halophila* have small rhizomes and therefore lower respiratory demands than species with large rhizomes. (iv) Seagrasses require 5 - 11% of surface irradiance at their lower depth limit.
Hemming *et al.*,	Review paper of nutrient	No specific location.	No specific spatial or	(i) Nitrogen fixation rates within	(i) Sources of nutrients:

(1991).	gains and losses from seagrass meadows.		temporal scales.	various seagrass meadows. (ii) NH_4 and NO_3 uptake rates of *Zostera marina*.	External from coastal zone and atmosphere, sedimentation and uptake by leaves, nitrogen fixation and internal recycling. (ii) Sources of losses: export of leaves and leaf fragments, leaching, nutrient transfer to foraging animals, denitrification, or diffusion from sediments to water column. (iii) Seagrasses meadows are open systems, representing both a nutrient source and sink at various times. Imbalances between losses and gains may account for fluctuations in annual seagrass biomass production.

Hillman *et al*., (1991).	Water quality, seagrass biomass and production and epiphyte loads.	Albany, Western Australia. 34°S.	3 sites: Princess Royal Harbour, Oyster Harbour and King George Sound. 2 seagrasses: *Posidonia australis*, *P. sinuosa*. Study carried out over 1 year.	(i) Salinity, temperature, dissolved oxygen, TSS and % organic content of TSS, NH_4, NO_3/NO_2, organic nitrogen, PO_4, organic phosphorus, SiO_4, Chlorophyll *a*. (ii) Seagrass biomass and production. (iii) Epiphyte biomass and production.	(i) Oyster Harbour was more nutrient-enriched than King George Sound and Princess Royal Harbour. (ii) Light was the dominant factor influencing seagrass growth at all three sites. (iii) Macroalgal smothering appeared to be cause of seagrass decline in Princess Royal Harbour, whereas epiphytes on the seagrass leaves appeared to cause decline in Oyster Harbour (epiphytes in this study includes periphyton).
Tomasko and Lapointe (1991).	Nutrient availability and epiphyte effects on *Thalassia testudinum*.	Florida Keys, USA 25°N.	Field study: 9 sites. 2 depths: 0.5 and 2.0 m One sampling time, all sites sampled within 30 day period. Lab study: 2 light levels. 2 nutrient levels	(i) Water column NH_4, NO_3/NO_2, soluble reactive phosphate (SRP), N:P ratio. (ii) Leaf turnover rate and production, plastochrone interval, areal biomass and production, turnover time. (iii) Epiphyte load.	Field Study: Nutrient inputs occur from a bird rookery and by 2000 septic tanks. An increase in nutrients was associated with: (i) An increase in epiphytes (partly related to leaf turnover time). (ii) A decrease in shoot density. (iii) A decrease in leaf area index. (iv) A decrease in biomass. Lab study: an increase in nutrients was associated with: (i) An increase in epiphyte levels. (ii) An increase in blade turnover time (decrease in turnover rate). (iii) A decrease in rhizome growth rate. A decrease in irradiance was associated with (i) A decrease in epiphytes under high nutrient conditions.
Bulthuis *et al*., (1992).	Nitrogen limitation of *H. tasmanica* growth in Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	5 month study at 5 sites. Nitrogen enriched at 100 g N m^{-2} Phosphorus enriched at 20 g P m^{-2}	(i) Water column and sediment DIN and PO_4. (ii) Seagrass biomass, leaf cluster density, canopy height, tissue nutrient concentrations, epiphyte biomass.	(i) Nitrogen is limiting in Port Phillip Bay, particularly in spring and summer. (ii) Nitrogen enrichment caused 50% increase in seagrass biomass, 40% increase in leaf cluster density and 20% increase in canopy height. (iii) Phosphorus enrichment caused an increase in phosphorus concentration in the leaves but no increase in leaf biomass, leaf cluster density or canopy height.
Burkholder *et al*., (1992).	Effect of NO_3 enrichment on *Zostera marina* decline.	North Carolina, USA. 35°N.	Mesocosm based study. 4 nutrient levels, Two 6 week run times:	(i) Temperature, salinity, pH, irradiance, water column NO_3, NH_4, TP, sediment NO_3 and NH_4 profiles. (ii) Seagrass shoot density, tissue	(i) Under low water movement regimes, Z. *marina* declined in all enrichment treatments, with the greatest decline at higher nutrient levels. (ii) Increasing water temperature and macroalgal loads increased the rate of *Z. marina* decline.

			Spring and Autumn.	carbon, nitrogen and phosphorus concentrations. (iii) Macroalgal biomass, (iv) Epiphytic microalgae cell abundance, (v) Amphipod grazer abundance.	(iii) High water NO_3 loads may have a direct physiological effect, thus causing declines which are not related to epiphyte loads.

Kenworthy and Fonseca (1992).	Use of fertiliser to promote growth of *Zostera marina* and *Halodule wrightii* transplants.	North Carolina, USA 35°N.	3 experiments over a 1 year period i.e. autumn, spring and late spring.	(i) Monthly temperature and salinity, (ii) % survival of transplants, increase in number of shoot and biomass. (iii) % of nitrogen or phosphorus release	(i) Nitrogen enrichment resulted in increases in vegetative reproduction, seagrass cover and leaf growth. (ii) There was no effect of nitrogen on overall survival of *Z. marina* or growth and survival of *Halodule wrightii.* (iii) Nitrogen X phosphorus interactions could not be studied due to problems with nitrogen and phosphorus release in the balanced fertiliser formulation.
Light and Woelkerling (1992).	Review of benthic flora in Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	No specific spatial or temporal scales.	No empirical data presented.	(i) The most extensive areas of seagrass occur on the western side of the Bay e.g. Swan Bay, Prince George Bank, Portarlington and southern margin of Corio Bay. 95% occurs in less than 5m of water. (ii) *Heterozostera tasmanica* is the dominant species. *Halophila ovalis* is restricted to small areas fringing *H. tasmanica* or *Caulerpa* beds. *H. ovalis* occurs in deeper waters than *H. tasmanica* and replaces *H. tasmanica* under low light levels.
Walker and McComb (1992).	Review paper on seagrass degradation in Australian waters.	Temperate and tropical Australian waters.	No specific spatial or temporal scales.	(i) Areal extent of losses and suggested causes of decline. (ii) No empirical water or sediment quality data presented.	(i) Measured seagrass losses are over 45 000 ha. (ii) Most losses are attributed to a reduction in light environments as a result of human activity. (iii) Reduction in light attributed to growth of epiphytes and/or deposition of suspended particles.
Valiela *et al*., (1992).	Review paper of sources and consequences of nutrient enrichment of coastal waters.	Waquoit Bay, Massachusetts. 42°N.	Documented changes in Waquoit Bay since the 1940's.	(i) Relationship between housing density and water column DIN. (ii) Describes changes in seagrass, macroalgae and macrofauna as a result of increased water column nutrient concentrations.	(i) Groundwater provides the major source of nutrients in this system. (ii) Nutrient enrichment has had a number of effects on the bay: 1° effects are an increase in phytoplankton and macroalgae. 2° effects are alteration of water column nutrient status, and increase in the frequency of anoxic events and degradation of the eelgrass environment. 3° effects are a change in benthic fauna due to habitat change and anoxic events.
Pedersen and Borum (1993).	Annual nitrogen budget for *Zostera marina*.	København, Denmark. 56°N.	1 year study.	(i) Water column DIN, NH_4 and NO_3, and interstitial NH_4. (ii) Seagrass above and below ground biomass, leaf growth and overall production. (iii) Seagrass tissue nitrogen concentrations, annual nitrogen assimilation, uptake, losses and reclamation.	(i) Maximum seagrass biomass was 700 g DW m^{-2}, Annual Production was 2388 g DW m^{-2} y-1, Nitrogen assimilation was 34.5 g N m^{-2} y^{-1}. (ii) Nitrogen requirements exceeded nitrogen assimilation from June to September (4 months). (iii) External nitrogen sources were low, between May and June, therefore recycling accounted for most nitrogen uptake during this time. (iv) 49% of nitrogen uptake was from water column, 51% from the sediments. (v) Uptake of external nitrogen supplied 73% of requirements, internal recycling supplied 27%. (vi) An increase in nitrogen concentration, stimulated a moderate growth of *Z. marina* but the overall conclusion is that at this location *Z. marina* is not seriously nitrogen limited.
Burkholder *et al*., (1994).	Effects of nitrate enrichment on *Zostera marina*, *Halodule wrightii* and *Ruppia maritima*.	North Carolina, USA. 3°N.	Mesocosm based study. 3 nutrient levels, (ambient, 2.5µM NO_3; low, 5µM NO_3; and moderate, 7.6µM). Two run times: Spring run = 12 wk duration,	(i) Temperature, salinity, irradiance, NO_3, NH_4, Total phosphorus. (ii) Seagrass shoot densities and tissue carbon, nitrogen and phosphorus concentrations. (iii) Macroalgal biomass. (iv) Abundance of amphipods, isopods and polychaetes.	(i) Shoot production was reduced under NO_3 enriched conditions. This was considered to be due to an adverse response by the seagrass to high NO_3 levels rather than due to effects of epiphytes. (ii) Production of *Halodule wrightii* and *R. maritima* was stimulated by NO_3 enrichment.

			Autumn run = 14 wks.		
Duarte (1995).	Review paper of relationships between nutrients and submerged aquatic vegetation.	No specific location.	No specific spatial or temporal scales.	(i) Light absorption efficiency, chlorophyll *a* density, and compensation irradiance, photosynthetic capacity and efficiency, and nutrient uptake efficiency for seagrasses, macroalgae and phytoplankton. (ii) This paper also cites a variety of good references for nutrient loadings on seagrasses.	(i) As nutrient loadings increase and light levels decrease, a shift occurs from slow growing, high C:N:P ratio seagrasses and macroalgae to faster growing macroalgae with moderate C:N:P ratios. (ii) As nutrient levels continue to increase and light levels continue to decrease there shift towards dominance by phytoplankton which have low C:N:P ratios. (iii) Slow growing seagrasses are effective competitors at low nutrient levels because their requirements for nitrogen and phosphorus are low relative to carbon, have access to sediment nutrient pools and are efficient at internal recycling. (iv) Phytoplankton are superior competitors when light is limiting because they are higher in the water column and able to use light efficiently.
Philippart and Dijkema (1995).	Temporal patterns of *Zostera noltii*.	Dutch Wadden Sea, 53°N.	Changes between the 1970's to 1980's at two sites: Terschelling and Groningen.	(i) Areal cover (km^2) of seagrass in 1972/73, and in 1987/88, (ii) % change in areal cover. (iii) No empirical data on water or sediment quality parameters presented.	(i) Percent change in areal cover of seagrasses: At Terschelling sites: Dekeeg: 0.15 to 0.23 km^2, +53%; Hoorn: 1.15 to 0.84 km^2, -27%. At Groningen sites: Linhorst/Homanpolder: 0 to 0.75 km^2, +100%; Emmanpolder 0 to 0.77 km^2, +100%. At a third site: Balgzand: 0.12 to 0.01 km^2, -0.92%. Total from all sites: 1.42 to 2.60 km^2, +83%. (ii) Areal cover of seagrass at the Terschelling sites decreased by 20% overall. (iii) There was a positive correlation with sediment clay content and negative correlation with the lugworm *Arenicola* at this site. (iv) Areal cover of seagrass at the Groningen sites was still expanding and there were no correlations with sediment content or lugworms. (v) Total seagrass cover had doubled between late 1970's and early 1980's, particularly due to establishment in the outer sedimentation fields. (vi) Macroalgae cover was < 1% at all sites (De Keeg/ De Ans = 25% cover due to drift), and there were no significant correlations between macroalgae and seagrass observed. (vii) The lug worm *Arenicola* was found inside and outside seagrass meadows, although *Z. noltii* had a negative correlation with lugworm faecal castings. Lugworms work equivalent of top 3 cm y^{-1} of sediment within seagrass meadows and top 20 cm y^{-1} outside seagrass meadows.
Van Lent *et al.*, (1995).	Light and nutrient manipulations of *Zostera marina*.	Southwestern Netherlands. 51-52°N.	2 sites (water depth = 1.25m). 2 treatments: Light and nitrogen enrichment. Light reduction = 70% of ambient. N enrichment = 190g m^{-2} Experiment run time of 2 months	(i) Irradiance, interstitial NH_4, interstitial NO_3 / NO_2. (ii) Shoot density, above and below-ground biomass.	(i) Light reduction severely reduced all growth parameters, and under these conditions nitrogen uptake could not be used for growth. (ii) In the perennial population: nitrogen enrichment caused an increase in above-ground relative growth rate, occurrence of flowering, and above ground biomass. (iii) Nitrogen limitation has thought to be reason for decline at Grevelingen since 1985.
Fitzpatrick and Kirkman (In press).	Effects of shading on *Posidonia australis* meadows.	Jervis Bay, New South Wales. 35°S.	3 experiments: seagrasses shaded for 91 days, 95 days and 104 days	(i) Light profiles under shaded and non-shaded treatments. (ii) Seagrass shoot density, seagrass biomass and production	(i) Seagrass density, biomass and production were significantly lower under shaded treatments. (ii) Epiphyte biomass was lower under shaded treatments, and community composition changed as fleshy macrophytes declined and encrusting invertebrates became dominant.

			respectively. Monitored for 17 months after removal of shading.	over time.	(iii) Seagrass shoot density declined from about 320 m-2 to 80 m-2 after 100 days of shading, and did not recover to pre-shading levels 17 months after the removal of shading. (iv) Shading in early summer had more severe effects on seagrass shoot density and growth than shading at the end of summer.

Table 2: Synopsis of information on changes in macroalgal communities in relation to changes in water or sediment quality.

Reference	Focus of Study	Location	Space/Time scales	Parameters Measured / Presented	Conclusions
Brown *et al.*, (1980).	Effects of sewage effluent on macroalgae.	Port Phillip Bay, Victoria. 38°S.	2 sites, 12 quadrats at each site. Sampled seasonally.	(i) Water column Total N, NH_4, Total P and PO_4. (ii) Macroalgal biomass, species composition and tissue nutrient concentrations.	(i) Macroalgae were influenced by type of substratum, wave action, water movement and proximity to drains. (ii) During the study, the major environmental influences were seawater temperature and irradiance. (ii) Nearshore, the macrophytes exhibited high tissue nitrogen concentrations, possibly as luxury consumption, whereas offshore the macroalgae were possibly nutrient limited.
Axelrad *et al*., (1981).	Effects of treated sewage discharge on benthic communities.	Port Phillip Bay, Victoria. 38°S.	3 sites, sampled monthly to bi-monthly over a 1 year period.	(i) Water column NH_4 and PO_4 concentrations. (ii) Median, minimum and maximum macroalgal biomass.	(i) Although Werribee provided approximately 50% of the nitrogen and phosphorus discharges into Port Phillip Bay annually, effects were limited to within a few hundred metres of the outfall. (ii) Macroalgae stands near the outfall were characterised by low species diversity, a dominance of opportunistic species, an absence of brown algae which were prevalent elsewhere in the bay, and occasional algal blooms.
Schramm *et al.*, (1988).	Effects of nitrogen and phosphorus addition on the productivity of *Fucus* and *Phycodrys*.	Kiel Bight, Western Balitc Sea. 54°N.	Communities sampled from 8 to 12 m water depth, twice per month. Laboratory batch experiments run for 2 weeks.	(i) Uptake rates and tissue concentrations of nitrogen and phosphorus with increasing levels of these nutrients in the water column. (ii) Macroalgal growth rates.	(i) Nitrogen and phosphorus concentrations were higher in the macroalgal bed than in the overlying surface waters. (ii) Macroalgae in this area were apparently not nutrient limited except for nitrogen limitation of *Phycodrys* in summer. (iii) Input into Kiel Bight : 23 000 tons N and 1500 tons P annually.
Lapointe and O'Connell (1989).	Effects of nutrient enrichment on the growth of *Cladophora prolifera*.	Harrington Sound, Bermuda, USA 32°N.	Experiments carried out over two week period. Pulsed with four nutrient treatments: NO_3 (160 µM), PO_4 (16 µM), NO_3+PO_4 and control (ambient seawater).	(i) Water column and pore-water nutrient concentrations. (ii) Photosynthesis versus irradiance (P v I), growth rate (doublings), tissue nutrient concentrations and alkaline phosphatase activity.	(i) Massed *Cladophora* blooms have been widespread over the past 20 years but no studies have conclusively linked these blooms to nutrient enrichment. (ii) Algal growth was limited by both nitrogen and phosphorus but primarily phosphorus. (iii) Nitrogen and phosphorus enrichment increased growth rates (decreased doubling times), and enhanced light-saturated photosynthetic capacity.
Lyngby (1990).	Nutrient availability and limitation of *Ceramium rubrum*.	Limfjord, Denmark. 57°N.	*Ceramium rubrum* transplanted to 8 sample areas. sampled monthly for 8 months.	(i) DIN and PO_4 of water column and of macroalgal tissue. (ii) Seasonal variation in nitrogen and phosphorus concentrations.	(i) Nitrogen was limiting for *C. rubrum* growth. (ii) *C. rubrum* may serve as a useful tool for monitoring eutrophication as tissues integrate fluctuating nutrient concentrations across sampling intervals.
Light and Woelkerling (1992).	Review of macroalgae in Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	Reviews current knowledge of bay-wide benthic vegetation from historical and recent work.	Presents information on species composition and distribution in the Bay.	(i) Throughout the Bay, there is little hard substrata onto which macroalgae can colonise. Only *Caulerpa* can make use of the unstable sediments. (ii) No macroalgae are found below 15m water depth within the Bay. (iii) Wind, current, sediment transport, substrate suitability and light attenuation with depth are reported as being the main factors influencing benthic macroalgae. (iv) Near the Werribee sewage outfall, ephemeral species dominate and there is an absence of brown algae, which are prevalent on other hard substrata in the Bay.

					(v) The absence of brown algae near the sewage outfall is attributed to reduced light intensity, smothering of plants due to sedimentation of particles, toxicity of some sewage constituents and grazing pressure due to increased abundance of grazers. (vi) Macroalgal biomass is higher in spring through summer and autumn. Blooms of *Cladophora* occur in late spring. *Griffithsia* and *Ceramium* wracks occur on the Werribee foreshore in late autumn. (vii) Higher algal tissue nitrogen concentrations corresponded with higher water column nitrogen concentration. However, annual species were not present in winter despite high water column nitrogen concentrations, indicating temperature and light effects.
McGlathery (1992).	Physiological controls of *Spyridia hypnoides* along a eutrophication gradient.	Baileys Bay, Bermuda. 32°N.	*Spyridia hypnoides* transplanted to sites within the inner (high nutrients) and outer (low nutrients) areas of the bay. 2 week study period.	(i) Water column NO_3/NO_2 concentrations. (ii) Macroalgal tissue nitrogen, protein, chlorophyll *a* and starch content. (iii) P vs I curves at low and high nutrient concentrations. (iv) Empirical data for macroalgal biomass and production not measured.	(i) In the inner harbour, rich in nutrients, physiological controls on algal growth influenced patterns of algal distribution. (ii) In the outer harbour, a low nutrient environment, algae were absent. (iii) The results of transplant procedures suggested that nitrogen demands exceed storage capabilities and possibly explained the absence of algae in the low nutrient environment.
Piriou and Ménesguen (1992).	Study of *Ulva* blooms.	Brittany, France. 49°N.	*Ulva* studied *in situ* using perforated bags. Growth of *Ulva* measured twice per month.	(i) Total nitrogen loadings from 3 years over a four year period. (ii) *Ulva* biomass from 3 years over a four year period. (iii) Oxygen production and water column carbon, nitrogen and phosphorus decline as a result of *Ulva* growth over a 6 hour period.	(i) *Ulva* blooms in areas with low water movement and high residual times. (ii) Large interannual variations occur due to interannual fluctuations in nitrogen loadings of rivers. (iii) Irradiance controls growth by stimulating growth in spring and promoting degradation in summer. (iv) Nitrogen limitation is suggested as nitrogen loadings vary cyclically whereas phosphorus is more stable.
Sfriso *et al*., (1992).	Interactions between nutrients and macroalgae in the Lagoon of Venice.	Northern Adriatic Sea. 45°N.	1 year study period.	(i) Sediment, water nutrient and oxygen concentrations at four sites. (ii) Macroalgal production and biomass. (iii) Contamination by PCB's, copper, and cadmium.	(i) *Ulva rigida* was the dominant macrophyte. (ii) During growth phases, *U. rigida* rapidly depleted dissolved inorganic nitrogen from the water column. (iii) During decomposition, oxygen was rapidly depleted causing a rapid uptake of nitrate and release of phosphate by the sediments. (iv) Thus, fluctuations in macroalgal biomass accounted for seasonal variations in nutrient concentrations.
Viaroli *et al*., (1992).	Growth and decomposition of *Ulva rigida*.	Northern Adriatic Sea. 45°N.	Phytoplankton sampled monthly from November 1987 to October 1989. *Ulva* sampled monthly from March 1989 to July 1990.	(i) Water column oxygen levels with water depth. (ii) Phytoplankton abundance with time. (iii) Water column inorganic nitrogen concentrations with time. (iv) *Ulva* tissue nutrient concentrations. (v) Empirical data of macroalgal biomass changes with time not presented.	(i) *Ulva* blooms suppressed phytoplankton and higher trophic groups shifted from grazing to detritus feeding. (ii) Decomposition of detritus and consumption of organic matter by detritivores resulted in oxygen depletion of the water column and dystrophic crises. (iii) Nitrogen regulated *Ulva* growth.

Fong *et al*., (1993).	Competition for nutrients between macroalgae, benthic microalgae and phytoplankton.	Tijuana Estuary, USA 32°N.	2 factors: nutrients and presence of benthic microalgae. 2 nutrient additions: low (1.2µM N, 0.01 µM P), high (77µM N, 5 µM P). 2 benthic microalgal treatments: present or absent. Experimental run time of 60 days.	(i) Phytoplankton chlorophyll *a* with time (integrated over entire water column). (ii) Biomass of attached macroalgae, floating macroalgae and benthic cyanobacterial mats.	(i) Benthic algae (attached macro- and cyanobacterial mats) were better competitors at high nutrient levels than phytoplankton or free-floating drift algae.
Neckles *et al*., (1993).	Effects of nutrient enrichment and grazing on epiphytes on seagrass.	Chesapeake Bay, USA 37°N.	Series of 1 week to 2 month experiments carried out. 2 nutrient levels: ambient (4 - 10.8 µM DIN, 0.7 - 1.6 µM PO_4 and enriched (10.6 - 37.8 µM, 1.8 - 3.4 µM PO_4).	(i) Irradiance, water temperature, DIN, phosphate. (ii) Abundance of grazers. (iii) Epiphyte biomass, seagrass growth.	(i) There was evidence of interactions between top-down (grazing) and bottom-up (nutrient) controls over epiphyte growth on seagrasses. (ii) The effects of grazers were more conspicuous than those of nutrients. (ii) Seagrass production declined when grazers were absent in late summer but otherwise was not influenced by any of the treatment combinations.
Horne *et al*., (1994).	Growth and consumption of macroalgae in estuaries.	Waquoit Bay, Massachusetts, USA. 42°N.	Four 4 day trials run at weekly intervals.	(i) Macroalgal growth in the presence and absence of grazers at high and low nutrient levels. (ii) Nutrient concentrations not stated.	(i) Seagrasses were replaced by algae as nutrient concentrations increased. (ii) Grazers consumed *Enteromorpha* and *Cladophora* but did not consume *Ulva* or *Gracilaria* to a great extent.
Peckol *et al*., (1994).	Growth, nutrient uptake and tissue nutrient concentrations of *Cladophora vagabunda* and *Gracilaria tikvahiae* in relation to nitrogen loading rates.	Waquoit Bay, USA. 42°N.	Studies carried out included site-specific growth rates (2 week experiment), nutrient uptake dynamics (75 hr experiment), and tissue composition (observations carried out over 1 year period).	(i) Water column NH_4, NO_3, and PO_4. (ii) Tissue chlorophyll *a* and *b* concentrations (iii) Tissue nitrogen and phosphorus concentrations and rates of uptake. (iv) Growth rate (doublings).	(i) *Cladophora vagabunda* and *Gracilaria tikvahiae* have become dominant macrophytes in Waquoit Bay, possibly due to increased nitrogen loading. (ii) These species are strongly influenced by and in turn strongly influence the nitrogen concentrations in the bay. (iii) These species remove a great deal of nitrogen from the water column and may be responsible for low summer water column nutrient concentrations. (iv) Enrichment experiments revealed that nitrogen limits macroalgal growth in summer, phosphorus in autumn.
Walker *et al*., (1994).	Relationships between nitrogen and epiphyte growth.	Marmion Lagoon, Western Australia. 31°S.	Two factors: nutrients and temperature. Two Nutrient additions: NH_4 and NO_3 added separately. Four temperatures. Experimental run times ranging from 35	(i) Water column NH_4 and NO_3 with time. (ii) Macroalgal (epiphyte) biomass and production with time.	(i) Over the range of nutrient additions provided, nitrogen did not stimulate macroalgal growth. (ii) Macroalgae were capable of taking in both forms of nitrogen and showed a preference for NH_4 only in experiments carried out in the dark. (iii) Temperature did not appear to have a major influence over macroalgal biomass or growth rates. (iv) Control of nutrient treatments was not successful and results are possibly influenced by artifacts.

			to 60 days.		
Pedersen (1995).	Nitrogen limitation of photosynthesis and growth of phytoplankton, ephemeral macroalgae, perennial macroalgae and seagrass.	Roskilde Fjord, Denmark. 56°N.	Nutrient treatments included controls (no addition), Nitrogen addition (20µM N), Phosphorus addition (8µM P). Incubations carried out over four days.	(i) Tissue concentrations of nitrogen, phosphorus and chlorophyll *a*. (ii) Algal growth rate.	(i) Unicellular and thin multicellular algae are more nutrient limited than large, perennial macroalgae. (ii) Growth rates of ephemeral algae and phytoplankton were stimulated by nitrogen but not phosphorus additions whereas perennial algae and seagrass were not stimulated by nutrient additions. (iii) The findings support the hypothesis that eutrophication results in a shift from large perennial macroalgae to small ephemeral algae and phytoplankton.
Rivers and Peckol (1995).	Interactive effects of nitrogen and dissolved inorganic carbon on *Cladophora vagabunda* and *Gracilaria tikvahiae*.	Cape Cod, Massachusetts, USA. 42°N.	Studies carried out include photosynthesis vs irradiance measures, growth experiments, NH_4 uptake experiments and tissue concentrations.	(i) Water column CO_2 concentrations above the algal mat over a 24 hour period. (ii) PvI curves. (iii) NH_4 uptake rate under ambient and enriched nutrient conditions.	(i) Dissolved inorganic carbon (DIC) is rarely considered limiting. However, in a high nitrogen environment, an increase in DIC can stimulate macroalgal photosynthesis. (ii) In summer DIC limits photosynthetic capacity of the algae due to an excess of nitrogen and low CO_2 tension in the water column.

Table 3: Synopsis of information on changes in benthic microalgal communities in relation to changes in water or sediment quality.

Reference	Focus of Study	Location	Space/Time scales	Parameters Measured / Presented	Conclusions
Axelrad *et al*., (1981).	Effects of treated sewage on benthic biota.	Port Phillip Bay, Victoria. 38°S.	2 sites sampled every six weeks over a 1 year period.	(i) Minimum and maximum annual salinity, NH_4, NO_3/NO_2, PO_4. (ii) Minimum and maximum microalgal biomass and production. (iii) Mean monthly nutrient or microalgal biomass data not provided.	(i) Production of benthic microalgae was 5 times higher near the sewage outfall than at the control site.
Hopkinson and Wetzel (1982).	Nutrient and oxygen fluxes in a benthic community.	Georgia Bight, USA 31°N.	1 site. *In situ* measurements of oxygen and nitrogen fluxes made using 4 acrylic enclosures.	(i) % C, NH_4, PO_4, NO_3/NO_2 concentration profiles in the sediment. (ii) Flux of oxygen, NH_4, NO_2, NO_3, DON, PO_4, DOP. (iii) Time course of NH_4 flux from the sediments.	(i) NH_4, NO_2, NO3 and PO_4 was released to the overlying water from the sediment. (ii) Oxygen uptake was equivalent to 1.1 g C m^{-2} d^{-1}. (iii) Benthos remineralised 55% of net primary production and 25% of total community metabolism. (iv) External sources of organic matter were required to balance carbon budget of inshore sites. (v) The benthos supplied 16% nitrogen and 53% phosphorus required by phytoplankton. (vi) Pore-water nutrient concentrations were indicative of a high level of denitrification i.e. 4.9 mg N m^{-2} d^{-1} by mass balance. The water column had low N:P ratios (1:1). (vi) This study supports the hypothesis that shallow marine sediments control the nitrogen and phosphorus available for water column production.
Davis and MacIntire (1983).	Effect of physical gradients on the production of benthic microalgae.	Netarts bay, Oregon, USA. 45°N.	3 sampling sites, on sand, fine sand and silt sediment-types. 50m transects at 4 depths, at each site. Sampled monthly between March 1980 and March 1981.	(i) Monthly sediment chlorophyll *a*, biomass and production. (ii) Primary production vs irradiance. (iii) No water quality data presented.	(i) Annual net primary production rates of 38 g m^{-2} in sand, 53 g m^{-2} in fine-sand and 21 g m^{-2} in silt were recorded. (ii) Complex non-linear relationship exists between sediment-type, tidal height, and season and their effects on benthic microalgae. (iii) These effects are more complex than has previously been reported.
Rasmussen *et al.*, (1983).	Factors affecting production of benthic microalgae.	Skallingen, Danish Wadden Sea. 55°N.	Primary production measured *in situ* at hourly intervals over 5 hr periods. Laboratory incubations of 2 hr durations.	(i) Microalgal production vs temperature and irradiance. (ii) No water or sediment quality parameters measured.	(i) Temperature shows an almost linear relationship with benthic microalgal abundance.
Colijn and de Jonge (1984).	Primary production of benthic microalgae.	Ems-Dollard Estuary, Netherlands.	Six stations sampled monthly between 1976 to 1978.	(i) Monthly water temperature and irradiance. (ii) Monthly biomass and production. (iii) No water or sediment quality data measured.	(i) Tidal influence had the highest correlation with benthic microalgal primary production. (ii) Temperature and irradiance did not correlated with production or assimilation.

Borum (1985).	Microalgal epiphyte communities on seagrass along a nutrient gradient.	Roskilde Fjord, Denmark. 56°N.	4 study sites chosen within the fjord, inner sites representing high nutrients, decreasing towards outer sites. Samples collected monthly over a one-year period.	(i) Total P, PO_4, Total N, NH_4, NO_3/NO_2 sampled monthly. (ii) Epiphyte and periphyton chlorophyll *a* sampled monthly.	(i) At nutrient poor sites a bimodal peak in periphyton chlorophyll *a* occurred in autumn and spring. In Summer, abundance was low due to high host seagrass leaf turn-over. (ii) In spring, phytoplankton were not stimulated by higher nutrient levels. (iii) In summer, both benthic and planktonic microalgae were stimulated by nutrients. (iv) Phytoplankton exhibited a 5-10x increase in abundance, whereas microalgal epiphytes experienced a 50-100x increase in relation to nutrient concentrations. (v) Therefore the effects of nutrients were most reflected in the abundance of benthic microalgae.
Graneli and Sundbäck (1985).	Response of planktonic and benthic microalgae to nutrient enrichment.	Oresund, Southwestern Sweden. 56°N.	Two field and two lab experiments were carried out. Water and sediment collected from two sites, representing enriched and non-enriched environments. 4 nutrient treatments : control, nitrogen, phosphorus and nitrogen + phosphorus addition.	(i) Chlorophyll *a* of phytoplankton and benthic microalgae in experimental treatments. (iii) Schematic models of nutrient budgets.	(i) An increase in nutrients increased the biomass of phytoplankton and benthic microalgae. (ii) At nitrogen rich sites, an increase in phosphorus stimulated phytoplankton production (nitrogen was not limiting in these areas). (iii) In treatments without sediment, phytoplankton accounted for uptake of inorganic nitrogen from the water column. (iv) In treatments with a sediment, benthic microalgae accounted for 20% uptake of inorganic nitrogen, with the other 80% being lost from the system through denitrification. (v) By producing oxygen, benthic microalgae keep sediments aerated and promoted phosphorus transport to overlying water.
Lukatelich and McComb (1986).	Distribution and abundance of benthic microalgae in a shallow estuary.	Peel-Harvey Estuary, Western Australia. 32°S.	4 sites sampled at fortnightly intervals over 16 month period, supplemented by two intensive surveys carried out at 36 sites on two occasions.	(i) Chlorophyll *a* with sediment depth at four sample stations, for three sample times. (ii) Chlorophyll *a* distribution in the estuary. (iii) Correlations between chlorophyll *a* and physico-chemical parameters. (iv) Chlorophyll *a* with Total Nitrogen, Total Phosphorus and % organic matter. (v) Chlorophyll *a* concentrations compared with other systems.	(i) Most chlorophyll was observed in the top 1 cm of sediment. (ii) Less than 10% of the chlorophyll was non-functional. (iii) There was greater biomass at shallow sites and in coarse sediments. (iv) Except during *Nodularia* blooms, the chlorophyll concentration of the sediments was 40 times that of the overlying water column. (v) In summer, resuspension of benthic microalgae accounted for much of the water column chlorophyll *a*. (vi) The role of benthic microalgae in overall primary production was emphasised.
Masini (1987).	Productivity of benthic microalgae.	Swan River Estuary, Western Australia. 32°S.	5 sites in lower Swan River.	(i) Light attenuation and chlorophyll *a* concentration profiles in the sediment. (ii) Comparisons between biomass and production with other community components provided.	(i) Biomass of benthic microalgae was greater than that in the overlying water column. (ii) Estimated production of benthic microalgae was greater than that estimated for seagrass meadows over a similar area.
Fielding *et al.*, (1988).	Biomass and production of benthic diatoms.	Langebaan Lagoon, South Africa. 33°S.	10 stations, representing high-,	(i) Diatom biomass in each zone at each site.	(i) The highest biomass of benthic microalgae occurred in sheltered areas. (ii) High biomass was recorded at 20-30 cm deep in the sediments.

			mid-, and low-shore intertidal and subtidal habitats, sampled on one occasion.	(ii) No water or sediment quality data measured.	(iii) Deep depths of benthic microalgae in the sediments was related to the activities of macrofauna in turning over the sediment. (iv) Benthic microalgal production rivalled that of phytoplankton and accounted for approximately 22% of total lagoon primary production.
Shaffer (1988).	Factors influencing benthic microalgal production.	Barataria estuary, Louisiana, USA. 29°N.	3000 laboratory incubations carried out over 30 day period.	(i) P v I curves for benthic microalgae. (ii) Daily gross primary production at sandy and muddy sites. (iii) Relative abundance of microalgal species at three sites- a muddy site, sandy site and sandy site experiencing aerial exposure. (iv) Wave energy, Chlorophyll *a*, irradiance, temperature, tidal height and salinity, initial dissolved oxygen. (v) Benthic microalgal production, biological activity, respiration.	(i) Production at the muddy site (27 g C m^{-2}) was twice that of the sandy site (14 g C m^{-2}), but greatest production occurred at the sandy site experiencing aerial exposure. (ii) Environmental factors, such as tidal height, light, wave height, meteorological events, interacted to regulate production.
Shaffer and Sullivan (1988).	Contribution of benthic microalgae to water column production through resuspension.	Mugu Lagoon, California. 34°N.	2 sites. Productivity and biomass measurements made every 2 days over a period of 3 to 4 weeks.	(i) Production of oceanic water and of Mugu lagoon water. (ii) Diel comparisons of production. (iii) Plots of production, light intensity, water temperature, tidal height. (iv) Nutrients not measured.	(i) Benthic diatoms increased water column production by several orders of magnitude. (ii) Benthic pennate diatoms accounted for 74% of the diatom taxa in the water column.
Sundbäck and Jonsson (1988).	Biomass and production of benthic microalgae.	Laholm Bay, Sweden. 56°N.	3 year study.	(i) Chlorophyll *a* and phaeophytin with depth. (ii) Production with depth and time of year. (iii) Water quality parameters were not presented in this paper.	(i) Production was regulated by an interaction of light, nutrients, sediment-type and water flow conditions. (ii) Production was limited by light at a depth of 5m, but this relationship was not linear, with some of the greatest production occurring at 15m. (iii) Primary production was highest from May to September i.e. summer, where production ranged from < 1 to 20 g C m^{-2} year. Settled phytoplankton accounted for some of this production. (iv) Bay-wide estimates of benthic microalgal production were 5-10 g m^{-2} y^{-1}, which was only 5-10% of bay-wide phytoplankton production. (v) In early stages of eutrophication, benthic microalgae benefit from increased nutrients, and in turn have a positive effect by increasing oxygen conditions and reducing the release of inorganic N and P from the sediments. As eutrophication progresses, turbidity impacts on benthic microalgae and the system progresses towards a phytoplankton dominated system.
Delgado (1989).	Abundance and distribution of benthic microalgae.	Ebro Delta, Spain. 43°N.	4 sites sampled for examination of spatial distribution. 1 site sampled monthly for 1 year to examine temporal patterns.	(i) Depth profiles of benthic microalgal distribution. (ii) Diatom abundance with time. (iii) No environmental data measured.	(i) Spatial heterogeneity between 10 cm to 10m scale was not significant. (ii) Resuspension and burial had major impacts on the benthic microalgae.

Masini (1990).	Benthic microalgae in Western Australian aquatic ecosystems.	Western Australia.	Range of marine and estuarine habitats sampled from the North-West Cape to the Blackwood Estuary, Western Australia.	(i) Sediment Total Nitrogen, NH_4, NO_3, PO_4 and Total Phosphorus. (ii) Sediment Chlorophyll *a*.	(i) Biomass and production was less important in deeper waters, due to lower light levels, than in shallow marine bays and estuaries. (ii) Between systems, benthic microalgal distribution was related to nutrient levels, but within systems, distribution was related to light availability. Benthic microalgal biomass was lower in more turbid waters an in sediments with a higher silt content.

Sundbäck and Snoejs (1991).	Effects of nutrient enrichment on benthic microalgae.	NE Skagerrak, Sweden. 58°N.	Mesocosm study. 2 nutrient treatments: enriched (85 µM DIN, 2.5 µM DIP) and ambient. Sediments collected from 0.2m water depth, incubated in 0.18m water depth.	(i) Abundance and biomass of diatoms, flagellates and cyanobacteria which comprise the benthic microalgae. (ii) Table of relative abundances of benthic microalgal taxa and nutrient loadings.	(i) An increase in nutrients caused an increase in filamentous cyanobacteria, diatoms and flagellates but did not cause a shift in dominance by the major taxa. (ii) Diatoms accounted for over 50% of the microalgal biomass and were not out-competed by any other group. (iii) Nitrogen + phosphorus addition favoured the production of larger diatom cells. (iv) Nutrient addition did not alter successional stages in the diatom community but increased the rate at which succession occurred.
Cahoon and Cooke (1992).	Production of benthic microalgae.	Onslow Bay, North Carolina, USA. 34°N.	*In situ* study from 1984 to 1989.	(i) Light attenuation and temperature regimes. (ii) Net respiration, net and gross production for each site. (iii) Dissolved oxygen plotted against net production. (iv) Light attenuation plotted with gross benthic production. (v) No nutrient data presented.	(i) Benthic microalgal production averaged 24.9 mg m^{-2} h^{-1} compared with integrated phytoplankton production of 27.4 mg C m^{-2} h^{-1}. (ii) Benthic biomass (chlorophyll *a*) always exceeded integrated phytoplankton production (average values = 18.1 and 8.2 mg m^{-2} respectively).
Daehnick *et al.*, (1992).	Primary production of benthic microalgae in seagrass beds	Mississippi Sound, USA. 30°N.	Monthly sampling carried out between June 1989 to June 1990.	(i) Monthly benthic microalgal biomass (chlorophyll *a*), and production. (ii) No water or sediment nutrient concentrations measured.	(i) Sand microflora contributed 8 - 42% of system primary production. (ii) Benthic microalgae were dominated year round by small, araphid, monoraphid and biraphid pennate diatoms. (iii) Water temperature and *H. wrightii* leaf density are the best predictors of chlorophyll *a* concentration (r^2 = 0.38). (iv) Temperature, tidal range, and light are best predictors of hourly production (r^2 = 0.72).
Light and Woelkerling (1992).	Review of benthic flora of Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	Review of knowledge at bay-wide scale.	(i) No empirical data presented.	(i) Few studies on benthic microalgae have been carried out in Port Phillip Bay. (ii) Production figures of benthic microalgae are high compared with other marine areas and are potentially very important in Port Phillip Bay.
Moncreiff *et al.*, (1992).	Contribution of seagrass, epiphytic algae, benthic microalgae and phytoplankton to primary production in a seagrass ecosystem.	Mississippi Sound, USA. 30°N.	Sampled monthly between June 1989 and June 1990.	(i) Average hourly production of epiphytes, seagrass, benthic microalgae and phytoplankton throughout study period. (ii) No nutrient data measured.	(i) Only 15% of the variation of hourly benthic microalgal production could be related back to a single environmental variable (e.g. light). (ii) Variations were best explained by irradiance, water temperature, tidal range and seagrass leaf density. (iii) Annual production of individual community components was: epiphytes = 905 g C m^{-2} y^{-1}, phytoplankton = 468, benthic microalgae = 339, and seagrass (*Halodule wrightii*) = 256. (iv) Diatoms were important elements of the epiphyte, benthic microalgal and phytoplankton communities.
Cahoon *et al.*, (1993).	Production of benthic microalgae.	Stellwagen bank, Massachusetts Bay, USA. 42°N.	3 sites sampled daily over 1 week period.	(i) Values of biomass and production for benthic microalgae. (ii) No water quality data presented.	(i) Benthic microalgal biomass, which averaged 39.8 mg m^{-2}, was higher than that of phytoplankton in the overlying water column, which averaged 25.9 mg m^{-2}. (ii) Irradiance never exceeded 1% surface PAR and was sometimes as low as 4.7 µE m^{-2} s^{-1} (water depth = 21-28 m). Thus, benthic microalgae have the potential to be important primary producers at very low ambient light levels.

Sabbe (1993).	Short-term fluctuations of benthic diatoms on a sand-flat.	Westerschelde Estuary, Netherlands. 51°N.	Sampled every 2 to 3 days over 2 month period.	(i) Temperature, wind speed, irradiance and organic content of sediments. (ii) Microalgal abundance. (iii) No other water or sediment quality parameters measured.	(i) Short-term fluctuations of epipelic diatoms were related to fluctuations in sky irradiance and % organic matter of the sediments.
Beardall and Light (1994).	Review of biomass, production and nutrient requirements of benthic microalgae.	Targeted towards Port Phillip Bay, therefore covers temperate coastal waters.	No specific spatial or temporal scales.	(i) Presents benthic microalgal abundance and production in appendices.	(i) Benthic microalgal biomass and production are influenced by temperature, light, depth, sediment-type, and nutrient availability. (ii) Large variations occur over small spatial scales. (iii) Few studies demonstrate a clear seasonality of benthic microalgae abundance. (iv) Generally benthic microalgal abundance is correlated with nutrients, although a decrease in benthic microalgae with increasing nitrogen loading has been reported.
Coleman and Burkholder (1994).	Nutrient enrichment of seagrass epiphytic microalgae.	Mesocosm facility, Pivers Island, USA. 35°N.	3 nutrient treatments: ambient (< 1 µM NO3), low (< 3.5 µM NO3), medium (< 7 µM NO3). Mesocosms sampled after 3 and 6 weeks.	(i) Cell abundance, and biovolume for each nutrient treatment after 3 and 6 weeks. (ii) Productivity of the community and of particular components of the community after 3 and 6 weeks.	(i) After 3 weeks: moderate nutrient enrichment increased the production of benthic microalgae, mostly of blue-green algae. (ii) After 6 weeks: both low and moderate nutrient enrichment enhanced algal growth mostly of small algae such as the diatom *Nitszchia closterium*. (iii) The data indicate a controlling influence of nutrients on community structure and species dominance among epiphytic microalgal.
Neckles *et al.*, (1994).	Response to nutrient enrichment and grazing of epiphytic auto- and heterotrophs.	Chesapeake Bay, USA. 38°N.	2 treatments: nutrients and grazers. 2 nutrient regimes: ambient (4 µM DIN, 0.8 µM PO_4), and enriched (10.8 µM DIN, 1.8 µM PO_4). 2 Grazer regimes: absent and present (300 isopods and 600 amphipods m^{-2}).	(i) Abundance of diatoms, cyanobacteria, heterotrophic flagellates and heterotrophic bacteria.	(i) Diatoms declined in abundance due to grazers but did not respond to nutrients. (ii) Cyanobacteria increased as a result of nutrient enrichment but were not affected by grazers. (iii) Although diatoms dominated all treatments, grazers influenced at community shift from diatoms towards cyanobacteria, particularly under nutrient enriched conditions.
Coleman and Burkholder (1995).	Response of epiphytic microalgae to nutrient enrichment.	Beaufort, North Carolina, USA. 35°N.	2 nutrient levels: low (ambient) and enriched (6 µM NO_3). Sites were sampled 6 days and 30 days after enrichment.	(i) Cell biovolume and abundance of different components of the epiphytic community.	(i) Nitrate enrichment stimulated the adnate monoraphid diatom *Cocconeis placentula* but inhibited dinoflagellates and the diatom *Melosira*. (ii) Total community production remained comparable between the two nutrient treatments, but community shifts, from dominance by the crustose red alga *Sahlingia subintegra* and dinoflagellates, towards dominance by *Cocconeis placentula*, indicated a regulating influence of nutrients.

Table 4: Synopsis of information on changes in macrofaunal communities in relation to changes in water or sediment quality.

Reference	Focus of Study	Location	Space/Time scales	Parameters Measured / Presented	Conclusions
Poore and Rainer (1974).	Distribution and abundance of soft-bottom molluscs.	Port Phillip Bay, Victoria. 38°S.	Sampled along a regular grid of 86 stations, approx 5 km apart. Fauna collected only once from each site, all stations sampled irregularly over 3.25 years.	(i) Sediment and water quality characteristics for 8 regions identified in the Bay. (ii) Presence/absence of species, divided into feeding-types, in the 8 regions. (iii) Abundance and biomass of feeding-types and of major species, represented as circle plots, at each sampling station in the Bay.	(i) Six molluscan feeding-types were identified: epifaunal and infaunal suspension-feeders, surface deposit-feeders, grazers, predators, scavengers. (ii) Infaunal suspension-feeders dominated marginal sandy habitats. (iii) Surface deposit-feeders dominated the central silt and clay sediments. (iv) Other feeding groups were less abundant and seldom dominant. (v) Main determinants of distribution were sediment type and food supply.
Poore and Kudenov (1976).	Study of benthic environment and fauna around Werribee sewage treatment plant.	Port Phillip Bay, Victoria. 38°S.	7 transects radiating from outfall, 5 sites on each transect. Samples taken at distances ranging from 10's to 100's of metres. All stations sampled once between 18-28 November, 1975.	(i) Relationship between water column and pore-water PO_4 and NO_3. (ii) Sampling stations divided into 5 zones. Reports mean salinity, PO_4, NO_3 and NO_2, NH_4, for each zone. (iii) Has abundances of fauna, divided into feeding-types, and of species which are of special interest (represented as circle plots). (iv) Also reviews effects of sewage on benthic communities.	Review of effects of sewage: (i) Growth of *Ulva* and *Enteromorpha* and phytoplankton blooms were associated with sewage discharge. (ii) A reduction in fauna occurs in relation to sewage discharge, with an abiotic zone around outfalls which may range from 100's of metres to several kilometres. (iii) Anoxia of sediments was generally the main cause of shift from macrofauna, meiofauna, microfauna and microfloral dominated system to a bacterial dominated system which rapidly consumes oxygen and are resistant to low oxygen tensions. (iv) Effects of Werribee treatment plant are less severe than those recorded elsewhere in the literature for sewage effluents. (v) An increase of deposit-feeding polychaetes and amphipods was characteristic of moderately polluted systems. (vi) P:B ratios increase in more polluted areas. Conclusions of this study: (i) Sediments were more sandy, and had a higher proportion of carbonate further from the outfall. (ii) Nutrient concentrations decreased rapidly with distance from the outfall. (iii) Fauna was rich and contained several euryhaline and opportunistic species. (iv) Suspension-feeders were 4x more abundant than deposit-feeders across all sample stations. Bivalve molluscs dominated the suspension-feeders and polychaete worms dominated the deposit-feeders. (iv) Fish used the area as nursery area where they consumed isopods, amphipods and polychaetes. (v) The P:B ratio of 2 for the macrofaunal community indicated a 'healthy' system.

Pearson and Rosenberg (1978).	Macrofaunal community succession in relation to eutrophication.	No specific location.	No specific spatial or temporal scales.	No empirical data presented.	(i) Organic enrichment of the sediments causes physical and chemical changes in the environment with resultant impacts on the fauna. (ii) An increase in organic matter in the sediments increases benthic respiration which in poorly flushed sites can lead to anoxia and mass mortality of the fauna. (iii) Within the immediate vicinity of sewage outfalls, the sediments are devoid of fauna. With increasing distance from the outfall there is an increase in faunal abundance, biomass and species diversity dominated by small, deposit-feeding 'enrichment' opportunists e.g. capitellid polychaete worms. (iv) Faunal abundance and biomass increase to a transition zone, the 'ecotone' point, where species diversity is highest representing an overlap of communities typical of polluted and non-polluted sites. On the polluted side of the ecotone point the community consists of few pollution-tolerant opportunistic species. On the non-polluted side of the ecotone point, species diversity declines to a relatively stable level and becomes dominated by large, long-lived species.
Poore and Kudenov (1978a).	The benthic environment around Werribee treatment plant.	Port Phillip Bay, Victoria. 38°S.	This study was based on sampling carried out for Poore and Kudenov (1976).	Same environmental parameters as given in Poore and Kudenov (1976), but no macrofaunal abundances presented.	(i) Common macrofaunal species were correlated with depth, sediment properties and interstitial phosphorus concentrations. (ii) At the outfall stations there were high faunal abundances, primarily scavengers and deposit feeders.
Poore and Kudenov (1978b).	The benthos of the Port of Melbourne.	Hobson's Bay and the Yarra River, Port Phillip Bay, Victoria. 38°S.	7 stations in the Yarra River and 4 in Hobson's Bay. Single samples taken at each station at 6 weekly intervals over a one year period.	(i) Temperature, salinity. (ii) Macrofaunal abundance, species richness, diversity and evenness. (iii) Population size and growth rates of *Theora fragilis*.	(i) *Theora* fragilis dominated muddy sediments and were more abundant in the lower reaches of the Yarra River and in Hobson's Bay. (ii) The Yarra River benthos exhibited characteristics of a stressed community with high abundances of opportunistic species e.g. the polychaete *Polydora*, and low species richness, diversity and evenness.
Poore and Rainer (1979).	Study of benthos in muddy habitats.	Port Phillip Bay, Victoria. 38°S.	3 sample sites: Corio Bay, Central basin and Martha Pt. Sampled quarterly for three years (1973-1975).	(i) Depth, sediment characteristics, Total nitrogen and Total phosphorus. (ii) Community statistics: abundance, richness, evenness and diversity. (iii) Abundances of dominant species at each station.	(i) Differences between stations and between years accounted for most of the statistical variation in abundances and species richness. (ii) The deposit feeding bivalve *Theora fragilis* and the crustacean *Callianassa limosa* dominated the fauna at each sampling site. (iii) Macrofaunal abundance varied seasonally but species composition was more irregular. (iv) Differences in community composition were related to differences in sediment-type but not to physico-chemical factors.
Beukema and Cadée (1986).	Responses of macrofauna to eutrophication.	Dutch Wadden Sea, Netherlands. 53-54°N.	15 year study (1969-1984). Annual sampling of 12 transects, each 1km long.	(i) Macrofaunal biomass, production, annual recruitment of bivalves. (ii) Does not present any data on sediment or water quality parameters.	(i) Biomass and production increased over the 15 year time period. (ii) Over half of the species present contributed to this increase. (iii) Reproductive success and growth rate of the bivalve *Macoma balthica* increased during this period. (iv) A causal relationship between simultaneous increases in nutrients, primary production and secondary production, although appeared likely, could not be proved. (v) In the well mixed Dutch Wadden Sea, detrimental events associated with eutrophication, such as hypoxia, were rare.

Friligos (1989).	Nutrient and oxygen conditions in an anoxic bay.	Elefsis Bay, Mediterranean, 38°N.	4 year study: from 1973-1976.	(i) O_2 concentration with time, (ii) PO_4, SiO_4, NO_2, NO_3, NH_4 in the water column over time. (iii) Ratio of total nutrients with background (ambient) nutrient levels. (iv) Biological interactions are not covered in this study.	(i) Elefsis Bay is most industrialised in Greece. (ii) Nutrient loads were higher and oxygen levels lower than other bays in the Aegean Sea. (iii) Nutrient and oxygen loads were related to eutrophication which was influenced by human activities.
Loo and Rosenberg (1989).	Eutrophication effects on bivalve feeding and benthic-pelagic coupling.	Laholm Bay, southwest Sweden. 56-57°N.	2 sites, 5-8m water depth 16 random samples at each site, samples taken at 5 occasions between 1985-86.	(i) Abundance, biomass and size-class structure of the benthic suspension-feeders *Cardium edule* and *Mya arenaria*. (ii) Environmental data not presented.	(i) Water depth is 10-20 m with a strong halocline at 15m. Water salinity above the halocline is 12-25‰, below the halocline is 32-34 ‰. (ii) Below the halocline - eutrophication induced hypoxia occurred on muddy bottoms in late summer to early autumn. (iii) Bivalves filtered the equivalent of all of the water to 5 m depth every three days (which was half of their estimated feeding capacity). (iii) The majority of phytoplankton were exported from the bay and not consumed by suspension-feeders in the bay.
Forbes and Lopez (1990).	Effects of food concentration, body size and oxygen tension on *Capitella* spp.	Long Island, USA 41°N.	3 experiments to test interactive effects of body volume, food concentration and oxygen levels on volume-specific growth rate.	(i) Oxygen tensions. (ii) *Capitella* growth rates.	(i) Growth of Capitella decreased in response to low oxygen and low food concentration. (ii) Small worms responded only to low oxygen concentrations. (iii) Under conditions of near hypoxia or food limitation, it is predicted that *Capitella* will experience size-dependent growth limitation with large worms declining more rapidly than small ones.
Grant and Thorpe (1991)	Effects of water turbidity on the soft-shelled bivalve *Mya arenaria*.	Nova Scotia, Canada. 45°N.	2 treatments: control and sediment-added. Short-term and long-term experimental run times (90 minutes and 35 days respectively).	(i) O_2 consumption and NH_4 excretion with time. (ii) O_2 consumption with sediment concentration.	(i) An increase in turbidity caused an decrease in ventilation rate and oxygen consumption and an increase in NH_4 excretion. (ii) Bivalves exposed to high turbidity utilised their reserves to meet nutritional requirements whereas control clams grew by 43%. (iii) Clams were tolerant to short-term levels of high turbidity but starved under conditions of long-term turbidity.
Bogdanos and Satsmadjis (1992).	Factors controlling benthic communities.	Messolonghi Lagoons, 38°N.	16 sampling stations distributed over lagoon e.g. 10 km x 30 km. Sampled seasonally between Dec 1983 to March 1984.	(i) Depth, sediment and nutrient characteristics, temperature and salinity for each sample site. (ii) Abundance and species richness for each sample site.	(i) In deeper areas, a halocline caused hypoxia and turbidity. In these areas the bivalves *Abra ovata* and *Mytilaster minimus*, and the polychaetes *Polydora ciliata* and *Nereis caudata* dominated. (ii) In shallower, well oxygenated areas, grazing amphipods dominated. (iii) At polluted sites the amphipods *Corophium volutator* and *Gammarus olivii* and the polychaete *Ficopomatus enigmatica* dominated.
Dauer *et al*., (1992).	Effects of low oxygen events on macrobenthos.	Chesapeake Bay 37-38°N.	Samples collected from range of habitats including: tidal freshwater, oligohaline-lower mesohaline, mesohaline and polyhaline.	(i) Salinity, temperature, oxygen, sediment physical and chemical characteristics. (ii) Macrofaunal community data were not presented.	Hypoxic events (defined at < 2mg O_2 l^{-1}), caused: (i) A decline in species diversity, biomass, and the proportion of deep-dwelling species. (ii) An increased dominance of opportunistic species e.g. euryhaline annelids. (iii) A decrease in dominance of long-lived molluscs and maldanid polychaetes. (iv) Hypoxic events were primarily restricted to upper reaches of Chesapeake Bay, at primarily freshwater or estuarine sites.

Desprez *et al.*, (1992).	Effects of eutrophication and anoxia on benthic macrofauna.	Bay of Somme, France. 50°N.	Single sampling station sampled seasonally from 1981 to 1991.	(i) Temperature, Somme River flow rates and NO_3 flux, (ii) Abundance of the polychaete *Pygospio elegans* and the bivalve *Cerastoderma edule*. (iii) Formulated a model of anoxia based on the oxygen demand of various components of the benthic community.	(i) Phytoplankton blooms were associated with high nitrogen loadings (NO_3 from runoff, NH_4 from bivalve populations). (ii) Phytoplankton blooms and high summer water temperatures caused water column anoxia. (iii) Mass mortalities of bivalves and other benthos over large areas occurred as a result of anoxia. (iv) The polychaete *Pygospio elegans* recovered more quickly than the bivalve *Cerastoderma edule*. (v) A change in the benthic community, i.e. disappearance of *C. edule* and proliferation of *P. elegans*, was also apparent at higher trophic levels with a change in the diet of two main predators of *C. edule*.
De Zwaan *et al.*, (1992)	Metabolism of bivalves at low oxygen concentrations.	North-western Adriatic. 45°N.	Tolerance to anoxia, oxygen consumption rate and body tissue metabolites of mussels tested in the laboratory.	(i) Survival (in days) of bivalves in anoxic water. (ii) O_2 tension and consumption rates.	(i) The introduced Indopacific bloodclam *Scapharca inaequivalis* was outcompeting native bivalves *Venus gallina* and *Mytilus galloprovincialis* in the north-western Adriatic Sea. (ii) *S. inaequivalis* was metabolically more efficient at low O_2 tensions because at low O_2 they were able to regulate O_2 consumption to a constant level, and their anoxic ATP use was half of that of the other species. (iii) In eutrophied areas with low O_2 levels, the introduced bivalve was more successful and progressively displaced the other species.
Flothman and Werner (1992).	Effects of eutrophication on benthic microalgae, meio- and macrofauna.	Konigshafen, German Wadden Sea. 55°N.	2 nutrient treatments: enriched and control (ambient). Experimental run-time of 95 days, with samples taken at 20, 85 and 95 days.	(i) Pore-water PO_4, NH_4, NO_3/NO_2 and SiO_4 concentrations with time. (ii) Chlorophyll *a*, benthic microalgae, meiofauna and macrofauna abundances with time.	(i) Benthic microalgae were nitrogen limited and increased in abundance in response to enrichment. (ii) The cyanobacteria *Merismopedia* dominated the benthic microalgae and was not heavily grazed by meio- and macrofauna. (iii) Meio- and macrofauna showed no response to an increase in biomass of benthic microalgae. (iii) Therefore an increase in abundance benthic microalgae, as a result of nutrient enrichment, did not necessarily mean that more food was available for meio- and macrofauna.
Josefson and Jensen (1992).	Effects of hypoxia on soft-sediment macrobenthos.	Southern Kattegat. 56-57°N.	(i) Recent sampling compared with two other studies to give 1911/1912; 1984; 1989 time-series.	(i) Mean biomass and abundances of fauna for total fauna, polychaetes, molluscs, echinoderms and crustaceans, and for individual species. (ii) Environmental data not reported.	(i) Water depth to 43 m. The greatest effects were observed in shallower waters i.e. 22-26 m. (ii) A change towards a smaller size-structure under hypoxic conditions was recorded, as hypoxia removed larger, older individuals. (iii) Although the effects of eutrophication on benthic communities has been the focus of a great deal of research, data showing clear quantitative effects on benthic fauna are sparse and very localised.
Poore (1992).	Review of soft-bottom benthic macrofauna of Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	No specific spatial or temporal scales.	No empirical data presented.	(i) Benthic macroinvertebrate communities were diverse in comparison with other geographical locations. (ii) The distribution of benthic macrofauna was related to sediment types. Muddy sediments typically had a lower species diversity than sandy sites. (iii) Callianassa limosa (Decapoda) and Theora lubrica (Bivalvia) are the dominant species in the Bay and are restricted to the muddy central basin. (iv) Benthic suspension-feeding molluscs are abundant in the Bay and are estimated to filter a volume equivalent to the entire Bay every 24 days.

					(v) Empirical data on community change in response to environmental change is non-existent for the Bay.
Sarda *et al*, (1992).	Effects of nutrient enrichment on benthic invertebrate populations in a salt marsh habitat.	Great Sippewissett Marsh, Massachusetts, USA 42°N.	2 plots, 10m radius. 3 sludge treatments: control (ambient), high (25 g wk^{-1}), very high (75 g wk^{-1}). Sampled seasonally in 1974-75, monthly in 1979, 1987, 1988.	(i) Carbon:nitrogen ratios in 1975 and 1987 in control and very high treatments. (ii) Responses of individual species to organic enrichment. (iii) Water-column and sediment nutrient concentrations not presented.	(i) Nutrient enrichment favoured species such as *Capitella capitata*, *Paranais littoralis* and *Streblospio benedicti*. (ii) Secondary production was three times higher in enriched treatments than in controls. (iii) The effects of enrichment declined in summer when epibenthic predators such as crabs and fish were most active. (iv) Bottom up control of macrofauna, through regulation of food-resources, occurs in spring to early summer and gives way to top-down control by predators later in summer.
Schaffner *et al.*, (1992).	Effects of hypoxia and anoxia on the benthos and on bioturbation.	3 systems: Chesapeake Bay, USA 38°N. Long Is Sound, USA 41°N. Baltic Sea, 55-60°N.	12 stations on 6 transects, 55 stations, and 16 stations sampled in the three sites respectively.	(i) Provides a good review of the effects of anoxia on the sediments. (ii) Grain size, total organic carbon, densities of *Clostridium perfringens* spores, temperature, salinity and dissolved oxygen.	(i) Gradient in bioturbation (0-20cm) is coincident with a gradient in O_2 stress. (ii) Low O_2 results in fewer large fauna, lower bioturbation and sediments become physically laminated. (iii) High O_2 results in more large fauna, higher bioturbation and well mixed sediments.
Stachowitsch (1992).	Study of two mortality events due to hypoxia and the subsequent recovery of the benthos.	Gulf of Trieste, northern Adriatic Sea. 45°N.	Mortality of benthos monitored for 14 days after anoxia, recovery of benthos monitored for 6 years.	(i) Biomass changes between 1983 to 1989. (ii) Percent composition of former species. (iii) Survival of major benthic fauna. (iv) Oxygen concentrations not presented.	(i) The benthos may be considered to represent a long-term 'memory' of eutrophication through their responses: i.e. behaviour, survival, recolonisation, to hypoxia and anoxia. (ii) 90% of fauna were lost in four days, followed by a slow recolonisation to pre-anoxic community biomass and composition. (iii) Pre-event biomass was 390 g with 66% of this biomass consisting of species which define the community. In subsequent years these values were: 1984: 60g, 1%; 1985: 192 g, 10%; 1986: 142, 11%; 1987: 61g, 39% (dredging for *Pecten jacobaeus* started); 1988: 2g, 0%; (small -scale anoxia), 1989: 18g, 0%.
Tamai (1993).	Tolerance of *Theora fragilis* to anoxia.	Hiroshima, Japan. 35°N.	Experimental run time of 96 hrs.	(i) Survival of *Theora fragilis* at varying O_2 concentrations.	(i) Under anoxia: *T. fragilis* survived for 2 days at 15°C and 1 day at 25°C. (ii) At O_2 concentrations of 1.3-1.4 mg l^{-1} : *T. fragilis* survived for 4 days without irreversible physiological injury. (iii) At O_2 concentrations of 2.2-2.4 mg l^{-1} : *T. fragilis* behaved as they would in the field. (iv) Conclude that *T. fragilis* has a high tolerance to low dissolved oxygen concentrations.

Forbes *et al*., (1994).	Physiological responses of soft-bottom fauna to hypoxia and organic enrichment.	Odense Fjord, Denmark. 55°N.	6 individual worms reared at 2 oxygen and 4 nitrogen levels.	(i) Percent of carbon, nitrogen and carbon:nitrogen ratio of food provided to animals. (ii) Body volume at different nitrogen concentrations at two oxygen levels. (iii) Growth rate at different nitrogen concentrations at two oxygen levels. (iv) Growth rate / body volume regressions for two oxygen levels.	(i) A trade-off occurs between food availability and the O_2 available to use this food in benthic environments. This trade-off is most critical for early colonisers of enriched sediments. (ii) Early colonisers in enriched sediments are dominated by small thread-like polychaetes in the *Capitella capitata* complex. (iii) These reach high densities but if the level of organic matter declines then they are replaced by larger slower growing species e.g. *Arenicola marina*, *Nereis diversicolor*, *N. virens* and *Scoloplos armiger*. (iv) No difference in sulphide or anoxia tolerance was recorded between these two groups. (v) O_2 limits the use of organic matter by infauna. Thus, the feeding rate-growth relationship is limited by O_2. (vi) O_2 limits the growth rate and assimilation efficiency of *Capitella* spp., with a less efficient conversion of food to ATP. (vii) As O_2 concentration declines from 187 to 35µM, the growth rate of *Capitella* decreases by 20-35‰ d^{-1}. (viii) At O_2 levels of 35µM Capitella ceases feeding and becomes quiescent and body volume shrinks by 20% d^{-1}. (ix) At a constant O_2 level, an increase in feeding rate is a response to increased nitrogen.
Fuller (1994).	Effects of pore-water hydrogen sulphide on feeding by *Clymenella torquata.*	Long Island Sound, Connecticut. 42°N.	Series of experiments carried out in the lab in experimental chambers.	(i) H_2S concentration in pore-water. (ii) Feedback effects of worms on H_2S concentration. (iii) Effects of H_2S on feeding rate (as measured by defecation rate).	(i) *Clymenella torquata* is a surface-feeding polychaete worm (head-down, 'conveyor-belt' feeder). (ii) Generally low oxygen and high H_2S concentrations are lethal to infauna and fish. However, *C. torquata* feeds at depths of 10-20 cm and is likely to encounter hypoxia and H_2S. (iii) H_2S concentrations in the field were 0-2.5 mM. In the lab, H_2S concentrations of 700-1000 µM caused a decrease in faecal production. (iii) Tolerance to H_2S increased with temperature. (iv). *C. torquata* modified the sediment H_2S concentration via tube-irrigation. (v) Thus, H_2S may have significant but not lethal effects on *C. torquata* and *C. torquata* has the capacity to modify H_2S concentrations in its environment.
Lim and Hong (1994).	Ecology of a macrobenthic community.	Chinhae Bay, Korea. 35°N.	12 sites sampled at 2 month intervals over 3 year period.	(i) Temperature, dissolved oxygen, sediment characteristics. (ii) Macrofaunal abundance and biomass.	(i) A high sediment organic content and water column hypoxia were observed related to summer water stratification. (ii) Hypoxia spread from inner bay to outer regions throughout summer. (iii) Recovery from hypoxia was observed in autumn as summer stratification of the water column started to disappear. (iv) Faunal communities were classified using principal component analysis based on water temperature, salinity, dissolved oxygen, sediment grain size and organic carbon content. The classification of community types was most strongly correlated with sediment organic carbon content.

Nilsson and Rosenberg (1994).	Hypoxic responses of benthic communities.	Brofjorden, Western Sweden. 58°N.	2 experiments carried out using cores taken from 28.5 m deep and 3 O_2 treatments: 'normoxia' (8.2 mg l^{-1}); mild hypoxia (1.0 mg l^{-1}), severe hypoxia (0.5 mg l^{-1}), plus a field control.	(i) Oxygen concentrations with time, redox potential profiles, (ii) Abundances and number of species in different treatments (iii) Responses of the urchin *Echinocardium cordatum* and the polychaete *Pectinaria koreni* to hypoxia. (iv) Responses of *Amphiura filiformis*, *Mysella bidentata* and *Labidoplax buskii* to hypoxia.	(i) The abundance and number of species were reduced under severe hypoxia in expt 1 and both mild and severe hypoxia in expt 2. (ii) Differences in macrofaunal responses between experiments related to differences in sediment redox potential with the more adverse effects in experiment 2 related to a more reduced sediment in experiment 2. (iii) Infauna emerged from sediments under hypoxic conditions. *Echinocardium cordatum* exhibited more adverse reactions to hypoxia than *Pectinaria koreni.*
Tamai (1994).	Tolerance of *Theora fragilis* to H_2S.	Hiroshima, Japan. 35°N.	Experimental run times of 48 hrs.	(i) LT50 and LT100 for *Theora fragilis* under varying concentrations of H_2S.	(i) In anoxic conditions: LT50 under 12-15µM H_2S was 23hr at 23°C; LT50 under 46-778µM H_2S was 15-40hr at 15°C; 15-21hr at 23°C. (ii)*Theora fragilis* has a low tolerance to H_2S and would not survive long in anoxic sediments.
Ueda *et al*., (1994).	Recovery of a marine benthic environment after tighter regulation of pollutants and dredging activities since 1970.	Dokai Bay, Japan 33°N.	Bay-wide study at 13 stations, 2 sampling times: May and August, 1990.	(i) Dissolved oxygen, chemical oxygen demand (COD), acid volatile sulphide (AVS), Hg, Cd at each station at one time. (ii) Water Column total nitrogen and total phosphorus from 1980-1991. (iii) Abundance of macrobenthos and of dominant species at each station at each time.	(i) Heavy metal contamination was low but organic enrichment was still high. (ii) The presence of organics increased the periods of anoxia which continue to impact on the sediments. (iii) *Theora lubrica* abundance did not show any relationship with oxygen over the range of oxygen levels measured.
Posey *et al*., (1995).	Interactive effects of nutrient enrichment and predation on macrofauna to test bottom-up vs top-down controls.	North Carolina, USA. 35°N.	6 treatments: 3 caging treatments (open, partial cage, fully caged) x 2 nutrient levels (ambient; enriched: N = 25 µM, P = 1.6 µM). 4 week experimental run time.	(i) Benthic chlorophyll, abundances of dominant taxa, abundances of surface and burrowing deposit feeders.	(i) In minus predator treatments there was an increase in the abundance of surface deposit feeders but no change in infaunal deposit feeders. (ii) Nutrient addition treatments caused an increase in macrofaunal abundance where predators were excluded. Nutrient enrichment also caused an increase in the size-structure of polychaete *Streblospio benedicti* population. (iii) Interactions between predation and nutrients were variable between years. (iv) Nutrient enrichment may be associated with changes in benthic communities (through microalgal production) but predators may regulate the degree of this response.
Widbom and Frithsen (1995).	Structuring effects of eutrophication on a marine soft-bottom community.	Narragansett, Rhode Island, USA. 42°N.	2 mesocosms: control + single nutrient spike (47 mmol PO_4 m^{-2}. 608 mmol NH_4 m^{-2}). 5 month study period.	(i) Nitrogen and phosphorus concentrations given at start of experiment (not measured during the experiment). (ii) Chlorophyll *a* levels. (iii) Carbon flux at different sediment depths. (iv) Change in biomass of abundant species and of feeding groups.	(i) A 12x increase in phytoplankton, as a result of nutrient enrichment, related to an increase in fresh detritus, as 12x increase in the abundance of *Mediomastus ambiseta* and 27x increase in *Polydora ligni* (both polychaetes), and an increase in the mud anemone *Cerianthopsis americanus*. (ii) Competition for space was the major controlling factor. (iii) There was no consistent or direct response by other taxa.

Table 5: Synopsis of information on changes in fish communities in relation to changes in water or sediment quality.

Reference	Focus of Study	Location	Space/Time scales	Parameters Measured / Presented	Conclusions
Axelrad *et al*., (1981).	Effects of sewage on benthic communities.	Port Phillip Bay, Victoria. 38°N.	2 sites, one offshore and one nearshore the sewage outfall.	(i) Biomass, species composition, dietary analysis and metabolic rates of fish.	(i) Fish biomass was the same at the two sites but near the sewage outfall it was dominated by juveniles and small species. At the offshore site, older and larger fish were more abundant. (ii) Food requirements of fish at the nearshore site were six times that of the offshore site. (iii) Offshore site was sampled with an otter trawl, nearshore site was with a seine net.
Nixon *et al*. (1986).	Review of nutrients and productivity of estuaries and coastal marine systems.	No specific location.	No specific spatial or temporal scales.	(i) Relationships between macrofaunal biomass with primary production from a variety of field and laboratory studies.	(i) The overall trend is for an increase in nutrients to result in a modest increase in primary production which is quickly consumed by heterotrophs. (ii) As nutrient inputs increase so does the rate of internal recycling, thus only a small proportion of this increment ends up in higher trophic levels. (iii) The amount of nitrogen or phosphorus bound up in animal tissue is very small proportion of the total nutrient budget, thus detecting increases in production of heterotrophs at higher trophic levels in response to eutrophication is difficult. (iv) Problems related with climate, hydrology, harvesting efforts and technology, and other forms of pollution make this assessment even more difficult. (v) Work in the MERL mesocosm facility, Rhode Island, USA, have shown general increases in primary and secondary production in response to nutrient enrichment but have not demonstrated a tight coupling between phytoplankton and benthic faunal biomass.
Koivisto and Blomquist (1988).	Effect of fish farming on natural fish stocks.	Baltic Sea. 55-60°N.	5 sites sampled between May 1985 to September 1986.	(i) Fish abundance, biomass and species richness over time. (ii) Catch rates at eutrophied and non-eutrophied sites. (iii) Length-frequencies of fish at 5 sites and mean perch length over time at 4 sites. (iv) Food choice of perch at 6 sites.	(i) Fish farming is a source of nutrients which can contribute to eutrophication. (ii) Nutrient enrichment has led to an increase in biomass and total abundance of fish. (iii) Community composition has shifted towards a cyprinid-dominated community. (iv) Perch growth rates have increased as a result of nutrient enrichment. (v) Perch diets have changed with a greater proportion of fish consumed. (vi) Near fish farms perch populations are dominated by juveniles and small fish.
Baden *et al*. (1990).	Effects of eutrophication on benthic communities including fish.	Review paper. South-east Kattegat, Sweden. 56-57°N.	No specific spatial or temporal scales.	(i) Water column oxygen concentrations with depth and with time. (ii) Temporal changes in macroalgal and benthic faunal communities. (iii) Demersal fish catch yields.	(i) Areas of the Baltic Sea are susceptible to anoxia as a result of the effects of eutrophication, due to relatively shallow waters and the development of a strong halocline. (ii) Periods of hypoxia are variable depending on hydrographic conditions which vary between years. (iii) Near the halocline benthic infauna were affected by low oxygen levels. At about 40% oxygen saturation fish moved away and lobsters emerged from burrows, at 15% saturation lobsters became immobilised and other infauna emerged from sediments, at 10% saturation lobsters died but infauna were able to tolerate conditions of 7-5% saturation for some weeks. (iv) After deoxygenation of the bottom, populations of flatfish and benthic infauna recovered whereas cod and lobster populations did not.
Gwyther (1990).	Fisheries productivity in Port Phillip Bay.	Review paper. Port Phillip Bay,	Review of knowledge on bay-wide scale.	(i) Compares nitrogen loading of Port Phillip Bay with other locations.	(i) General response of fish to chronic nutrient addition is the increase in early growth rate.

		Victoria.		(ii) Presents Figure 19 from Nixon *et al*., (1986) relating fisheries yield with primary production.	(ii) No consistent trend has been observed between increased fish growth rate, and increased plankton or benthos. (iii) Presently there is no evidence that the nutrient load to Port Phillip Bay has had any adverse effects on fish.
Hansson and Rudstam (1990).	Review paper on eutrophication effects on Baltic fish communities.	Baltic Sea. 55-60°N.	From 1920's to present.	(i) Presents information on annual fisheries yield from 1920's to present.	(i) Changes in species composition have been recorded e.g. increases in pikeperch and decreases in whitefish, in relation to eutrophication. (ii) Total fish catches, dominated by herring, sprat and cod have increased dramatically over the last 50 years. This was considered to be related to intensified fishing efforts, eutrophication and possible reduced predation by sea mammals. (iii) Effects of eutrophication may be different for different species depending on their specific habitat requirements and reproductive characteristics.
Keller *et al*., (1990).	Effects of eutrophication on the growth of Atlantic menhaden *Brevoortia tyrannus*.	MERL Mesocosm study, Rhode Island, USA 42°N.	Experiment run-time of 32 weeks.	(i) Nitrogen, phosphorus and silicon concentrations. (ii) Mean lengths of fish (fish lengths are not related back to biomass). (iii) Mean instantaneous mortality rates. (iv) Relationship between food biomass and asymptotic size.	(i) Increased nutrient loading increased the abundance of phyto- and zooplankton. (ii) Increased food availability increased the growth rate and size of *Brevoortia tyrannus*.
Lee *et al*. (1991).	Review paper of the effects of eutrophication on fisheries.	No specific location.	No specific spatial or temporal scales.	(i) Presents relationships between phosphorus loading, chlorophyll *a*, secchi disk depth, water column oxygen and fish yield for fresh-water systems.	(i) Increased phosphorus loading increased water column chlorophyll *a*, turbidity, oxygen tensions (initially) and resulted in increased fish yield. (ii) However, although an increase in nutrients may increase the quantity of fish, they may also decrease the quality of the fish by stimulating a shift in species composition towards undesirable species. (iii) Marine waters are relatively nutrient depleted, nitrogen limited, and processes are more difficult to measure. (iv) In the Adriatic Sea, an increase in nutrients has caused phytoplankton blooms, depletion of water column oxygen and ultimately, fish kills. (v) In Japan, dinoflagellate blooms have had major effects on coastal fish culture.
Gray *et al*., (1992).	Distribution and abundance of fish larvae in relation to sewage plumes.	Sydney, New South Wales. 34°S.	3 sewage outfalls and 3 non-polluted sites sampled on three occasions over 9 months. Sampled at surface and 20m depth.	(i) Temperature and salinity profiles. (ii) Fish larvae number of taxa and number of individuals.	(i) Patterns of distribution of fish larvae were not consistent between sampling times or between polluted or non-polluted sites. (ii) Patterns of distribution more closely reflect patterns of spatial heterogeneity than effects related to the sewage plumes.
Isaksson and Pihl (1992).	Effects of changes in macrophyte communities on macrofauna.	Eastern Skaggerak Sea. 57-59°N.	Two sites sampled irregularly between 1982 to 1990.	(i) Epibenthic faunal biomass with time. (ii) Biomass of dominant species related to epiphyte and vegetation cover.	(i) An overgrowth of filamentous algae has been associated with a reduction in the quantity of epibenthic fauna. (ii) Eels have increased in abundance in response to the increase in filamentous algae, whereas plaice have declined.
Kerr and Ryder (1992).	Review paper of the effects of eutrophication on coastal marine fisheries.	No specific location.	No specific spatial or temporal scales.	No empirical data presented.	(i) Eutrophication may have direct effects through reducing the suitability of habitats, influencing community change towards undesirable species or transferring the effects through the biota. (ii) Although an increase in nitrogen and primary production in the sea may be considered a desirable attribute, excessive production leads to the development of zones of anoxia.

					(iii) Although the effects of eutrophication on fisheries are recognisable they are difficult to quantify due to large scales of variability around measured of abundance, growth rates and yield levels.
Nicholson (1992).	Review of commercial fisheries in Port Phillip Bay.	Port Phillip Bay, Victoria. 38°S.	No specific spatial or temporal scales.	No empirical data linking water or sediment quality parameters to fisheries yields presented.	(i) Port Phillip Bay supports a variety of fisheries including finfish, abalone, squid, scallops and mussels. (ii) Nutrients may affect fisheries by altering suitable habitats, e.g. loss of seagrass meadows. (iii) Contamination by toxic dinoflagellates leads to bitter taste or buildup of paralytic shellfish poisoning (PSP) toxins, or mortality of fish species. (iv) Suggested parameters for monitoring the effects of nutrient discharge in Port Phillip Bay include dissolved oxygen, organic nitrogen levels and chlorophyll *a* levels.
Pihl (1992).	Effects of oxygen depletion on demersal fish.	SE Kattegatt, Sweden. 56°N.	Sampled irregularly over four years.	(i) Water column oxygen levels. (ii) Total biomass of fish.	(i) Increased nitrogen may result in increased coastal primary production, sedimentation rates and benthic respiration rates. (ii) An increase in benthic respiration may deplete oxygen levels which then has rapid and severe effects on the benthic fauna. (iii) Reduction of oxygen levels to < 3mg l^{-1} may lead to up to 80% depletion of the total fish biomass. (iv) Species composition changed in response to low water column oxygen, with flatfish becoming dominant at lower oxygen levels.
Edgar *et al.* (1993).	Effects of seagrass loss on commercial fisheries.	Western Port Bay, Victoria.	Sampling carried out at a variety of sites, at three monthly intervals between August 1989 and August 1990.	(i) Epifaunal and infaunal biomass and abundance data for a variety of vegetated and unvegetated sites.	(i) Epifaunal production was considerably higher in vegetated habitats. (ii) Positive correlations existed between fish production, seagrass biomass and epifaunal crustacean production. (iii) The effects of seagrass loss on commercial species could only be demonstrated for 2 species: six-spined leatherjacket and blue rock-whiting. (iii) Effects of loss of seagrass were mostly restricted to small weed-fish which inhabited seagrass meadows but were not of any direct commercial importance.

8. FIGURE CAPTIONS

Figure 1.

(a) Changes in seagrass shoot density in relation to water column dissolved inorganic nitrogen concentration.

(b) Changes in seagrass shoot density in relation to water column ammonium concentration.

(c) Changes in seagrass shoot density in relation to water column nitrate+nitrite concentration.

Figure 2.

(a) Changes in seagrass shoot density in relation to sediment pore-water dissolved inorganic nitrogen concentration.

(b) Changes in seagrass shoot density in relation to sediment pore-water ammonium concentration.

Figure 3.

(a) Changes in seagrass above-ground biomass in relation to water column dissolved inorganic nitrogen concentration.

(b) Changes in seagrass above-ground biomass in relation to water column ammonium concentration.

(c) Changes in seagrass above-ground biomass in relation to water column nitrate+nitrite concentration.

Figure 4.

(a) Changes in seagrass above-ground biomass in relation to sediment pore-water dissolved inorganic nitrogen concentration.

(b) Changes in seagrass above-ground biomass in relation to sediment pore-water ammonium concentration.

Figure 5.

(a) Changes in annual seagrass above-ground production in relation to water column dissolved inorganic nitrogen concentration.

(b) Changes in annual seagrass above-ground production in relation to water column ammonium concentration.

(c) Changes in annual seagrass above-ground production in relation to water column nitrate+nitrite concentration.

Figure 6.

Changes in annual seagrass above-ground production in relation to sediment pore-water dissolved inorganic nitrogen concentration.

Figure 7.

Seagrass leaf production in relation to irradiance (after Walker *et al*., 1994; circles refer to *Posidonia sinuosa*, triangles refer to *Amphibolis antarctica*, open symbols = culture at 18°C, closed symbols = culture at 23°C).

Figure 8.

Decline in seagrass shoot density under light reduction manipulations. Light reduction is presented as a percentage of surface irradiance (after Bulthuis, 1983).

Figure 9.

Relationship between periphyton biomass on seagrass leaves and light attenuation at the leaf surface. (Light attenuation reported as a percentage of surface irradiance).

Figure 10.

Decline in seagrass production in relation to light attenuation caused by epiphytes.

Figure 11.

Changes in macroalgal biomass in relation to water column total nitrogen.

Figure 12.

(a) Changes in macroalgal biomass in four bays in the Lagoon of Venice, in relation to water column dissolved inorganic nitrogen concentration (after Sfriso *et al*., 1992).

(b) Changes in macroalgal biomass, averaged within seasons, in four bays in the Lagoon of Venice, in relation to water column dissolved inorganic nitrogen concentration (after Sfriso *et al*., 1992).

(c) Changes in macroalgal biomass, averaged within seasons, in relation to water column dissolved inorganic nitrogen (after Sfriso *et al.*, 1992).

Figure 13.

(a) Changes in macroalgal epiphyte biomass (per cm^2 of seagrass leaf) in relation to water column dissolved inorganic nitrogen concentration (after Walker *et al*., 1994).

(b) Changes in macroalgal epiphyte biomass (per cm^2 of seagrass leaf) in relation to water column ammonium concentration (after Walker *et al*., 1994).

(c)Changes in macroalgal epiphyte biomass (per cm^2 of seagrass leaf) in relation to water column nitrate concentration (after Walker *et al*., 1994; * = batch culture; ** = continuous culture).

Figure 14.

(a)Changes in macroalgal epiphyte growth rate (per cm^2 of seagrass leaf) in relation to water column ammonium concentration (after Walker *et al*., 1994).

(b)Changes in macroalgal epiphyte growth rate (per cm^2 of seagrass leaf) in relation to water column nitrate concentration (after Walker *et al*., 1994).

Figure 15.

Changes in macroalgal growth rate (wet weight) in relation to water column dissolved inorganic nitrogen concentration (after Schramm *et al*., 1988).

Figure 16.

Changes in macroalgal growth rate (dry weight) in relation to water column dissolved inorganic nitrogen concentration (after Pedersen, 1995).

Figure 17.

(a)Changes in macroalgal epiphyte biomass in relation to irradiance (after Walker *et al*., 1994; open symbols: summer; closed symbols: winter).

(b)Changes in macroalgal epiphyte production in relation to irradiance (after Walker *et al*., 1994; open symbols: summer; closed symbols: winter).

Figure 18.

(a)Changes in periphyton biomass on seagrass leaves in relation to water column dissolved inorganic nitrogen concentration (after Hillman *et al*., 1991; PRH: Princess Royal Harbour; OH: Oyster Harbour; KGS: King George Sound; open symbols: *Posidonia australis*, closed symbols: *Posidonia sinuosa*).

(b)Changes in periphyton biomass on seagrass leaves in relation to water column ammonium concentration (after Hillman *et al*., 1991; PRH: Princess Royal Harbour; OH: Oyster Harbour; KGS: King George Sound; open symbols: *Posidonia australis*, closed symbols: *Posidonia sinuosa*).

(c)Changes in periphyton biomass on seagrass leaves in relation to water column nitrate+nitrite concentration (after Hillman *et al*., 1991; PRH: Princess Royal Harbour; OH: Oyster Harbour; KGS: King George Sound; open symbols: *Posidonia australis*, closed symbols: *Posidonia sinuosa*).

Figure 19.

Changes in benthic microalgal production in relation to irradiance.

Figure 20.

Relationships between benthic and phytoplanktonic microalgal production.

Figure 21.

(a) Changes in macrofaunal density in relation to water column total nitrogen concentration (* data from Poore and Rainer (1974) includes molluscs only).

(b) Changes in macrofaunal density in relation to water column dissolved inorganic nitrogen concentration (* data from Poore and Rainer (1974) includes molluscs only).

Figure 22.

(a) Changes in macrofaunal density, averaged within seasons, in relation to water column dissolved inorganic nitrogen concentration (after Bogdanos and Satsmadjis, 1992).

(b) Changes in macrofaunal species richness, averaged within seasons, in relation to water column dissolved inorganic nitrogen concentration (after Bogdanos and Satsmadjis, 1992).

Figure 23.

Change in the biomass of molluscs, divided into feeding-groups, in relation to water column total nitrogen concentration (after Poore and Rainer, 1974; Epi = epibenthic, Inf = Infaunal, SF = suspension-feeders, DF = deposit-feeders).

Figure 24.

(a) Changes in macrofauna biomass in the Dutch Wadden Sea in relation to total nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(b) Changes in macrofauna biomass in the Dutch Wadden Sea in relation to dissolved inorganic nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(c) Changes in macrofauna biomass in the Dutch Wadden Sea in relation to nitrate loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(d) Changes in macrofauna biomass in the Dutch Wadden Sea in relation to ammonium loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

Figure 25.

(a)Changes in macrofauna production in the Dutch Wadden Sea in relation to total nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(b)(b)Changes in macrofauna production in the Dutch Wadden Sea in relation to dissolved inorganic nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(c)Changes in macrofauna production in the Dutch Wadden Sea in relation to nitrate nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

(d)Changes in macrofauna production in the Dutch Wadden Sea in relation to ammonium nitrogen loading of the Rhine River (Macrofauna data after Beukema and Cadée, 1986; Nitrogen data after Nienhuis, 1992).

Figure 26.

(a)Changes in macrofauna density in relation to water column oxygen concentration.

(b)Changes in macrofauna density, divided into taxonomic groups, in relation to water column oxygen concentration (after Ued *et al.*, 1994).

Figure 27.

(a)Changes in water column oxygen concentration in relation to water column total nitrogen concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(b)Changes in water column oxygen concentration in relation to water column dissolved inorganic nitrogen concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(c)Changes in water column oxygen concentration in relation to water column nitrate+nitrite concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(d)Changes in water column oxygen concentration in relation to water column ammonium concentration in Port Phillip Bay (after MMWB and FWD, 1973).

Figure 28.

(a)Changes in fish biomass in relation to water column total nitrogen concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(b)Changes in fish biomass in relation to water column dissolved inorganic nitrogen concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(c)Changes in fish biomass in relation to water column ammonium concentration in Port Phillip Bay (after MMWB and FWD, 1973).

(d)Changes in fish biomass in relation to water column nitrate+nitrite concentration in Port Phillip Bay (after MMWB and FWD, 1973).

Figure 29.

Changes in fisheries yield in relation to primary production in estuarine and coastal systems (adapted from Nixon *et al*., (1986); data drawn from 35 studies - refer to Nixon *et al*., (1986) for full details).

Figure 30.

Changes in fish biomass in relation to water column oxygen concentration (open symbols: after MMWB and FWD, 1973; closed symbols: after Pihl, 1992).

Figure 1

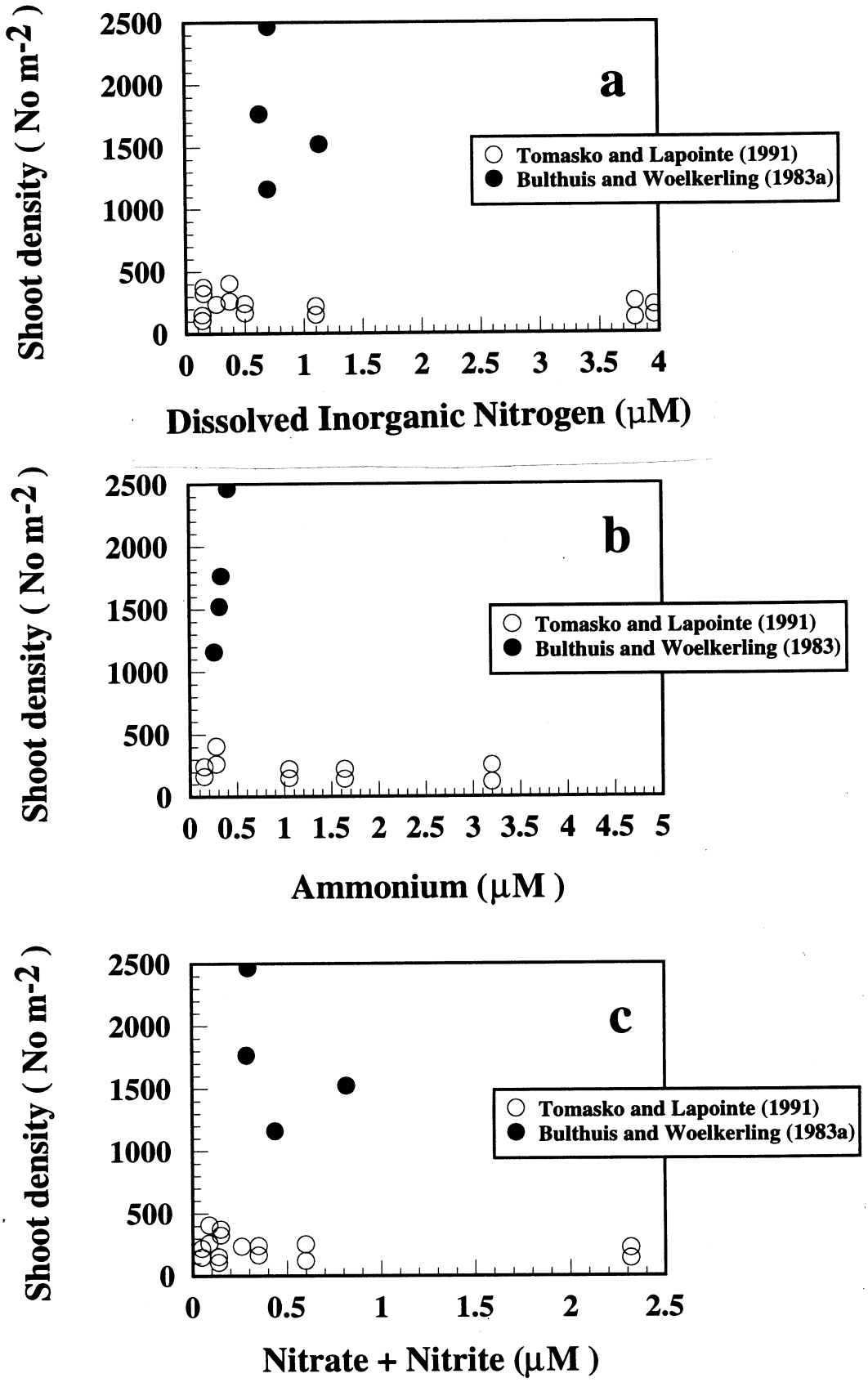
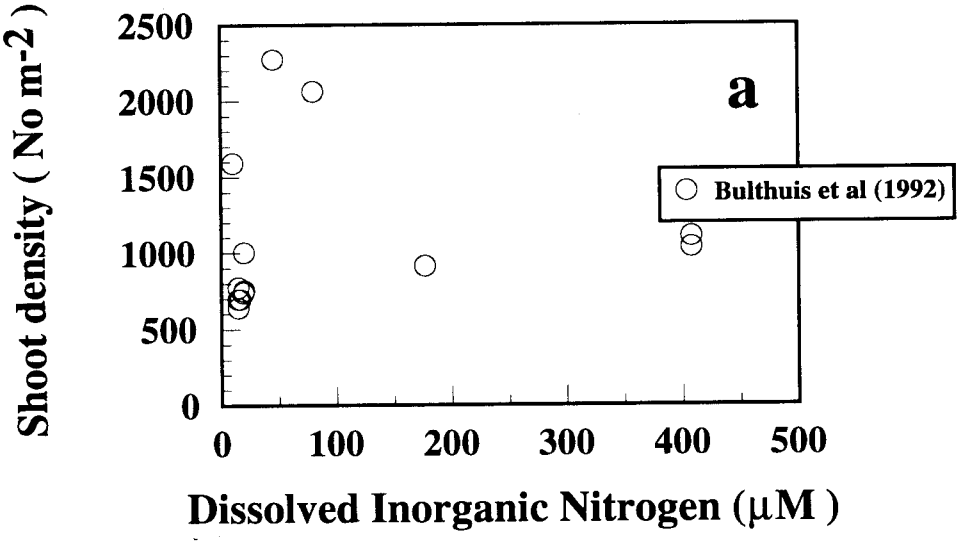

a
Shoot density (No m-2)
2500
2000
1500
1000
500
0
0 0.5 1 1.5 2 2.5 3 3.5 4
Dissolved Inorganic Nitrogen (µM)
Tomasko and Lapointe (1991)
Bulthuis and Woelkerling (1983a)
b
Shoot density (No m-2)
2500
2000
1500
1000
500
0
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5 5
Ammonium (µM)
Tomasko and Lapointe (1991)
Bulthuis and Woelkerling (1983)
c
Shoot density (No m-2)
2500
2000
1500
1000
500
0
0 0.5 1 1.5 2 2.5
Nitrate + Nitrite (µM)
Tomasko and Lapointe (1991)
Bulthuis and Woelkerling (1983a)

Figure 2


Shoot density (No m-2)
2500
2000
1500
1000
500
0
a
Bulthuis et al (1992)
0
100
200
300
400
500
Dissolved Inorganic Nitrogen (µM)

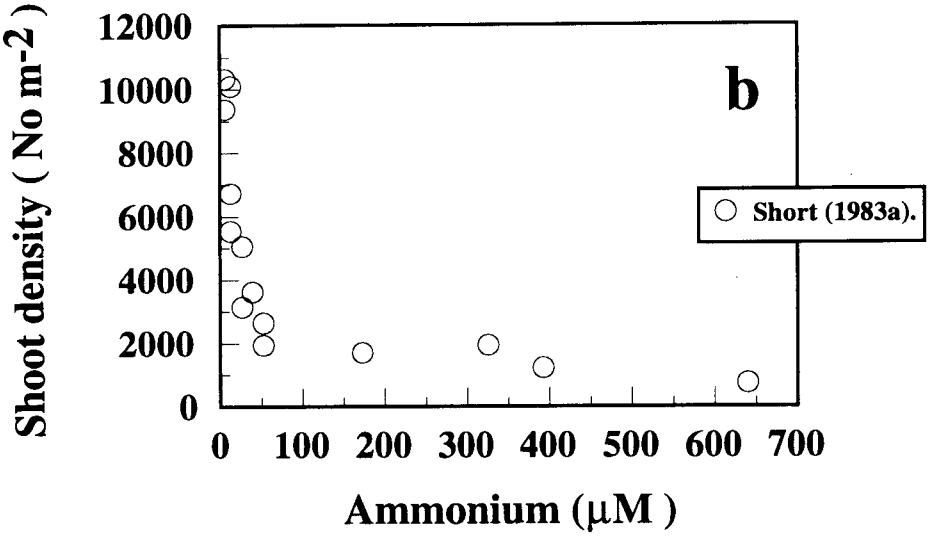
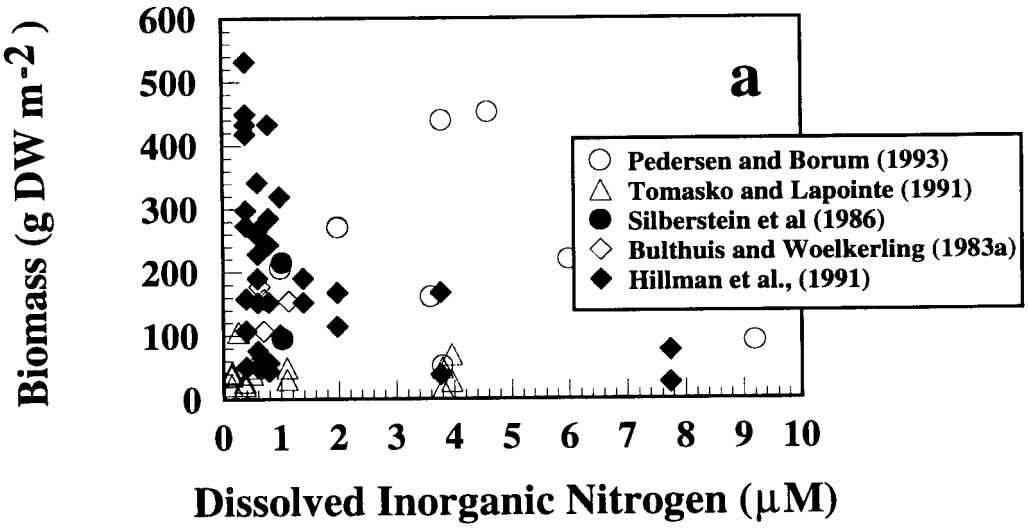
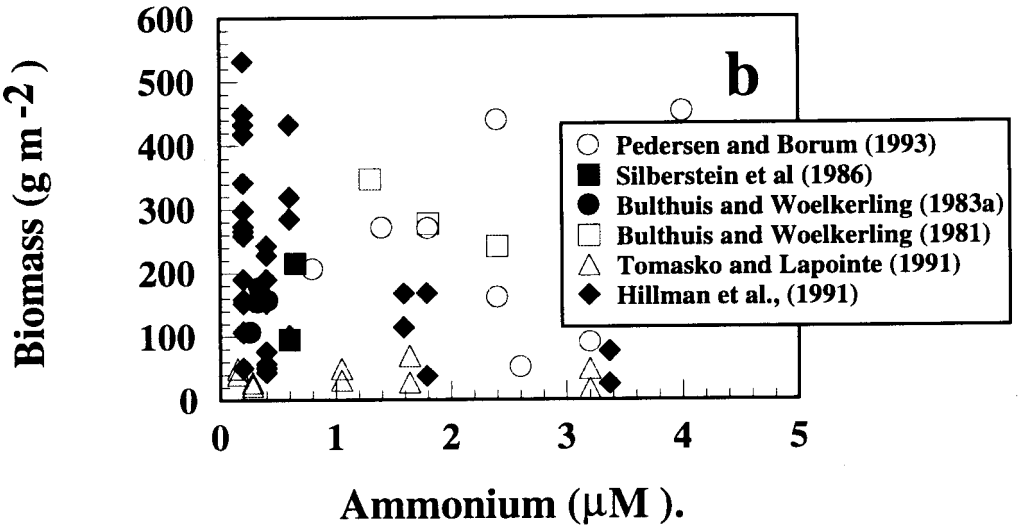

Shoot density (No m-2)
12000
10000
8000
6000
4000
2000
0
b
Short (1983a).
0
100
200
300
400
500
600
700
Ammonium (µM)

Figure 3


a
Biomass (g DW m-2)
600
500
400
300
200
100
0
0 1 2 3 4 5 6 7 8 9 10
Dissolved Inorganic Nitrogen (µM)
Pedersen and Borum (1993)
Tomasko and Lapointe (1991)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983a)
Hillman et al., (1991)


b
Biomass (g m -2)
600
500
400
300
200
100
0
0 1 2 3 4 5
Ammonium (µM).
Pedersen and Borum (1993)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983a)
Bulthuis and Woelkerling (1981)
Tomasko and Lapointe (1991)
Hillman et al., (1991)

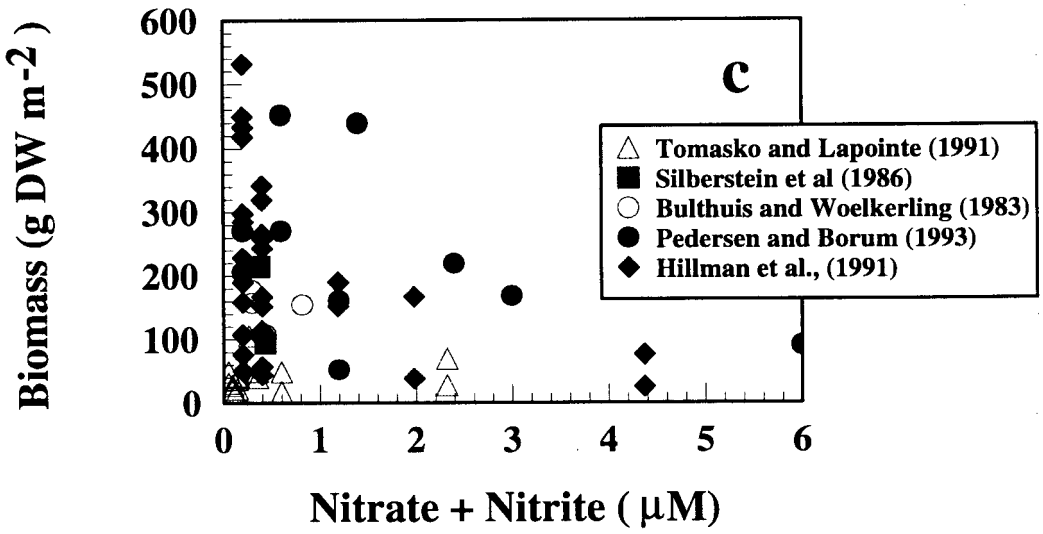
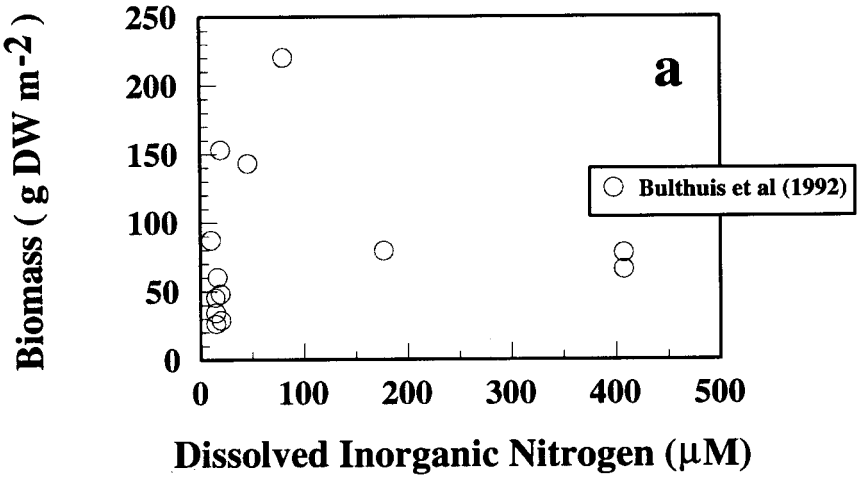

c
Biomass (g DW m-2)
600
500
400
300
200
100
0
0 1 2 3 4 5 6
Nitrate + Nitrite (µM)
Tomasko and Lapointe (1991)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983)
Pedersen and Borum (1993)
Hillman et al., (1991)

Figure 4


a
Biomass (g DW m-2)
250
200
150
100
50
0
0
100
200
300
400
500
Dissolved Inorganic Nitrogen (µM)
Bulthuis et al (1992)

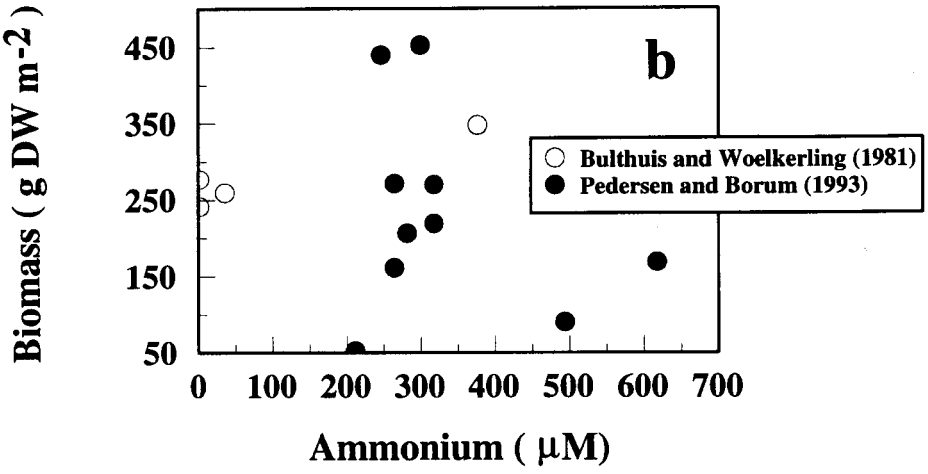

b
Biomass (g DW m-2)
450
350
250
150
50
0
100
200
300
400
500
600
700
Ammonium (µM)
Bulthuis and Woelkerling (1981)
Pedersen and Borum (1993)

Figure 5

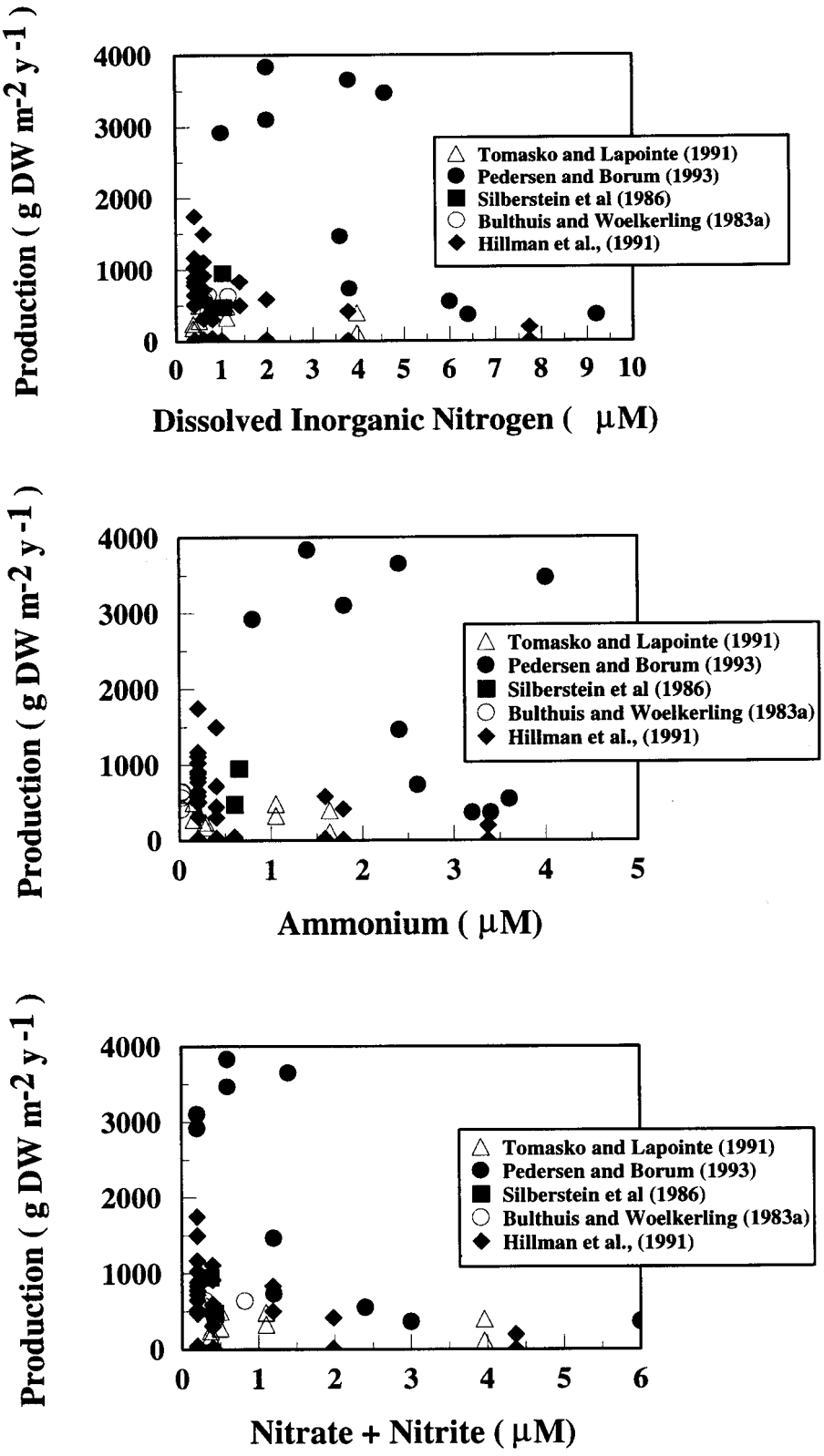

Production (g DW m-2 y-1)
4000
3000
2000
1000
0
0 1 2 3 4 5 6 7 8 9 10
Dissolved Inorganic Nitrogen (µM)
Tomasko and Lapointe (1991)
Pedersen and Borum (1993)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983a)
Hillman et al., (1991)
Production (g DW m-2 y-1)
4000
3000
2000
1000
0
0 1 2 3 4 5
Ammonium (µM)
Tomasko and Lapointe (1991)
Pedersen and Borum (1993)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983a)
Hillman et al., (1991)
Production (g DW m-2 y-1)
4000
3000
2000
1000
0
0 1 2 3 4 5 6
Nitrate + Nitrite (µM)
Tomasko and Lapointe (1991)
Pedersen and Borum (1993)
Silberstein et al (1986)
Bulthuis and Woelkerling (1983a)
Hillman et al., (1991)

Figure 6

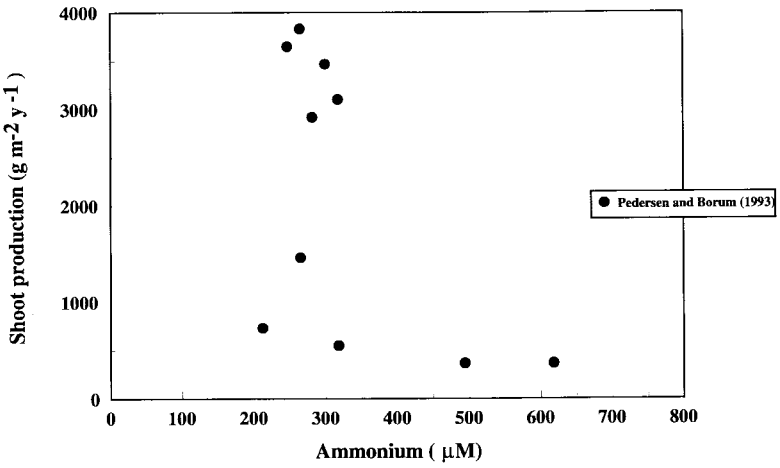


Figure 7

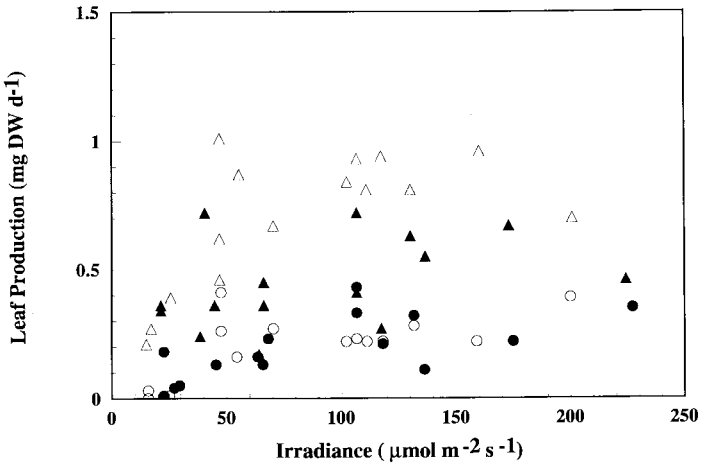


Figure 8

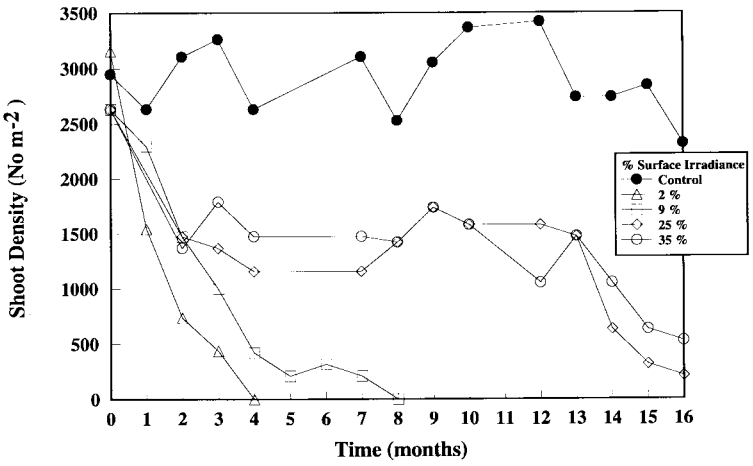


Figure 9

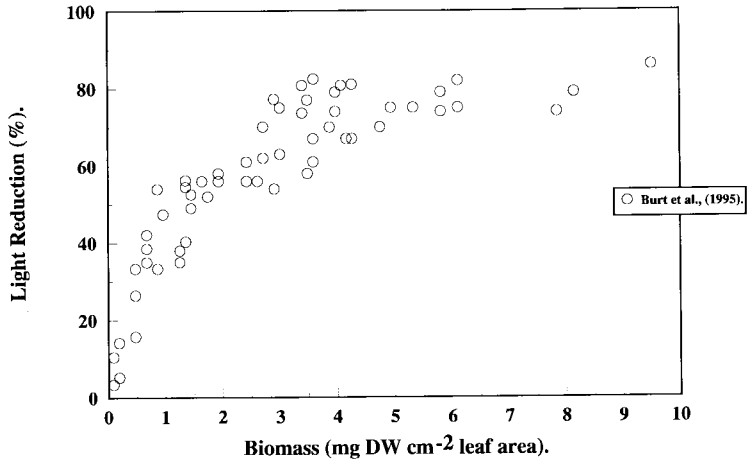


Figure 10

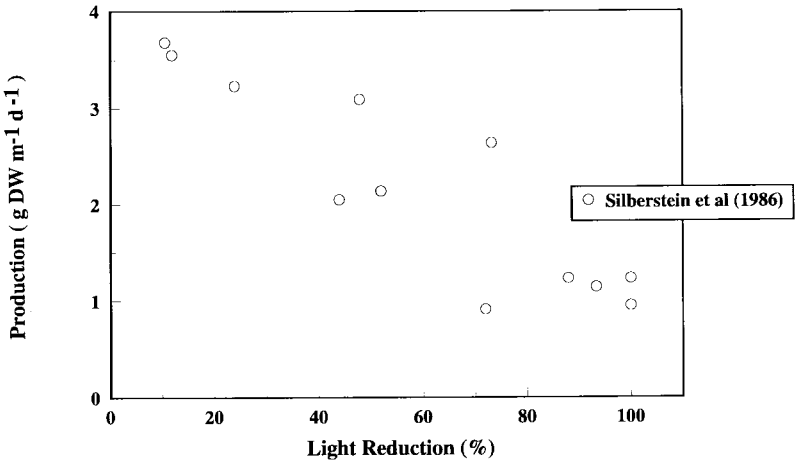


Figure 11

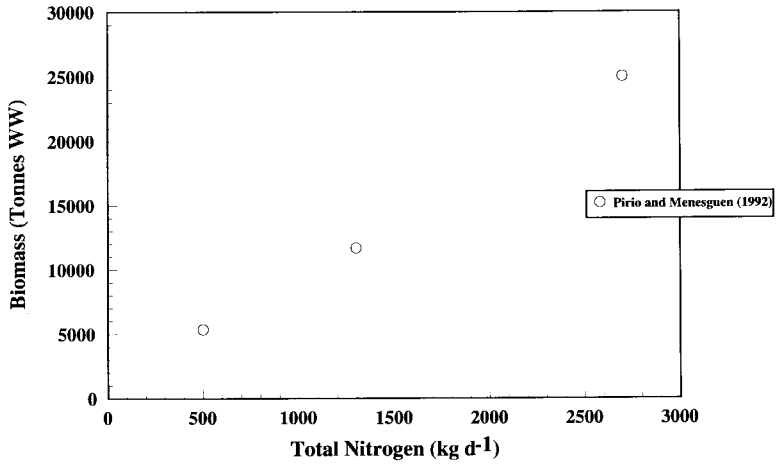


Figure 12

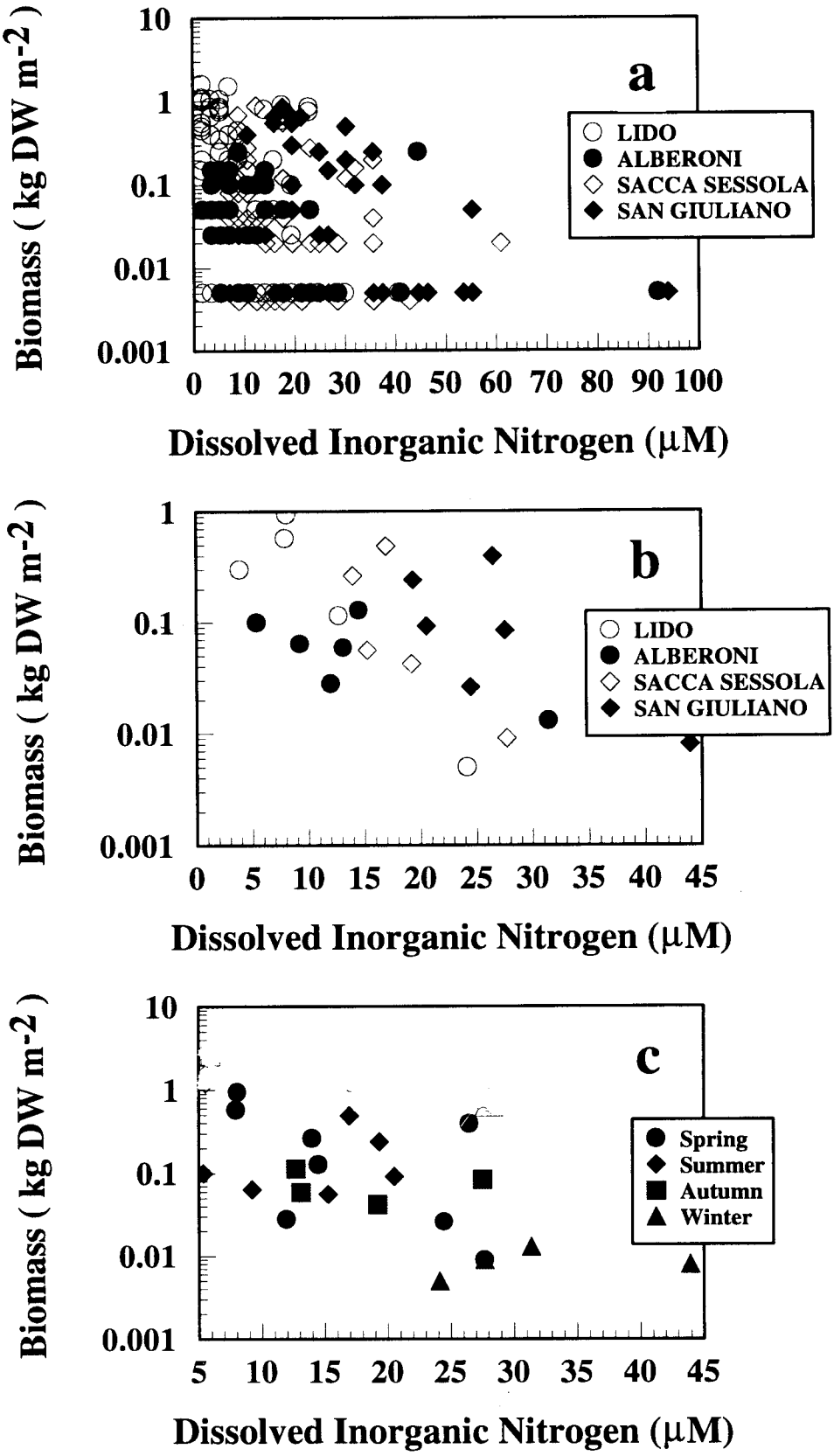

a
LIDO
ALBERONI
SACCA SESSOLA
SAN GIULIANO
Biomass (kg DW m-2)
10
1
0.1
0.01
0.001
0 10 20 30 40 50 60 70 80 90 100
Dissolved Inorganic Nitrogen (µM)
b
LIDO
ALBERONI
SACCA SESSOLA
SAN GIULIANO
Biomass (kg DW m-2)
1
0.1
0.01
0.001
0 5 10 15 20 25 30 35 40 45
Dissolved Inorganic Nitrogen (µM)
c
Spring
Summer
Autumn
Winter
Biomass (kg DW m-2)
10
1
0.1
0.01
0.001
5 10 15 20 25 30 35 40 45
Dissolved Inorganic Nitrogen (µM)

Figure 13

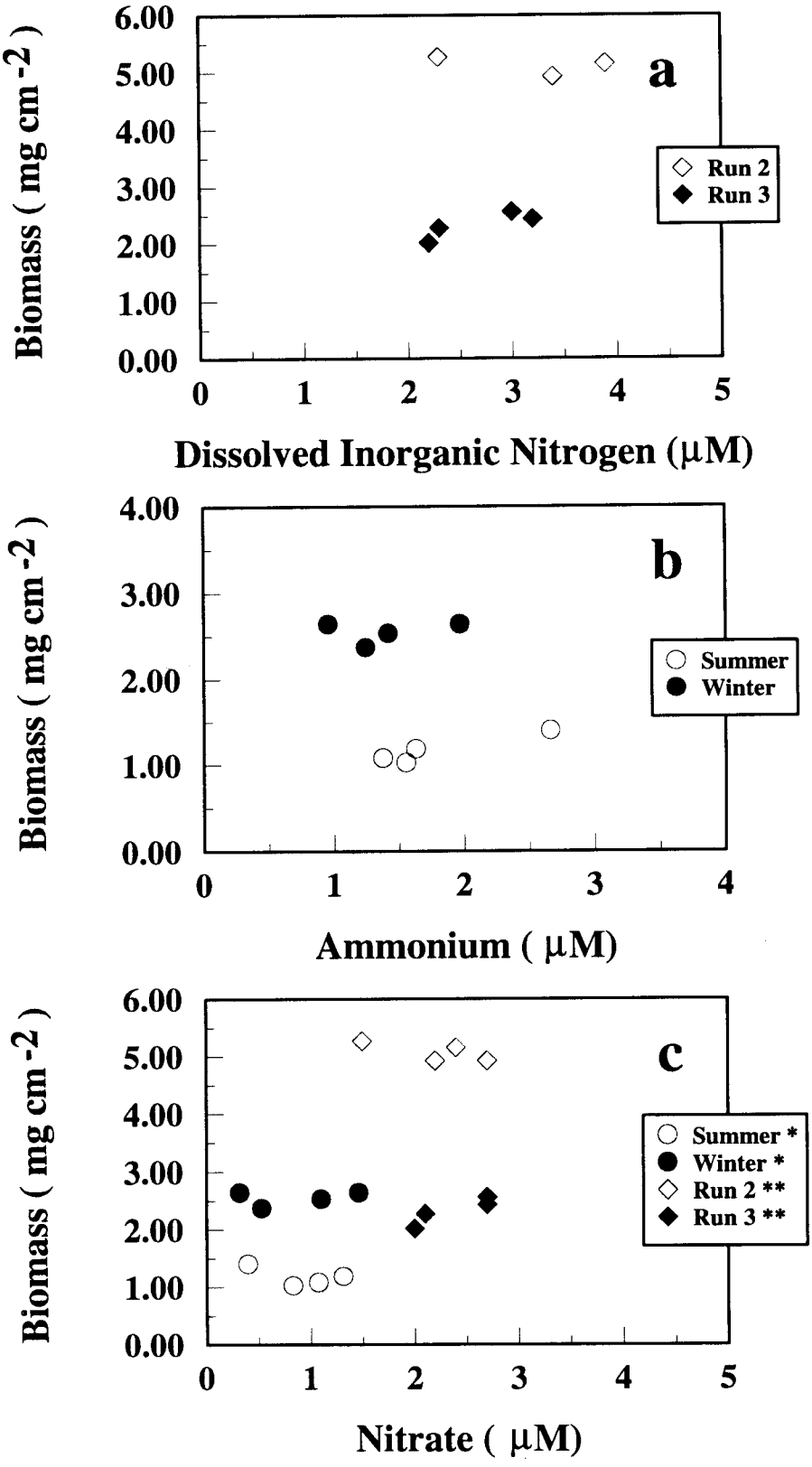

a
Biomass (mg cm -2)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0
1
2
3
4
5
Run 2
Run 3
Dissolved Inorganic Nitrogen (µM)
b
Biomass (mg cm -2)
4.00
3.00
2.00
1.00
0.00
0
1
2
3
4
Summer
Winter
Ammonium (µM)
c
Biomass (mg cm -2)
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0
1
2
3
4
5
Summer *
Winter *
Run 2 **
Run 3 **
Nitrate (µM)

Figure 14

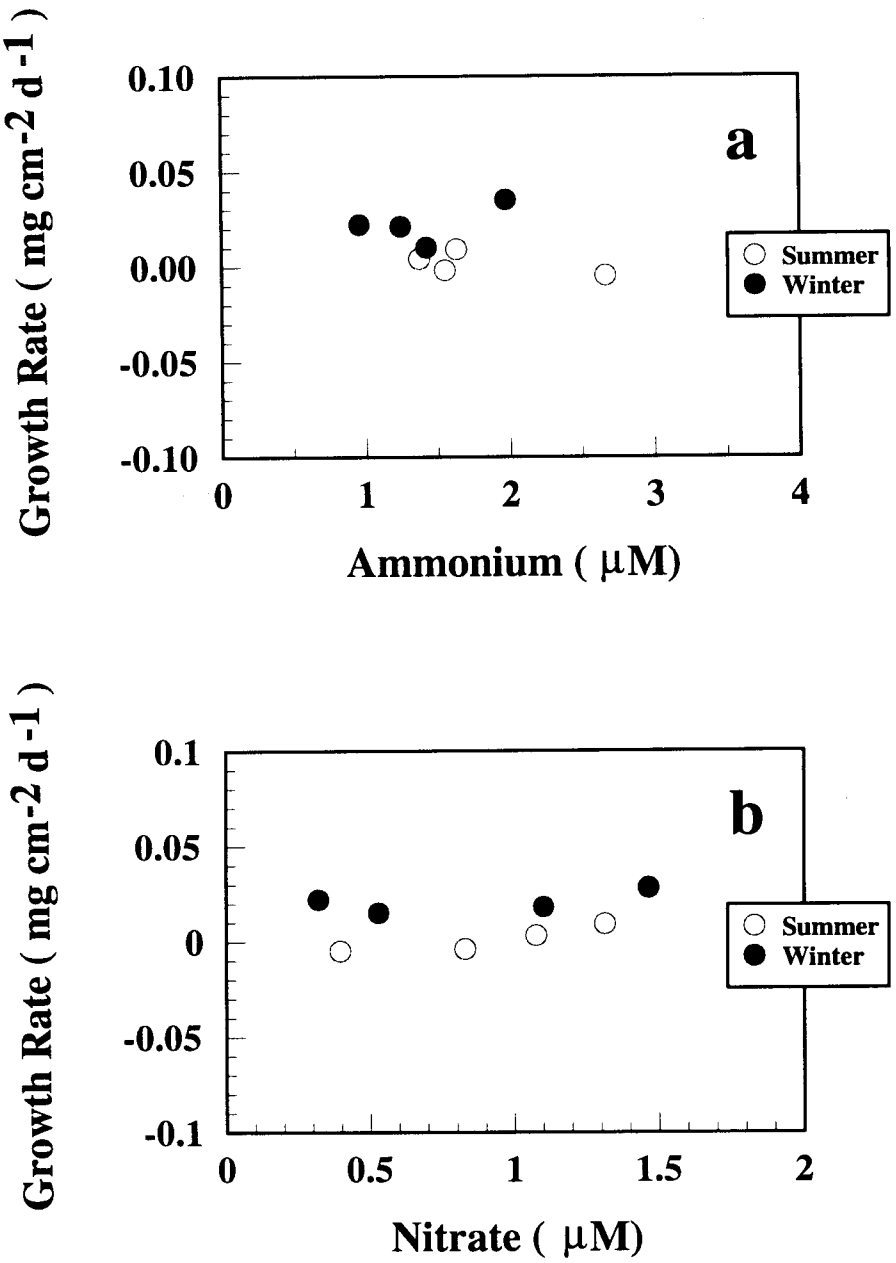

Growth Rate (mg cm-2 d-1)
0.10
0.05
0.00
-0.05
-0.10
0
1
2
3
4
a
Summer
Winter
Ammonium (μM)
Growth Rate (mg cm-2 d-1)
0.1
0.05
0
-0.05
-0.1
0
0.5
1
1.5
2
b
Summer
Winter
Nitrate (μM)

Figure 15

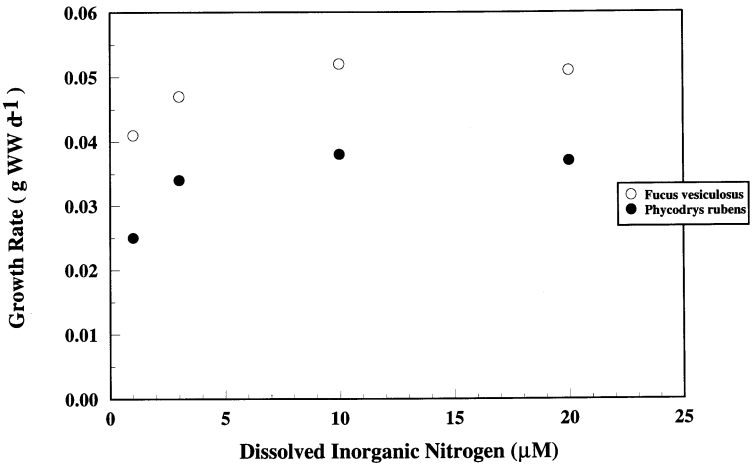


Figure 16

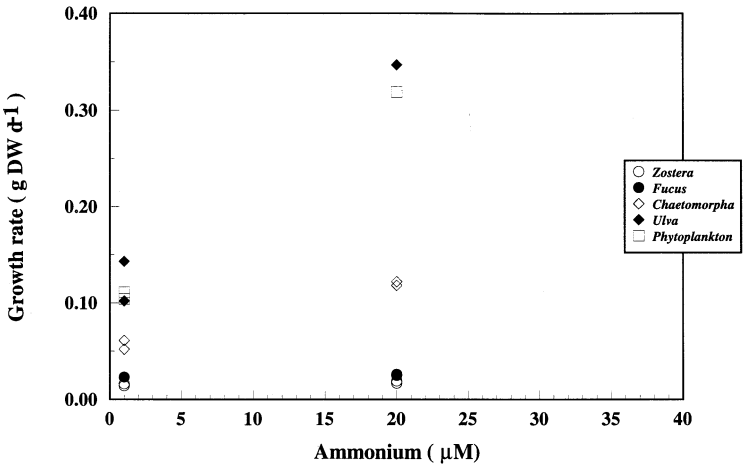


Figure 17

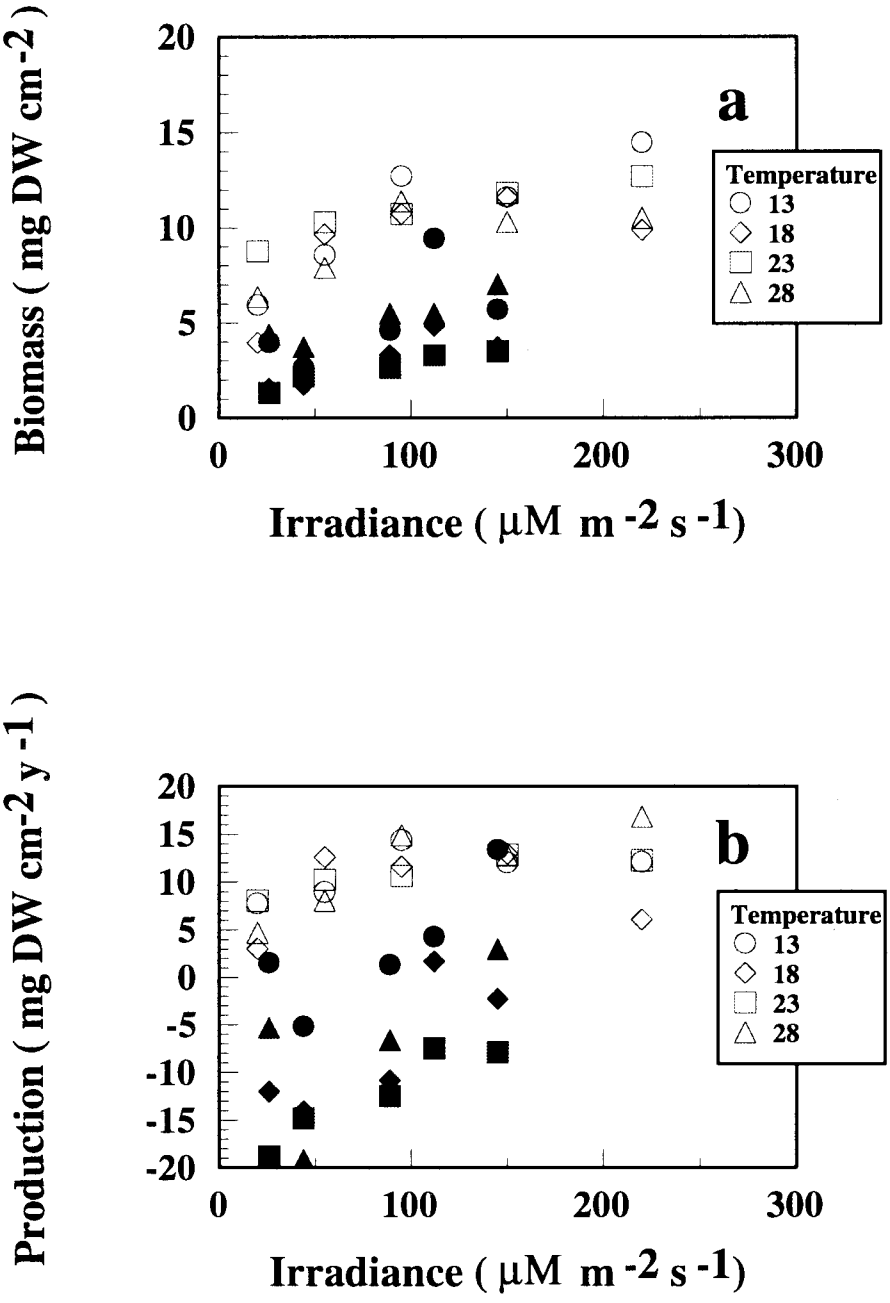

Biomass (mg DW cm-2)
20
15
10
5
0
0
100
200
300
Irradiance (µM m -2 s -1)
a
Temperature
13
18
23
28
Production (mg DW cm-2 y -1)
20
15
10
5
0
-5
-10
-15
-20
0
100
200
300
Irradiance (µM m -2 s -1)
b
Temperature
13
18
23
28

Figure 18

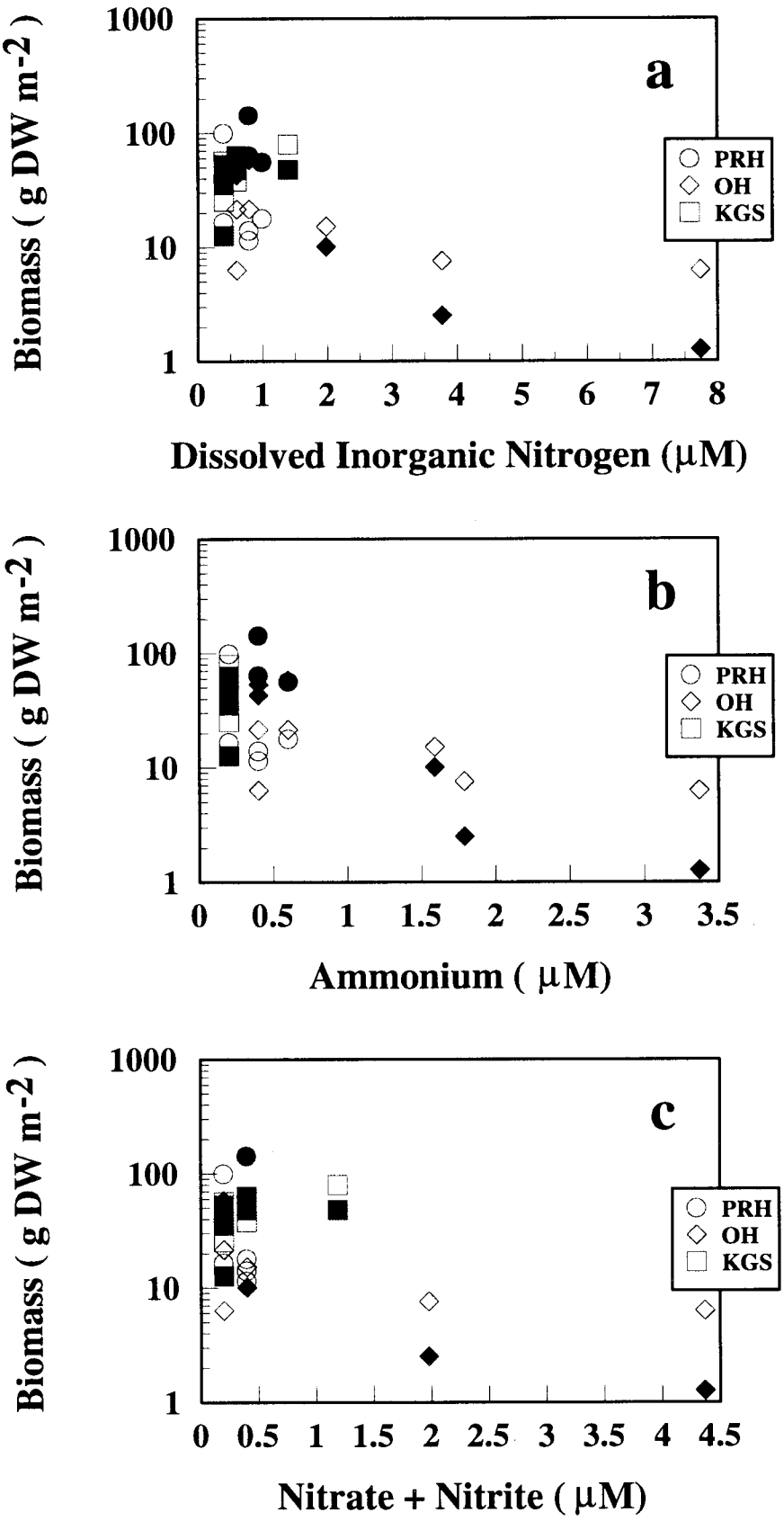

a
b
c
PRH
OH
KGS
Biomass (g DW m-2)
1000
100
10
1
0
1
2
3
4
5
6
7
8
Dissolved Inorganic Nitrogen (µM)
0
0.5
1
1.5
2
2.5
3
3.5
Ammonium (µM)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Nitrate + Nitrite (µM)

Figure 19

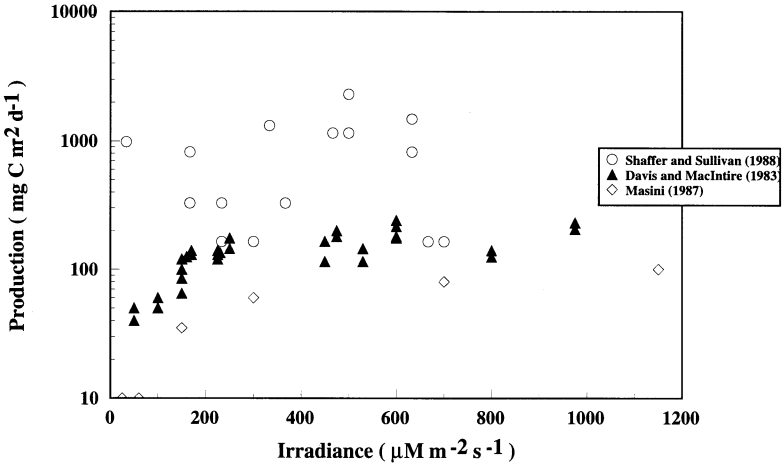


Figure 20

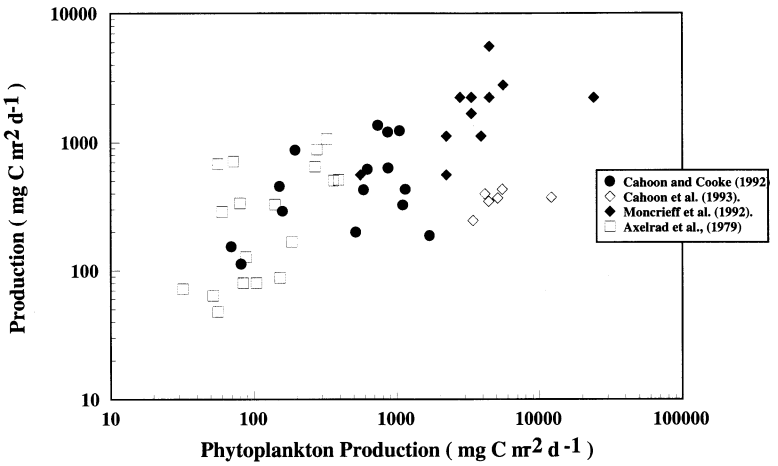
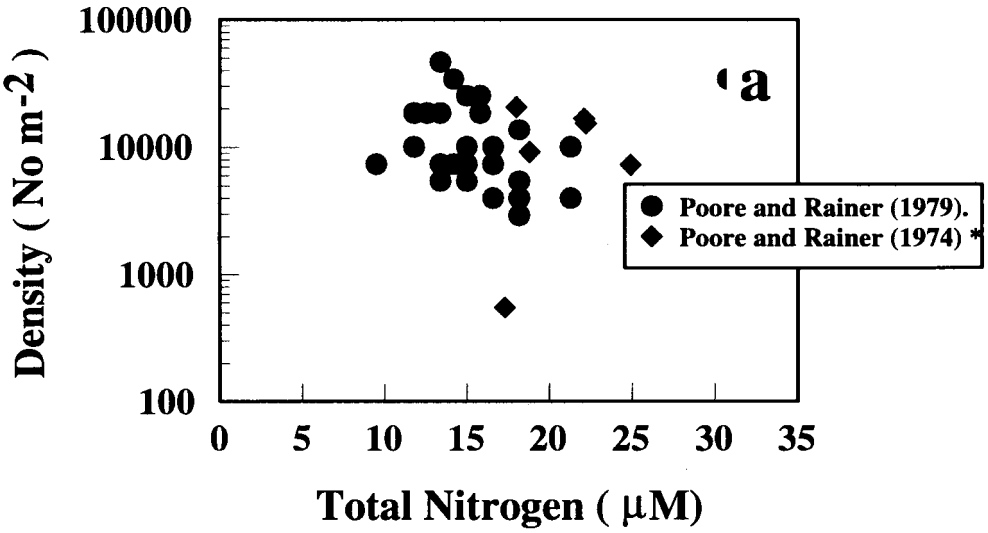


Figure 21


100000
10000
1000
100
Density (No m-2)
'a
Poore and Rainer (1979).
Poore and Rainer (1974) *
0
5
10
15
20
25
30
35
Total Nitrogen (μM)

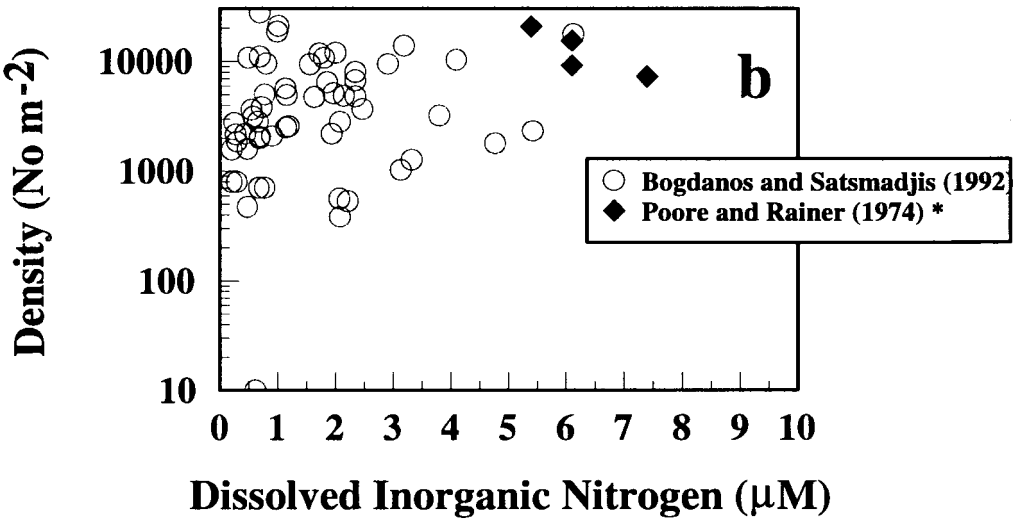
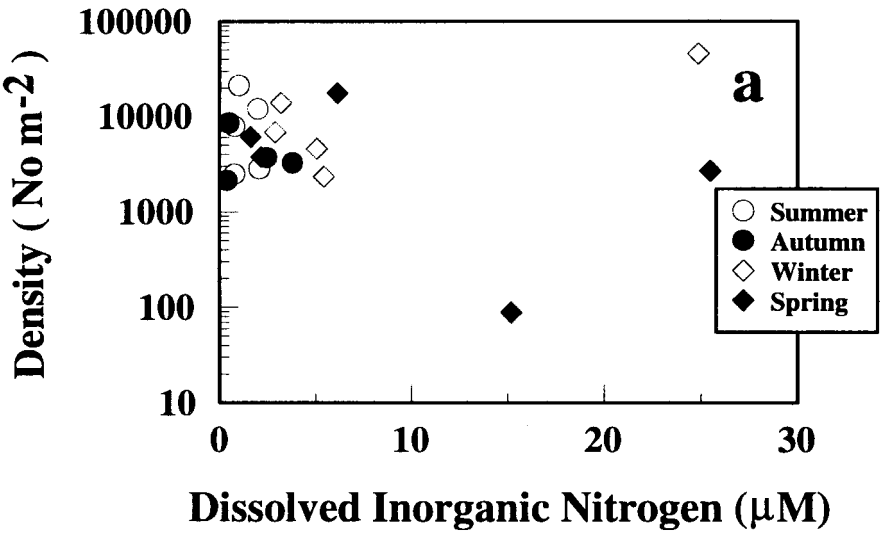

10000
1000
100
10
Density (No m-2)
b
Bogdanos and Satsmadjis (1992)
Poore and Rainer (1974) *
0
1
2
3
4
5
6
7
8
9
10
Dissolved Inorganic Nitrogen (μM)

Figure 22


100000
10000
1000
100
10
Density (No m-2)
a
Summer
Autumn
Winter
Spring
0
10
20
30
Dissolved Inorganic Nitrogen (μM)

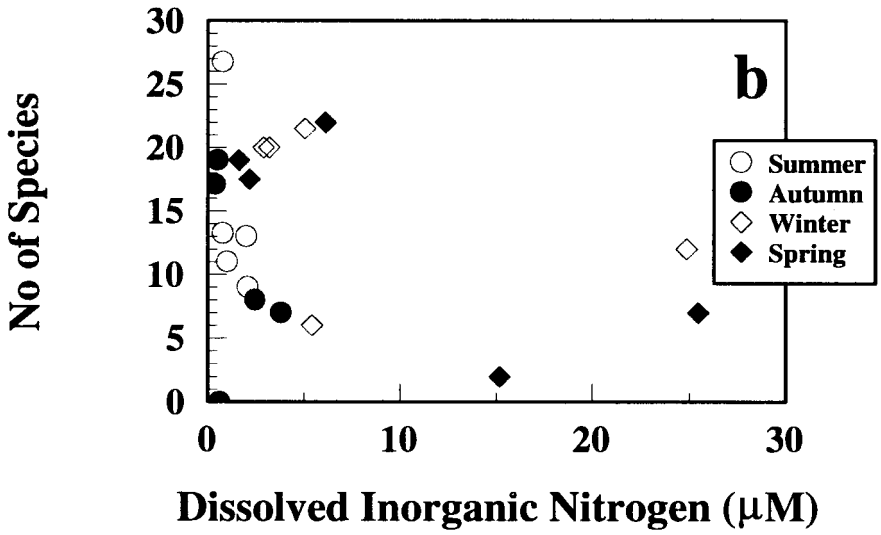

30
25
20
15
10
5
0
No of Species
b
Summer
Autumn
Winter
Spring
0
10
20
30
Dissolved Inorganic Nitrogen (μM)

Figure 23

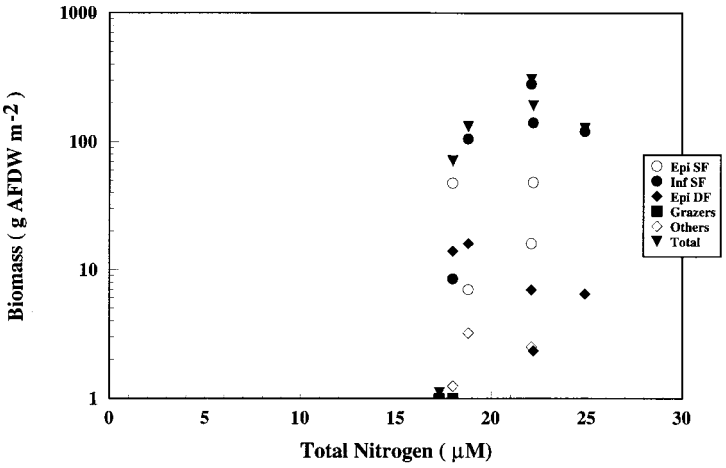


Figure 24

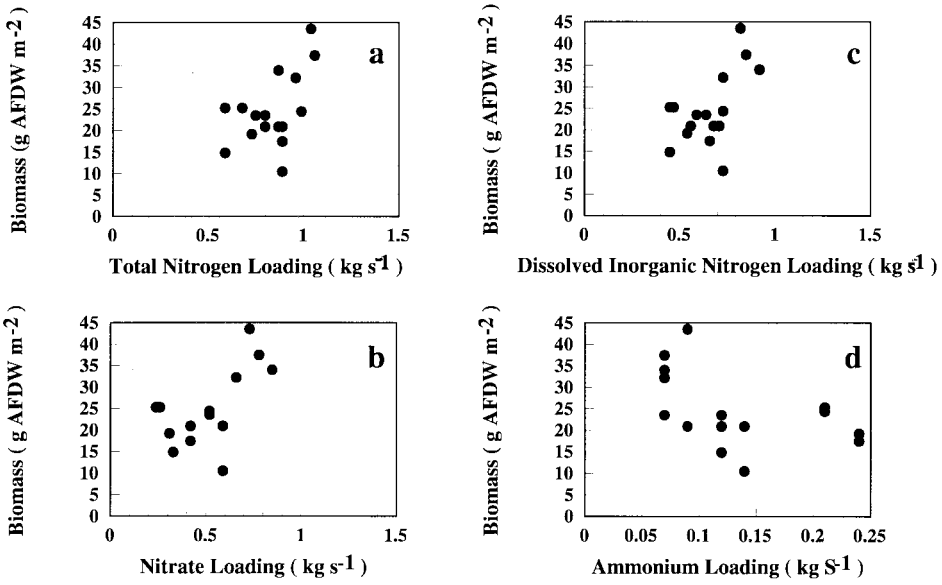


Figure 25

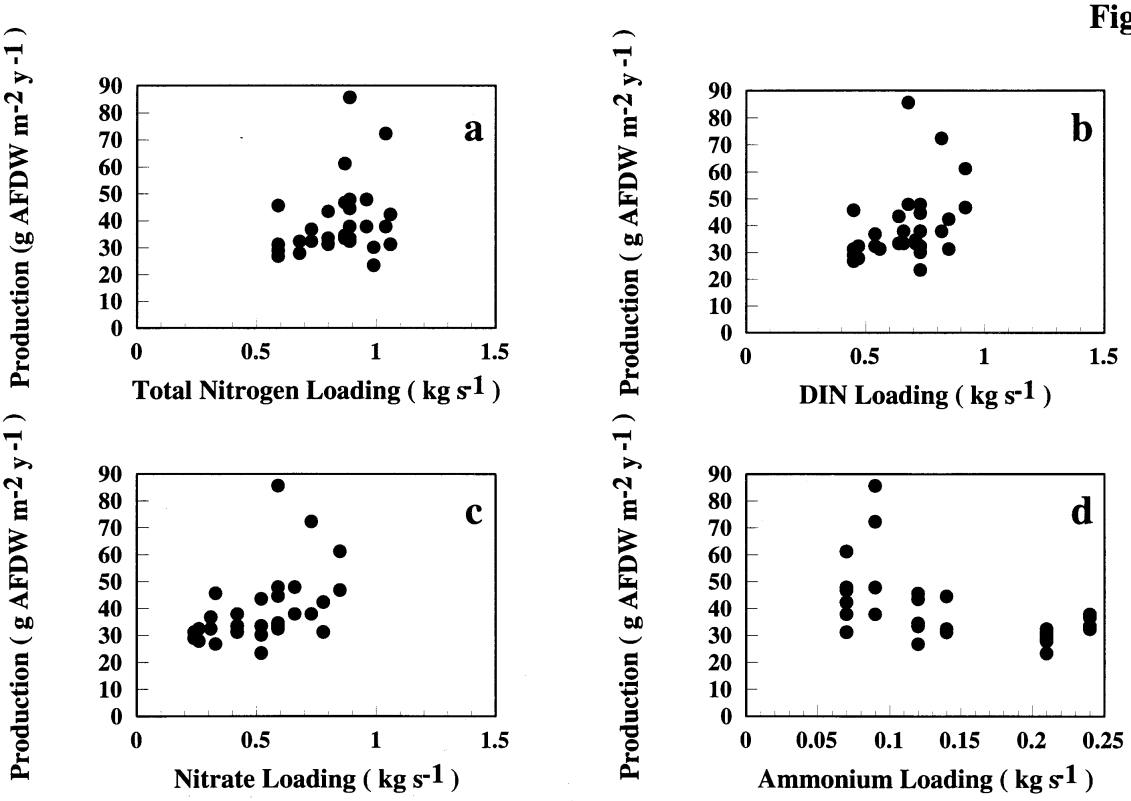
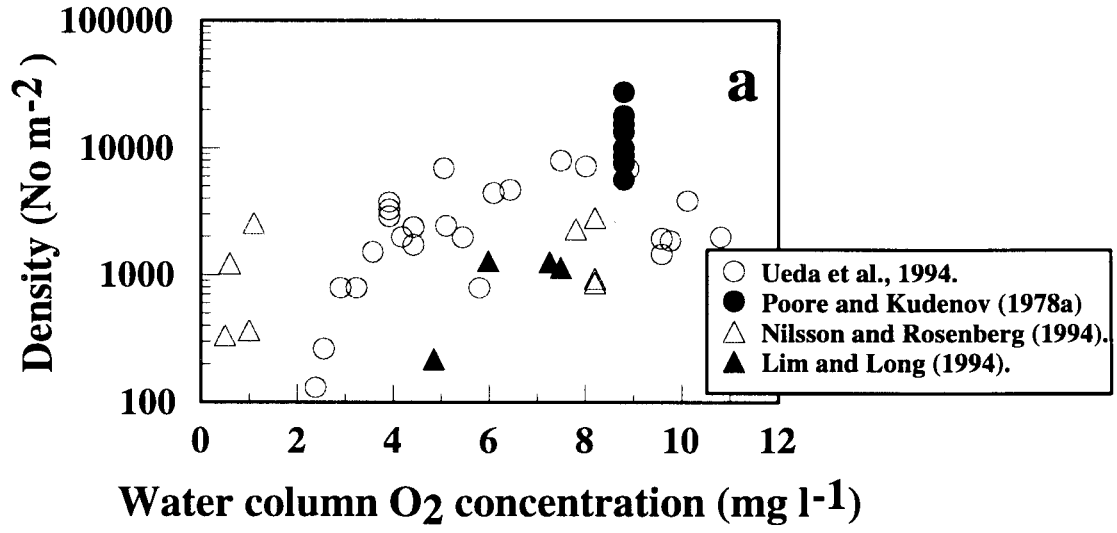

Production (g AFDW m-2 y-1)
a
Total Nitrogen Loading (kg s-1)
b
DIN Loading (kg s-1)
c
Nitrate Loading (kg s-1)
d
Ammonium Loading (kg s-1)

Figure 26


100000
10000
1000
100
Density (No m-2)
a
0
2
4
6
8
10
12
Water column O2 concentration (mg l-1)
Ueda et al., 1994.
Poore and Kudenov (1978a)
Nilsson and Rosenberg (1994).
Lim and Long (1994).

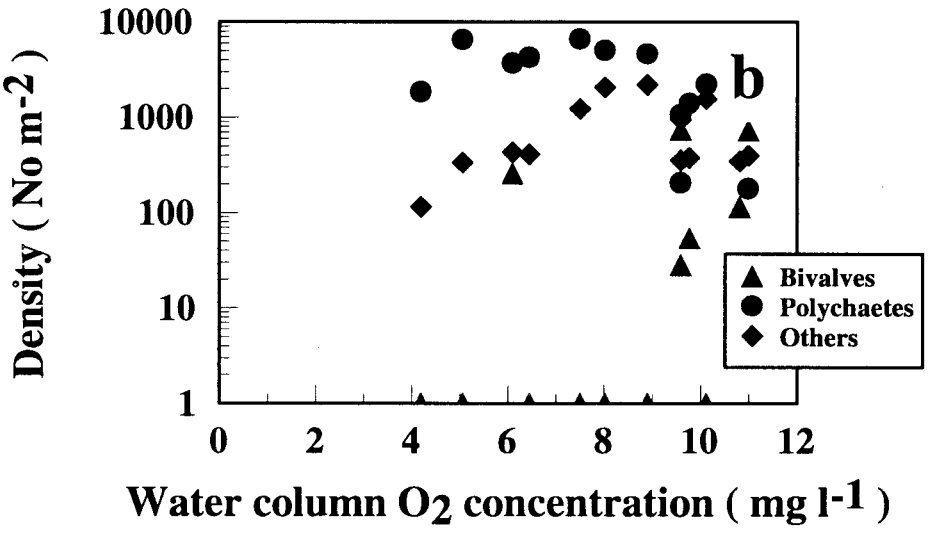

10000
1000
100
10
1
Density (No m-2)
b
0
2
4
6
8
10
12
Water column O2 concentration (mg l-1)
Bivalves
Polychaetes
Others

Figure 27

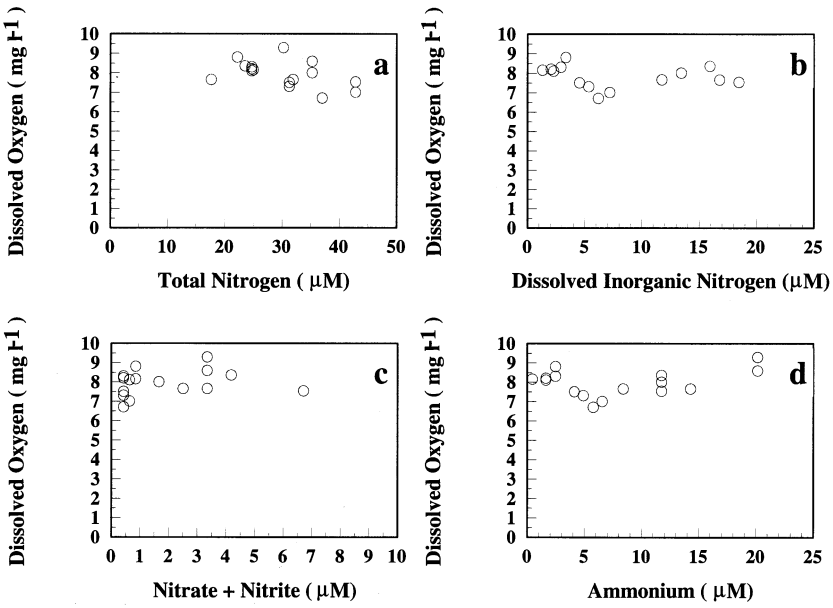


Figure 28

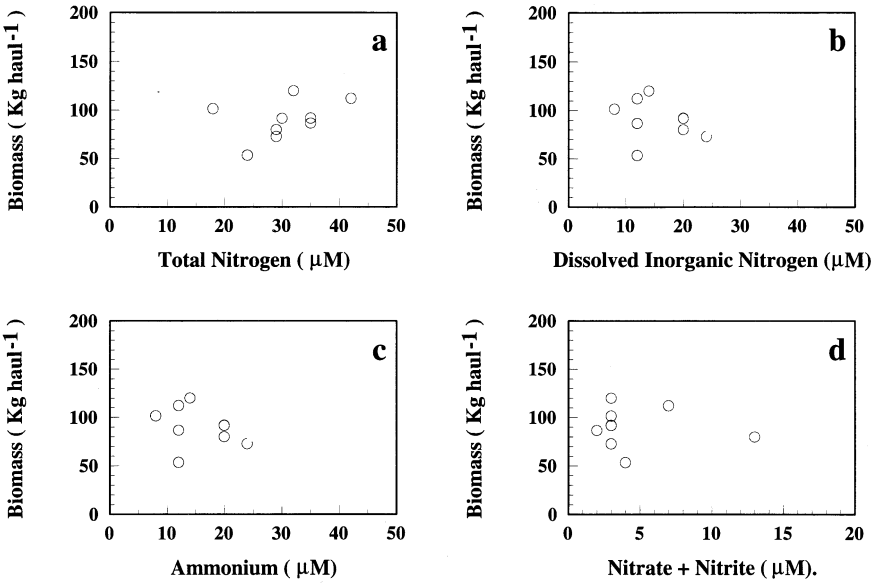


Figure 29

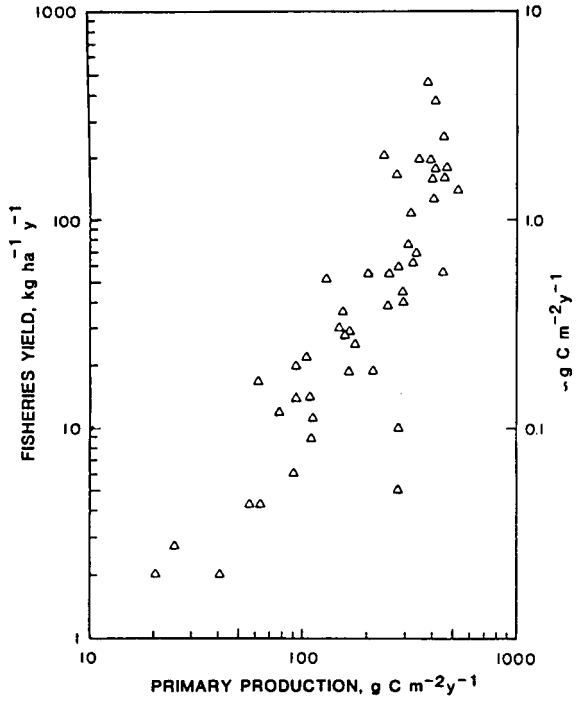


Figure 30